VULNERABILITY ASSESSMENT OF FOREST ECOSYSTEMS IN INDIA

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Introduction

Climate change and forests

Ensuring survival of life forms on planet earth has been a matter of concern for mankind during the last many decades. The intricate dependence of human survival on the health of forests has long been recognized. Forest ecosystems play an important role in the global biogeochemical cycle and exert significant influence on the earth's climate (Stephenson, 1990). Around half of the increase in global average surface temperature has been attributed to human activities (IPCC, 2014). Rapid industrialization during the last century has thus brought in the added dimension of the impact of human activities on earth's climate and their potential impact on the already fragile and threatened forest ecosystem. Effects of climate on the evolution of a forest type have been recognized, and is considered as the most important determinant of vegetation patterns globally with significant influence on the distribution, structure and ecology of forests (Kirschbaum et al.1996). The boundaries of forest biomes are known to closely follow patterns of temperature and/or moisture regimes (Stephenson, 1990). This interconnectedness of climate and forests thus implies that a dramatic change in one will influence the other (FAO, 2013). Through the inferences from paleoecological records, it has emerged that forest vegetation has the potential to respond within years to a few decades of climate change (IPCC, 2014). Fischlin (2007) report that 20–30% of the plant and animal species would be at increased risk of extinction if the global average temperature increase exceeded 2–3°C above the pre-industrial level. According to Intergovernmental Panel on Climate Change (2014), climate and non-climate stressors are projected to impact forests during the 21st century leading to large-scale forest die-back, biodiversity loss and diminished ecological benefits. It has been projected by IUFRO that the existing forests that are functioning as carbon sinks would later become a net source of CO_2 later in the century.

Significance of Vulnerability Assessment of India's Forests

India is one among the 18 mega diversity countries and is endowed with 8 % of the world's biodiversity, and hosts 4 biodiversity hotspots including Western Ghats, the Eastern Himalayas, the Indo- Burma and the Sundaland. India is home to about 7.6 % of mammalian, 12.6 % of avian, 6.2 % of reptilian, and 6.0 % of flowering plant species (https://en.wikipedia.org/wiki/Portal:Indian_wildlife). India is home to 2.9 %, of IUCN-designated threatened species, that includes the Asian elephant, the Asiatic lion, the Bengal tiger, the Indian rhinoceros, the mugger crocodile, and the Indian white-rumped vulture (https://en.wikipedia.org/wiki/Wildlife_of_India). Habitat of these endangered flora and fauna are India's forests. As per the State of Forest Report, 2017, India has 708273 sq km of forests, which comes to 21.54 % of geographic area of the country (FSI, 2017). India is endowed with diverse forest types ranging from tropical wet evergreen forests in the northeast and the southwest, to tropical dry thorn forests in central and western India. The forests of India are classified under 16 major types comprising 221 sub-types (Champion and Seth, 1968). Around 200,000 villages are classified as forest villages (Ravindranath et al., 2004). In addition to the dependence on forest resources by these communities, these forests provide a range of ecosystem services like functioning as catchment areas for water and as carbon sinks. These diverse forests also make available a diversity of forest produce thereby helping meet the wood, food and feed demands of India's growing population.

Climatic stressors include rising CO_2 concentrations, increased/ decreased rainfall patterns and associated drought and flooding, drought associated risks like forest fires, rising sea levels and associated flooding and salinity. Global mean temperatures in 2017 were 1.1 °C ± 0.1 °C above pre-industrial levels (WMO, 2017). Global mean sea level has been rising at a rate of ~3 ± 0.4 mm/y since 1993 (Nerem, et al., 2018) and has been projected to rise by 0.2 meters to 2.0 meters by 2100 (Melillo, et al., 2017). These climatic stressors are known to affect forests in terms of species composition, biodiversity and productivity. Migration of species towards higher latitudes/ elevations, spread of invasive species, decrease in area of socio-economically important species, asynchrony of flowering plants and associated fauna and leading to threats on endangered species are the other likely impacts of these stressors. The changes in the vegetation or forest type may be taken as an indicator of the vulnerability of the forest ecosystems to projected climate change (Rabindranath et al., 2006). Available studies have reported the likely change in vegetation of India's forests to the extent of 30.6% by 2035 and 45.9% by the end of the century (Gera, 2018). IPCC defines vulnerability as "The degree to which a system is susceptible to or unable to cope with, adverse effects of climate change, including climate variability and extremes. Vulnerability is a function of the character, magnitude, and rate of climate variation to which a system is exposed, its sensitivity, and its adaptive capacity" (IPCC, 2001). The study of the vulnerability of natural systems to climate change and variability, and their ability to adapt to changes in climate hazards, is a relatively new field of research (Brooks, 2003). It has been widely recognized that certain forest types are more vulnerable to climate change while certain forests types benefit from the altered CO_2, temperature and moisture regimes. The importance of a identification and scientific evaluation of the most vulnerable forest types has therefore been recognized for focusing on climate mitigation efforts. This status paper elaborates on the methodologies used for assessment of vulnerable forest types and vulnerability assessment studies undertaken in the India's forests.

Methodology for forest ecosystem vulnerability assessment

Assessing the vulnerability of forest ecosystems to climate change is important to determine appropriate mitigation and adaptation strategies. A methodology provides full framework for guiding the assessment of vulnerability (UNFCCC 2005). An ecosystem model can provide results about the vulnerability of ecosystem services to climate change. Various methods and tools are available for assessing the vulnerability of forests, forest ecosystem services and forest-dependent people or economic sectors (Locatelli et al., 2008). The tools and methods generally used for vulnerability assessment at different levels of complexity, range from simple tools and methods (e.g. using expert judgment or comparing with similar cases) to complex ones (e.g. simulation of integrated socio-ecological systems or dynamic vegetation modeling). The methodologies described in this section have essentially been quoted from the CIFOR's working paper 43 by Locatelli et al (2008).

Generic methods and tools can be applied to diverse systems for analysing vulnerability interactively with stakeholders (e.g. cognitive mapping or expert judgment) and for building empirical models from observations (e.g. meta analysis or data mining). Indicators, fuzzy systems, and uncertainty analysis can be applied for various purposes. Numerous ecosystem models can be used for studying the impacts of climate change on forests. Some models are restricted to specific ecosystem processes (e.g. the productivity of managed forests, forest perturbations or specific ecosystem services). Simple bioclimatic models can represent the distribution of ecosystems and help assessing ecosystem vulnerability to climate change. Other simple ecosystem models deal with community and landscape dynamics, with an emphasis on the interactions between species or patches of ecosystems. Other simple ecosystem models work on biogeochemical cycles in ecosystems.

Generic methods and tools

Expert judgment is a method for eliciting informed opinions from experts of a specific topic. An expert is defined as 'anyone especially knowledgeable in the field and at the level of detail being elicited' (Meyer and Booker, 1991). It is a useful method when resources are lacking for conducting an in-depth analysis of scientific literature, collecting data or modeling.

Empirical Models from Observations When observations are available about a phenomenon (e.g. forest fires) and possible explanatory variables (e.g. climate or human activities), empirical models can be built. These models aim at establishing a relationship between an observed impact and explanatory variables and can be used for testing the effects of changes (e.g. climate change or adaptation practices) on the phenomenon.

Meta-analysis is a statistical technique for combining the quantitative findings of different studies. It has the advantage of producing quantitative results about impacts and uncertainties (Arnqvist and Wooster, 1995). In an impact or vulnerability assessment, meta-analysis can be used for example for summarising the results of different studies of the impacts of climate change on ecosystems or human health. Meta-analysis has been applied to study the effect of global warming on biodiversity (Root et al. 2003; Parmesan, 2006) and soils (Rustad et al. 2001), the effects of elevated CO_2 on plants (Curtis and Wang, 1998).

Data mining consists of sorting through large datasets and picking out relevant information. Data mining is a more powerful tool than classical statistics for searching patterns in voluminous data (Witten and Frank, 2005). It can reveal complex relationships between a dependent variable and explanatory variables. Data mining methods include classification of trees, classification rules and artificial neural networks. Examples of applications include modelling forest fire (Javier Lozano et al. 2008), forecasting drought (Mishra and Desai, 2006), modelling deforestation (Mas et al. 2004), modelling rainfall-runoff relationships (Dawson et al. 2006), or modelling the distribution of vegetation in future climate (Hilbert and Ostendorf, 2001).

Uncertainty analysis Many methods and tools exist for analyzing uncertainties (New and Hulme, 2000). The most common approach is the application of different climatic or socio-economic scenarios and the presentation of the range of outcomes. Another approach can involve applying different ecosystem models or different representations of a social system, for exploring a different sensitivity or adaptive capacity. It is also possible to combine different scenarios with different system models. In addition to the simple presentation of the range of outcomes, more formal methods can be applied, such as Monte Carlo analyses or Bayesian methods (Katz, 1999). Zaehle et al. (2005) describe uncertainty analyses in forest and global vegetation modelling.

Specific ecosystem services: Some models deal with specific ecosystem services, such as hydrological services. Empirical or process-based hydrological models can be used for assessing the impacts of climate and land-use change (or impacts of climate change on ecosystems) on hydrological regimes (Ewen and Parkin 1996; Parkin et al. 1996; Bathurst et al. 2004).

Simple Ecosystem Models

Bioclimatic models are widely used tools for assessing the impacts of climate change on species or ecosystems. Such models are static and link the geographical distribution of species or ecosystems to their environment (Guisan and Zimmermann, 2000). The simplest bioclimatic methods applied to ecosystems are based on existing classifications using environmental characteristics to predict ecosystem distribution (Leemans et al. 1996). Empirical models are also used for modeling the distribution of ecosystems, e.g. with tools such as BIOCLIM (Beaumont et al. 2005) or with an artificial neural network (Hilbert and van der Muyzenberg, 1999). These models can be applied for studying the future distribution of ecosystems under climate change (Hilbert and Ostendorf, 2001).

Locatelli and Imbach (2008) studied the vulnerability of protected areas to climate change in Central America. The sensitivity was assessed with the displacement of Holdridge life zones under changing climate. Regarding the distribution of species, models can be built from observations and applied with climate change scenarios for predicting potential future distributions. Different methods can be used for modelling species distribution (Guisan and Zimmermann, 2000), such as rectilinear models (Miles et al. 2004), regression tree analysis (Iverson and Prasad. 2001), linear models, additive models, classification trees and artificial neural networks (Thuillier et al. 2006).

Community and landscape dynamics: Goudriaan et al. (1999) studied the interactions between species in an ecosystem and between ecosystem patches in a landscape. Price and Flannigan (2000) developed the patch level, gap models simulate dynamics of tree regeneration, growth and mortality and represent successional dynamics of forests over long periods of time. Examples of application include studying the distribution of trees under scenarios of climate change (Sykes et al. 1996) and developing forest management strategies for adaptation to climate change (Lindner, 2000). Schmitz et al. (2003) give examples of models representing the trophic interactions in ecosystems for studying the effects of climate change, for instance a dynamic system, linking climate with three trophic levels (plants, herbivores and carnivores) and illustrating the interactions among level in food webs. These interactions can determine the effects of climate change on ecosystems. Landscape models simulate the interaction between spatially connected patches (Goudriaan et al. 1999).

Integrated Ecosystem Models

Many models integrate different components, for example the distribution of ecosystem types and the functioning of these ecosystems in terms of biogeochemical cycles. These models are generally complex, especially the dynamic global vegetation models. They are generally applied at a global or continental scale but can also be used for studies at a more local scale.

Equilibrium models: Peng (2000) predicted the distribution and functioning of ecosystems under the assumption of equilibrium conditions of climate and vegetation. The BIOME3 model predicts ecosystem state in terms of plant types, total leaf area index and net primary production (Haxeltine and Prentice, 1996). These outputs allow classifying ecosystems into biomes for comparison with vegetation maps. MAPSS was applied in Mesoamerica for assessing the impacts of climate change on ecosystems' hydrological functions. The model requires input about monthly climate (precipitation, temperature, humidity and wind speed) and soils. The outputs of the model include vegetation characteristics (such as leaf area index of trees, shrubs and grasses), monthly soil moisture, surface runoff and base flow.

Dynamic models: Dynamic global vegetation models (DGVMs) are the most advanced ecosystem models for studying the impacts of climate change on ecosystems. They link dynamically vegetation structure and functioning, and simulate how climate change and natural disturbances affect ecosystem dynamics and processes (Peng, 2000). Opposite to equilibrium models, they can simulate transient changes in ecosystems. Examples include IBIS (Foley et al. 1996; Foley et al. 2005), LPJ (Sitch et al. 2003), MC1 (Daly et al. 2000), and Orchidee (Krinner et al. 2005). These models require a high level of expertise in ecosystem modelling.

Integrated ecosystem models, static or dynamic, consider many ecosystem processes and are generally complex. Many methods and tools are available for analysing the vulnerability of ecosystems or social systems, methods are lacking for integrating them into vulnerability assessments of coupled socio-ecological systems. Even if different tools and methods can be applied separately to ecosystems and social systems, the challenge is to link them into an integrated assessment. Ecosystem tools are generally quantitative, while social methods are often qualitative. Time horizons and spatial scale differ also greatly between large-scale, long-term ecosystem modelling and local, short-term social vulnerability assessment. The challenge is to build methods that facilitate the links among the different approaches of vulnerability.

Vulnerability Assessment of Forests in India

Climate is one of the most important determinants of vegetation patterns globally and has significant influence on the distribution, structure and ecology of forests (Kirschbaum et al., 1995). India is a mega-biodiversity country where forests account for about 21.54% (70 million ha) of the geographical area (FSI, 2017). With nearly 200,000 villages classified as forest villages, there is obviously large dependence of communities on forest resources (Ravindranath et al., 2004). Thus it is important to assess the likely impacts of projected climate change on forests and develop and implement adaptation strategies for both biodiversity conservation and the livelihoods of forest dependent people (Ravindranath et al., 2006). Forests in India are already subject to multiple stresses, including over extraction, pest outbreaks, fuel wood collection, livestock grazing, forest fires and other anthropogenic pressures. Climate change will be an additional stress, which may have an overarching influence on forests, through other stresses (pest incidence and diseases etc.,) (Gopalakrishnan et al., 2011). Despite utility of the forests and ecological importance, forests in India are degrading due to number of pressures like diversion of forest lands for development purposes, unsustainable harvest of forest products, encroachments, forest fires, invasive species and various other biotic interferences (Gera, 2016).

The impacts of climate change on forests in India are assessed based on the changes in area under different forest types, shifts in boundary of forest types, and net primary productivity (NPP) (MoEF, 2012). As per the Second National Communication to the UNFCCC, 2012, the existing assessments are based on (i) spatial distribution of current climatic variables, (ii) future climate projected by relatively high-resolution regional climate models for two different periods for the A1B climate change scenario, and (iii) vegetation types, NPP, and carbon stocks as simulated by the dynamic model Integrated Biosphere Simulator (IBIS v.2). The IBIS model is designed around a hierarchical, modular structure, which is based on four modules, namely, (i) the land surface module, (ii) vegetation phenology module, (iii) carbon balance module, and (iv) vegetation dynamics module. These modules, though operating at different time steps, are integrated into a single physically consistent model. The state description of the model allows trees and grasses to experience different light and water regimes, and competition for sunlight and soil moisture determines the geographic distribution of plant functional types and the relative dominance of trees and grasses, evergreen and deciduous phenologies, broadleaf and conifer leaf forms, and C3 and C4 photosynthetic pathways. Scenarios of climate change: SRES scenario A1B is considered for two future time-frames: (i) timeframe of 2021–50 (atmospheric CO_2 concentration reaches 490 ppm), which is labelled as "2035" and (ii) time frame of 2071–2100 (atmospheric CO_2 concentration reaches 680 ppm), which is labelled as "2085". Observed climatology for the period 1961–91 was treated as the baseline for the simulations (MoEF, 2012).

Using climate projects of the Regional Climate Model of the Hadley Centre (HadRM3) and the dynamic global vegetation model IBIS for A2 and B2 scenarios Chaturvedi et al., (2011) reported that 39 and 34% of forest grids in India are likely to undergo change of forest type under the A2 and B2 scenarios, respectively by the end of this century. This study also concluded that the upper Himalayas, northern and central parts of Western Ghats and certain parts of central India are most vulnerable to projected impacts of climate change, while North-eastern forests are more resilient. In a similar study, Gopalakrishnan et al., (2011) have reported that at the national level, about 45% of the forested grids are likely to undergo change. The vulnerability assessment in the study showed that the vulnerable forested grids are spread across India. However, their concentration is higher in the upper Himalayan stretches, parts of Central India, northern Western Ghats and the Eastern Ghats. The study also reveals that in contrast, the north-eastern forests, southern Western Ghats and the forested regions of eastern India were estimated to be least vulnerable.

Himalayan ecosystems are projected to be extremely sensitive to future climate (Chaturvedi et al., 2011). Further, Himalayan ecosystems are highly vulnerable due to the stress caused by forest land diversion, increasing pressure from human population, exploitation of natural resources, infrastructure development, mining, and other related challenges. The effect of these stressors is likely to be exacerbated due to climatic changes, which would be additional (Ravindranath et al., 2006). Analysis of temperature trends in the Himalayan region shows that temperature increases are greater in the uplands than that in the lowlands (Shrestha et al., 1999). Gopalakrishnan et al., (2011) have reported that the high-altitude mountainous forests (sub-alpine and alpine forests, the Himalayan dry temperate forest and the Himalayan moist temperate forests) are susceptible to the adverse effects of climate change.

While there are national level assessments studies for impact of climate change on forests. However such studies are lacking at the regional level (Sujata Upgupta et al., 2015). On regional level, Sharma et al., (2013) had attempted to assess the inherent vulnerability of forests using a methodological approach. This methodological approach was applied at local scale to Aduvalli Protected Forest, Kopal division of Chikamagalur district of Karnataka in Western Ghats in South India, where a vulnerability index value of 0.248 was estimated. Results of the case study indicate that 'preponderance of invasive species' and forest dependence of community are the major sources of vulnerability for Aduvalli Protected Forest.

Climate change is expected to increase species losses. Changes in phenology are expected to occur in many species. The general impact of climate change is that the habitats of many species will move poleward. Species that make up a community are unlikely to shift together (MoEF, 2012). A study conducted by Singh et al (2012) on the alpines of Uttarakhand reveals shift of treeline ie., *Betula utilis* from the year 1970 to 2006 due to the impact of ongoing warming under the background influence of increasing levels of GHGs. A study in Arunachal Pradesh in 2011 by Bharali and Khan, reported the phenological changes in some floral species (Rhododendron species and Orchids).

The second communication of India to UNFCCC, MoEF, 2012 reports that ecosystems dominated by long-lived species will be slow to show evidence of change and slow to recover from the climate-related stress. Climate change and modelling studies on tree species like sal (*Shorea robusta*), teak (*Tectona grandis*), eucalyptus, and pine (*Pinus* spp.) have been undertaken for A2 and B2 climate change scenario. Test run studies on teak and sal trees, highly characteristic of central India, have indicated that there would be a net increase in primary productivity with increase in temperature and rainfall, but this would also lead to a dieback with the induced stress to nutrient availability. The report also states that the enhanced levels of CO_2 are expected to lead to an increase in the NPP of forest ecosystems, with more than 75% of the grids showing an increase in NPP. Even in a relatively short span of about 50 years, most of the forest biomes in India seem to be highly vulnerable to the projected change in climate. Further, it is projected that by 2085, 77% and 68% of the forest grids in India are likely to experience shift in forest types under A2 and B2 scenarios, respectively. Indications point towards a shift to wetter forest types in the north-eastern region and drier forest types in the central and north-western region, in the absence of human influence. Increasing atmospheric CO_2 concentration and climate warming could also result in the doubling of NPP under the A2 scenario and nearly 70% increase under the B2 scenario (MoEF, 2012).

Ravindranath et al., (2006) had estimated the impact of climate change on net primary productivity (NPP in g C/m2 per year) under the current and GHG scenarios. In their study it was observed that among the dominant vegetation types (tropical xerophytic shrubland, tropical deciduous forest, warm mixed forest and tropical semi-deciduous forest), the NPP increases by 1.35 to 1.57 times under the GHG scenarios (A2 and B2) over the current scenario of NPP. The NPP under tropical evergreen forest increases by 1.5 times under the GHG scenarios. The rate of increase on NPP was lower for cool conifer forest, cold mixed forest and temperate deciduous forest. Generally the rate of increase is higher for warmer vegetation types.

Assessment of vulnerability is an urgent task because any adaptive measures undertaken would need time to develop before the adaptive capacities actually build-up (Seidl and Lexer 2013). Vulnerability assessments are necessary at local scale (forest stand or patch) as well as larger scales like landscapes, ecoregions and biomes and serve different objectives. While the assessments at larger scales would assist in identification of vulnerable forest areas and to prioritize them for efficient resource allocation (Næss et al. 2006), the assessments at local scale are necessary for designing site specific forest resilience enhancement measures. The results of inherent vulnerability assessment of forest would inform development of appropriate forest management practices and policies to restore disturbed forests, as restored forests would have higher adaptability than un-restored forests under climate change (Ciccarese et al. 2012).

Knowledge Gaps in Vulnerability Assessment

The MoEF report 2012 states that although climate change is a global issue for discussion, there are some gaps and constraints visible in the knowledge of vulnerability assessment, adaptation and mitigation aspect of forestry. Key knowledge gaps include the linkages between impacts of climate change and adaptation and mitigation options. Despite the emergence of more and more regional and country specific studies on climate change in India in recent years, knowledge gaps remain huge. There is an urgent need for undertaking more research at regional level to better understand the climate change and its impact, risks and vulnerability, adaptation needs, and mitigation potential at local levels.

The forestry sector in India has the potential to be a major source or sink of CO_2 in the future. The uncertainty in the estimates of inventory in the forestry, land use and land use change is shown to be higher than other sectors such as energy transformation, transportation, industrial processes, and even agriculture. The availability and access to information on activity data, emission coefficients, and sequestration rates in the forestry sector in India are limited, and the uncertainty of the data is high, as in most countries. Thus, there is a need for improvement in the information generation processes for the inventory so as to reduce the uncertainty involved in the estimation of GHG inventory in the forestry sector (MoEF, 2012).

Conclusions:

Considerable knowledge gaps exists for the purpose of modelling future climate change impacts and bringing up with robust adaptation strategies. Knowledge gaps include uncertainty in the estimates of inventory in the forestry, land use and land use change, and inadequate knowledge on the relationship between climate and ecosystem responses. There is therefore an urgent need for developing regional and national level dynamic vegetation models for assessing climate change impacts on forest ecosystems and biodiversity. Ecological studies on endemic and endangered species in relation to climate variability and change, and understanding changes in the phenological patterns of vegetation and its impact on associated fauna, primarily at the species level are a prerequisite for developing adaptation strategies and practices to reduce vulnerability of forests to climate change.

Summary

India's forests harbours several endemic and endangered species. The rapidly growing human population and attendant development needs have already pushed the forests and their dependent life forms to the precipice of irreversible destruction. The added dimension of climate change and its potential impact on the survival of forests calls for immediate studies for the identification of the most vulnerable forest areas where in concerted conservation/ mitigation efforts could be taken up. Vulnerability assessment methodologies including generic approaches, simple ecosystem models and integrated ecosystem models as reviewed by Locatelli et al (2008) have been briefed.

Few studies have already been taken up in India for assessment of vulnerability of India's forests to climate change. The impacts of climate change are assessed based on the changes in area under different forest types, shifts in boundary of forest types, and net primary productivity (NPP). Several studies have tried to evaluate the changes in the forest ecosystems due to the changes or projected climate change scenarios. It is projected that by 2085, 77% and 68% of the forest grids in India are likely to experience shift in forest types under A2 and B2 scenarios, respectively (MoEF, 2012). In another study it has been observed that the upper Himalayas, northern and central parts of Western Ghats and certain parts of central India are most vulnerable to projected impacts of climate change, while North-eastern forests are more resilient. Himalayan ecosystems are projected to be extremely sensitive to future climate.

Besides national level assessments, there are number of studies on regional basis assessing the vulnerability of the forests. Regional level climate change studies have assessed shift in tree line of *Betula utilis* in the alpine vegetation in Uttarakhand. In similar such studies, phenological changes in Rhododendron and orchids have been reported from Arunachal Pradesh. However such studies are staggered spatially and do not reveal changes occurring to the landscape. More such regional studies could help better understand the climate change and its impact, risks and vulnerability, adaptation needs and mitigation potential. Importantly there is urgent need to devise research strategies to evaluate the ecological assessment of endemic and endangered species vis-a-vis the climate change scenarios. Uncertainty in estimates of inventory in forestry, land use and land use change calls for refinement of information generation processes in the forestry sector.

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CHANGING ORTHOPTERA (ARTHROPODA: INSECTA) DIVERSITY IN NILGIRI SHOLAS AND GRASSLANDS, A SIGN OF CLIMATE CHANGE?

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Introduction

Orthoptera is one of the largest orders of the class insecta, and includes the well known grasshoppers, locusts, crickets, and katydids. They form a dominant group of herbivorous insects throughout the world, and their high diversity, functional importance and sensitivity to disturbance make them potentially useful bioindicators for land management. They are known to occur in a wide variety of habitats, ranging from the littoral zone of the sea shore to grasslands, forests and mountaintops, well above the tree line. There are models that explain that the number of species in the 100m altitudinal bands increases steeply with altitude until 1,500 m above sea level, and between 1,500 and 2,500 m, little change in the number of species is observed, while above this altitude, a decrease in species richness is evident (Mathew and Mohandas, 2001). However, certain models indicate that insect distributions should be expected to shift towards higher latitudes, and altitudes (Régnière *et al*., 2009). The montane forests are the stunted ever green forests locally known as 'sholas'. They are found only above 1500 m in the glens, hollows and valleys of the mountains. Nilgiris sholas are situated in the higher mountain tracts of the southern Western Ghats, at an altitude above 1800 m, interspersed with rolling grasslands. In the sholas the trees are stunted with crooked branches thickly laden with moss and other epiphytes. Nilgiris sholas are unique in terms of their vegetation and species diversity. The natural vegetation in the sholas and the grasslands depleted very fast due to introduction of commercially valuable fast growing trees like Wattle, Eucalyptus, Cypress and Pine to provide pulp for the Rayon and paper industries by English during 19th Century. Fortunately by late eighties, there was a shift in Government policies. Further plantations of wattle and Eucalyptus were stopped. Experiments are now on to reconvert these plantations into sholas. Studies have shown that majority of the endemic plants of the Nilgiris tract are highly threatened and many are already extinct because of loss of habitat due to anthropogenic pressure. Since orthopteran insects are good indicators of climate and landscape changes, and no authentic record of

Orthoptera in theses sholas was available, an attempt has been made to study the diversity of Orthoptera in Nilgiris shola forests.

Study sites

There are three locations each with a total of six sites under Nilgiris North, and South Forest Divisions viz., Kothagiri Longwood shola, Uppati shola, Nedugula shola in former and Avalanche cauliflower shola, ninth mile shola and Parson's valley shola in latter respectively selected for the study. They are located between 11º 12' 68.2" N and 11º44' 18.00" N latitude with the elevation ranges from 1937 m MSL to 2295 m MSL.

Sampling and analysis of data

The entire vegetation was covered during the intensive search out method, which involved hand picking the insects from the vegetation after locating them; sweep nets were also used for collecting specimens. Sanjayan (1994) showed that this was the best sampling method for species of Orthoptera. Orthoptera were observed between 0700 hrs to 1300 hrs. Collected specimens were narcotized with menthol crystals brought to the laboratory and air-dried for identification. All the specimens were examined carefully and identified specimens were labeled and preserved in insect boxes. A cotton wad immersed in preservative (Phenol, Naphthalene, and Para dichlorobenzene in equal ratio) was kept in the corner of the box to restrict ant and fungal attack. The specimens collected were identified using various publications of Rentz (1979), Tanton and Shishodia (1972), Ingrisch (1990, 2002), Ingrisch and Shishodia (1997,1998,2000), Shishodia (2000a, b), Shishodia and Tandon (1990), Naskrecki (1994, 1996a,b, 2000), Naskrecki and Otte (1999) and Senthilkumar *et al*. (2001, 2002). As a measure of α-diversity (diversity within a habitat), the most popular and widely used Shannon's diversity index (H′) was calculated since it is well accepted that all species at a site, within and across systematic groups contribute equally to its biodiversity (Ganeshaiah *et. al*., 1997). In addition, Simpson's diversity index (λ) and coverage estimators were also calculated as per Colwell (2004) using the software EstimateS 7.

Results and discussion

The study of Orthoptera of the Shola Forests has come up with promising results. Fifteen genera and 15 species including an unknown gryllid and two unidentified acridid were recorded from Nilgiris Shola forests and grasslands (Table 1). Seven species belonged to the family Acrididae, 6 species to Tettigoniidae. The family Gryllidae was represented by only two species. A greater diversity of short-horned grasshoppers was recorded in all the shola forests under study followed by tettigoniids. It is common belief that natural ecosystems, still untouched by man, are characterized by a great diversity of animal and plant species. These heterogeneous conditions form the basis of a stable and well-balanced environment in which population oscillates within certain limits (Senthilkumar *et al*. 2006). This study on Orthoptera has again supported the fact that a heterogeneous and undisturbed habitat like the forestlands harbour greater number of insect species. This observation is supported by the study of acridids diversity in Tamil Nadu (Senthilkumar *et al*., 2009). The species recorded namely, *Orthacris maindronii*, *Hetracris pulcher*, *Gastrimargus africanus*, *Phaleoba infumata*, *Mecopoda elongata*, *Mirrollia cerciata* and *Hexacentrus major*, were earlier found in the low to mid elevations, lowland forests in particular. (Sanjayan *et al*., 2002; Senthilkumar *et al*., 2009) None of these species were reported earlier in high altitudes. (Senthilkumar, 2002). It is evident from the study of Ching Chen *et al*. (2009) that tropical insect species have undertaken a shift towards higher altitudes, confirming the global reach of climate change impacts on biodiversity. The species richness in shola forests under Nilgiris North and South divisions were similar (Table 2.). However, the species composition differed. The species such as *Mirrollia cerciata, Hexacentrus major, Hetracris pulcher, Elaemaea securigera* and *Phaneroptera gracilis* were found only in the Cauliflower shola, Parson's valley shola, Nedugula shola and Uppati sholas respectively. The species namely *Orthacirs maindronii, Gryllodes sigillatus, Gastrimargus africanus* and *Phaleoba infumata* were recorded in more than four locations. The occurrence of the rare species like *Mirrollia cerciata*, unknown gryllid and unknown acridid in Avalanche Cauliflower shola indicate that the habitat is unique with characteristic vegetation types. Grasshoppers diversity was predicted to decrease significantly and species rich locations were predicted to move towards higher altitudes (Maes *et al.,* 2010). The large turnover rates were predicted to occur at higher altitudes for grasshoppers.

Shannon's diversity index was calculated as a measure of diversity within a habitat. The diversity indices $H^{'}$, and λ appear useful as they incorporate both species richness and evenness into a single value. Shannon's (H') diversity index appears to have more value (1.43) (Table 3). The present study indicates that orthopteran species are more diverse in Nilgiris Shola forests. However, the Shannon's index gave high values in Nedugula followed by Longwood and Avalanche shola forests. Simpson's diversity index, 'λ', also gave high value for aforementioned sites. It indicates that the shola forests and grasslands in these locations are occupied by species with more individuals. The availability of host plants in the habitat is vital for insect colonization. The type of vegetation in a habitat influences not only species presence, but also the number of individuals. Though the study sites fall under Nilgiris North and South divisions, the assemblage of orthopteran community varies and the similarity index was worked out to understand the closely related sites between Nilgiris North and South divisions. The dendrogram (Fig.1.) showed the similarity between sites of two different divisions in relation to Orthoptera diversity. Nedugula shola forest in Nilgiris North division is grouped under Ninth mile and Avalanche sholas in Nilgiris South division. However, Parsons' valley shola in Nilgiris South is grouped under Longwood and Uppati sholas in Nilgiris North Division. At middle latitudes, distribution shifts towards higher latitudes and altitudes seem to be prevalent, especially in highly mobile and polyphagous species (Ching Chen *et al*. 2009). Detailed models of the responses to climate of each insect species are needed to predict distribution changes with any accuracy. However, it seems difficult to make general predictions about the responses of major forest insect species from the point of view of climate change in their current ranges. There is an increasing risk of "invasion" into increasingly hospitable temperate ecosystems by the more mobile species. However, certain models indicate that insect distributions should not be expected to expand, but rather to shift towards higher latitudes and altitudes (Régnière, *et al*., 2009)**.**

It may be concluded that upward elevation shifts of grasshopper species in Nilgiris shola forests and grasslands are consistent with responses to the climate change observed in the region, either as a direct physiological response to climate or as a consequence of altered interactions with other species. If plant elevation increases this could be facilitating elevation increases by the insects that feed on them. It is too early to judge whether these responses are due to climate change. But the Nilgiris shola forests become important climate change refugia for low elevation species. However, high mountains will only become important refugia for low-elevation species if surrounding lowland forests and other natural habitats are maintained. The conservation of lowland forest will permit lowland species to survive locally and so be available to colonize upwards while also minimizing additional regional impacts on climate change associated with lowland deforestation. High tropical mountains and their surrounding lowland habitats represent some of the most important locations in the world to maintain biodiversity in the face of climate change. Our study would advocate that possible conservation and policy measures to mitigate the potentially strong impacts of climate change on insect diversity in Nilgiris should be much more proactive and flexible than is the case presently. Considering the importance of the sholas and to protect this cluster of rare and endangered species permanently, Tamilnadu Forest Department, has made chain-link fence under the Hill Area Development Programme. In 2008, 225 hectares of plantation was again reconverted into Shola forests by Nilgiris North Forest Division**.** 100 hectares of the exotic species were cleared in the Mukurti National Park. It has resulted in the up-gradation of the degraded area and augmentation of the dwindling shola species.

Conclusion

Climate change and habitat destruction have been linked to global declines in vertebrate biodiversity, including mammals, amphibians, birds, and fishes. However, invertebrates make up the vast majority of global species richness, and the combined effects of climate change and land use on invertebrates remain poorly understood. The vast majority of research on insect responses to altered climatic factors has focused on butterflies and beetles in temperate ecosystems, with a strong bias on diversity of Orthoptera. Studies regarding, tropical forest insects are still very incipient. The present study fulfils the felt need. The study on distribution and diversity of Orthoptera in Nilgiris upland shola forests and grasslands showed that the species found only distributed in lowland forests are now observed in high altitude evergreen forests. At higher elevations, we observed clear upward shifts in the elevational ranges of species, with the influence of global warming. It supported the prediction that the shifts of species towards higher altitudes seem to be prevalent, especially in highly mobile insects. It is evident from our study on the diversity of grasshoppers in Nilgiris shola forests that tropical insect species have undertaken refuge at high altitudes, confirming the global reach of climate change impacts on biodiversity.

Summary

Uplands are expected to provide refuges for insects subject to lowland habitat loss, but information on their response to climate change has been lacking. It was predicted that at middle altitudes, there is a significant reduction in diversity of grasshoppers. However, shifts towards higher altitudes seem to be prevalent, especially in highly mobile and polyphagous species. It is evident from our study on the diversity of grasshoppers in Nilgiris shola forests that tropical insect species have undertaken refuge at high altitudes, confirming the global reach of climate change impacts on biodiversity. The species found distributed only in lowland forests are now recorded in the high altitudinal stunted wet evergreen forests locally known as sholas. This is a case where upland forests provide refuges when lowland sites are subject to climatic fluctuations.

Acknowledgements

The authors are grateful to the Director, IFGTB, Coimbatore for providing facilities during the course of the study and Forest Department, Tamilnadu for granting permission to work in protected areas.

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Table 1. Orthoptera insect fauna in Nilgiri sholas.

S. No.	Diversity index	Family	Avalanche	Longwood	Nedugula	Ninethmile	Parson's valley	Uppati
1.	*Orthacris maindroni* Bolivar	Acrididae	-	+	-	+	+	-
2.	*Oxya fuscovittata* (Marsh.)	Acrididae	-	+	-	-	-	-
3.	*Gryllodes sigillatus* (Walker),	Gryllidae	-	+	+	+	-	-
4.	*Phlaeoba infumata* Brun.	Acrididae	+	+	+	+	-	-
5.	*Elimaea* (Orthelimaea) *securigera* (Brun.)	Tettigoniidae	-	-	-	-	-	+
6.	*Phaneroptera gracilis* Burm.	Tettigoniidae	-	-	-	-	-	+
7.	*Heteracris pulcher* (Bol.)	Acrididae	-	-	+	-	-	-
8.	*Gastrimargus africanus* (Saus.)	Acrididae	+	-	+	-	-	-
9.	*Mirrolia cerciata* Hebard.	Tettigoniidae	+	-	-	-	-	-
10.	*Mecopoda elongata* (Linn.)	Tettigoniidae	+	-	-	-	-	-
11.	*Euconocephalus incertus* (Walk.)	Tettigoniidae	-	-	-	+	-	-
12.	*Hexacentrus major* Redtenb.	Tettigoniidae	-	-	-	-	+	-
13.	Unknown Acridid 1	Acrididae	-	-	-	-	-	+
14.	Unknown Acridid 2	Acrididae	+	-	-	-	+	-
15.	Unknown gryllid 1	Gryllidae	-	-	+	-	-	-
	No. of species		5	4	5	4	3	3

Table 2. Species richness and diversity of Orthoptera in Nilgiris sholas.

	Location	Division	Latitude ° N	Longitude ° E	Altitude M (MSL)	No. of species	H'- Shanon's index
1.	**Longwood shola**	Nilgiris North	11.26	76.52	1970.6	4	1.34
2.	**Uppati shola**	Nilgiris North	11.30	76.54	1937.1	3	0.91
3.	**Nedugula shola**	Nilgiris North	11.36	76.53	1941.2	5	1.43
4.	**Avalanche shola**	Nilgiris South	11.12	76.35	2036.0	5	1.29
5.	**Ninthmile shola**	Nilgiris South	11.44	76.62	1946.0	4	1.24
6.	**Parson's valley shola**	Nilgiris South	11.38	76.58	2295.0	3	0.99

Table 3. Diversity indices of Orthoptera in Nilgiris sholas

S. No.	Diversity index	Avalanche	Longwood	Nedugula	Ninethmile	Parson's valley	Uppati
1.	Species richness	5	4	5	4	3	3
2.	Singletons	2	0	0	1	0	0
3.	Unique	2	0	0	1	0	1
4.	ACE	7.01	4	5	4.34	3	3
5.	ICE	7.16	4	5	4.42	3	3.88
6.	Chao 1	5.75	4	5	4.5	3	3
7.	Chao 2	5.75	4	5	4.5	3	3.12
8.	Jack 1	6.75	4	5	4.87	3	3.87
9.	Jack 2	7.60	4	4.55	5.62	1.71	3.98
10.	Bootstrap	5.79	4	5.12	4.37	3.20	3.44
11.	MM mean	5.99	4.52	5.75	5.30	4.30	5.59
12.	Colewel	4.73	3.91	4.99	3.87	2.98	2.98
13.	Alpha diversity index	2.29	1.07	1.50	1.59	1.35	1.35
14.	Shannon index	1.29	1.34	1.43	1.24	0.99	0.91
15.	Simpson's index	3.47	3.99	3.91	3.82	2.89	2.81

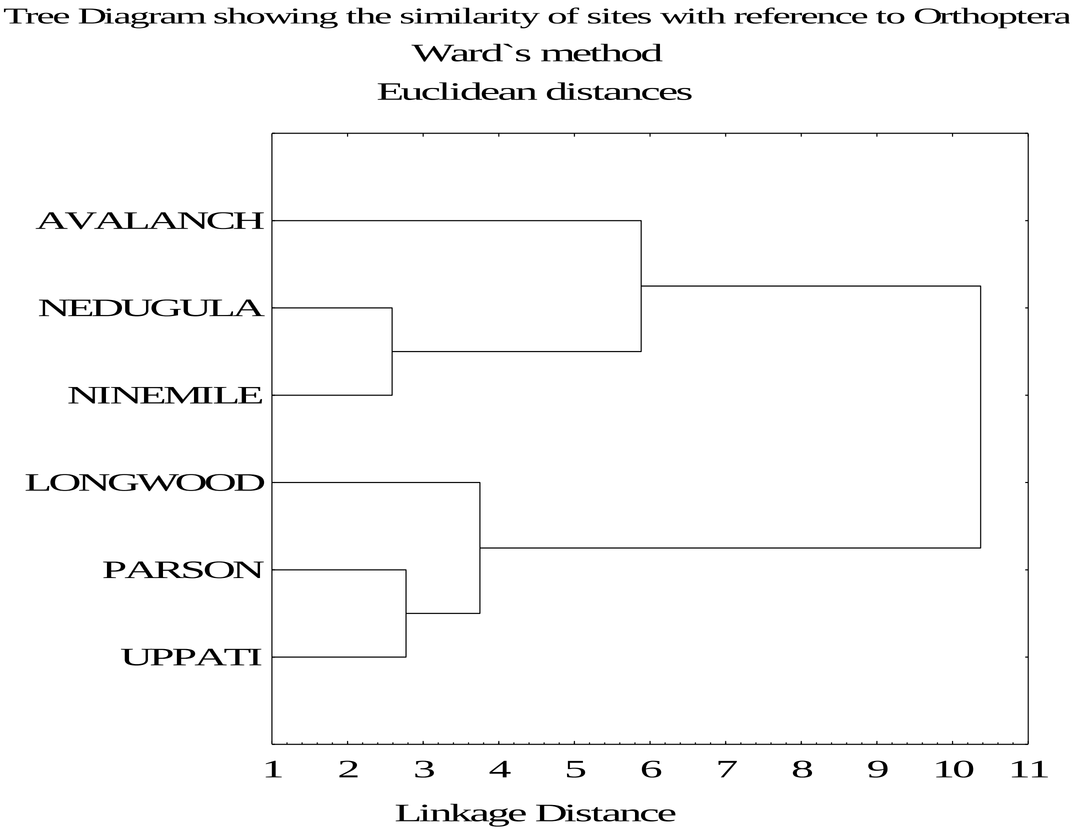

Fig. 1. Dentrogram showing the similarity of sites in realtion to Orthoptera species assemblages.

Mitig Adapt Strateg Glob Change
DOI 10.1007/s11027-010-9257-7

ORIGINAL ARTICLE

Impact of climate change on Indian forests: a dynamic vegetation modeling approach

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Received: 3 March 2010 /Accepted: 13 August 2010

Abstract We make an assessment of the impact of projected climate change on forest ecosystems in India. This assessment is based on climate projections of the Regional Climate Model of the Hadley Centre (HadRM3) and the dynamic global vegetation model IBIS for A2 and B2 scenarios. According to the model projections, 39% of forest grids are likely to undergo vegetation type change under the A2 scenario and 34% under the B2 scenario by the end of this century. However, in many forest dominant states such as Chattisgarh, Karnataka and Andhra Pradesh up to 73%, 67% and 62% of forested grids are projected to undergo change. Net Primary Productivity (NPP) is projected to increase by 68.8% and 51.2% under the A2 and B2 scenarios, respectively, and soil organic carbon (SOC) by 37.5% for A2 and 30.2% for B2 scenario. Based on the dynamic global vegetation modeling, we present a forest vulnerability index for India which is based on the observed datasets of forest density, forest biodiversity as well as model predicted vegetation type shift estimates for forested grids. The vulnerability index suggests that upper Himalayas, northern and central parts of Western Ghats and parts of central India are most vulnerable to projected impacts of climate change, while Northeastern forests are more resilient. Thus our study points to the need for developing and implementing adaptation strategies to reduce vulnerability of forests to projected climate change.

Keywords Climate change · Forest · Forested grids · Forest vulnerability index · Impact of climate change · India · Model

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1 Introduction

Climate is one of the most important determinants of vegetation patterns globally and has significant influence on the distribution, structure and ecology of forests (Kirschbaum et al. 1996). Several climate–vegetation studies have shown that certain climatic regimes are associated with particular plant communities or functional types (Walter 1985). It is therefore logical to assume that changes in climate would alter the distribution of forest ecosystems. Based on a range of vegetation modeling studies, IPCC 2007 suggests potential forest dieback towards the end of this century and beyond, especially in tropics, boreal and mountain areas (Miles 2002; McClean et al. 2005). The most recent report from International Union of Forest Research Organization (Seppälä et al. 2009) paints a rather gloomy picture about the future of the world forests in a changed climate as it suggests that in a warmer world, the current carbon regulating services of forests (as carbon sinks) may be entirely lost, as land ecosystems could turn into a net source of carbon dioxide later in the century.

Assessments of potential climate change impacts on forests in India (Ravindranath and Sukumar 1996; Ravindranath and Sukumar 1998; Ravindranath et al. 2006) were based on BIOME model (versions 3 and 4)—which being an equilibrium model, does not capture the transient responses of vegetation to climate change. The recent study (Ravindranath et al. 2006) concludes that 77% and 68% of the forested grids in India are likely to experience shift in forest types for climate change under A2 and B2 scenarios, respectively. In addition there have been two regional studies, the first focusing on potential climate change impacts on forests in the northern state of Himachal Pradesh (Deshingkar 1997) and the second in the Western Ghats (Ravindranath et al. 1997). These studies indicated moderate to large-scale shifts in vegetation types with implications for forest dieback and biodiversity. The studies conducted for India so far have had several limitations, e.g., coarse resolution of the input data as well as the use of BIOME which is an equilibrium model with limited capability in categorizing plant functional types and dynamic representation of growth constraints.

Impacts of climate change on forests have severe implications for the people who depend on forest resources for their livelihoods. India is a mega-biodiversity country where forests account for more than one fifth of the geographical area. With nearly 173,000 villages classified as forest villages, there is a large dependence of communities on forest resources in India (Kishwan et al. 2009). India has a large afforestation programme of over 1.32 Mha per annum (Ravindranath et al. 2008), and more area is likely to be afforested under programmes such as 'Green India mission' and 'Compensatory Afforestation Fund Management and Planning Authority' (CAMPA). Thus it is necessary to assess the likely impacts of projected climate change on existing forests and afforested areas, and develop and implement adaptation strategies to enhance the resilience of forests to climate change.

The present study investigates the projected impacts of climate change on Indian forests using a dynamic global vegetation model (DGVM). It specifically assesses the boundary shifts in vegetation types, changes in NPP and soil carbon stocks, as well as the vulnerability of existing forests to future climate change.

2 Status of forests in India

According to the Forest Survey of India (FSI) "all lands, more than one hectare in area, with a tree canopy density of more than 10% is defined as Forest" (FSI 2009). The status of forests and forest management systems contribute to the vulnerability of forests to climate change.

2.1 Forest area

The Forest Survey of India has been periodically estimating the forest cover in India since 1987 using remote sensing techniques (FSI 1989). It can be observed from Fig. 1 that the forest cover in India has nearly stabilized and further it is increasing marginally over the years. In addition to forest cover, FSI has also included the tree cover in its 2001, 2003, 2005, and 2007 assessments.

2.2 Distribution of forest types

Indian forests are extremely diverse and heterogeneous. Classification of Indian forest types is available from two main sources—one by Forest Survey of India (FSI 2001) and another by Champion and Seth (1968). Due to forest heterogeneity, Forest Survey of India’s classification scheme has a pan-Indian ‘miscellaneous forest’ category (with no dominant species), which accounts for 63% of forest area. This large miscellaneous category makes the FSI classification rather unattractive for further analysis. However, Champion and Seth (1968) classify Indian forests into 16 distinct forest types. Hence, we use the Champion and Seth classification for further analysis. The distribution of forest types in India according to Champion and Seth (1968) is shown in Fig. 2.

2.3 Carbon stocks in Indian forests

Estimates for forest carbon stocks, including biomass and soil carbon from literature are shown in Fig. 3. Forest carbon stocks including biomass and soil carbon for the year 1986 are estimated to be in the range of 8.5 to 9.5 GtC (the studies differ in the methods used). According to an FAO study, total forest carbon stock was estimated to be 10 GtC for 2005. Thus, carbon stocks in Indian forests may not have declined. Additionally, Kishwan et al. (2009) estimate that the carbon stock in biomass as well as soil has increased by 377 Mt C between 1995 and 2005. Forest soil carbon accounts for over 50% of the total forest carbon stock according to different estimates (Fig. 3).

2.4 Afforestation trend in India

India initiated large-scale afforestation under the social forestry programme starting in the early 1980s. Figure 4 presents the progress of afforestation in India for the period 1951–2005. It can

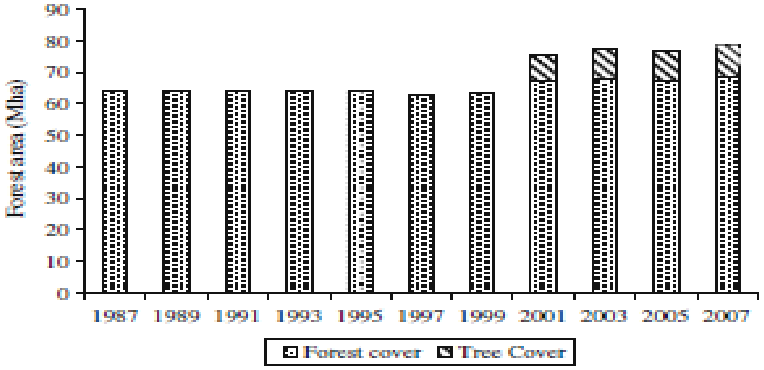


Fig. 1 Trends in area under forest and tree cover (FSI 1989–2009)

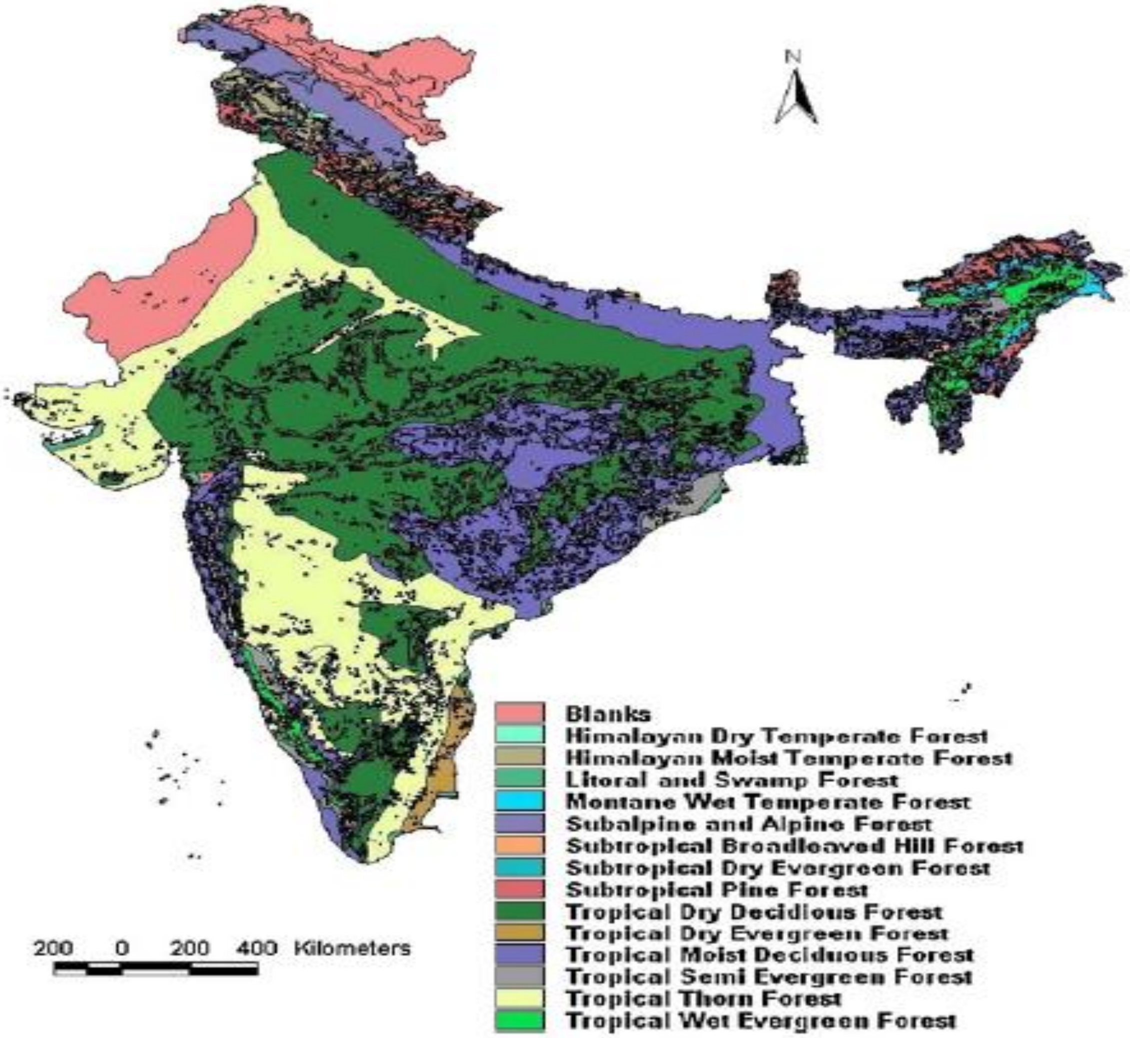


Fig. 2 Forest types of India (Champion and Seth, 1968). "Blanks" indicate that the region is not classified by Champion and Seth

be seen from Fig. 4 that the cumulative area afforested in India during the period 1980–2005 is about 34 Mha at an average annual rate of 1.32 Mha (Ravindranath et al. 2008).

3 Methods

The impacts of climate change on forests in India are assessed based on the changes in area under different forest types, shifts in boundary of forest types and NPP. This assessment was based on: (i) spatial distribution of current climatic variables, (ii) similar data for future climate projected by relatively high-resolution regional climate models for two different

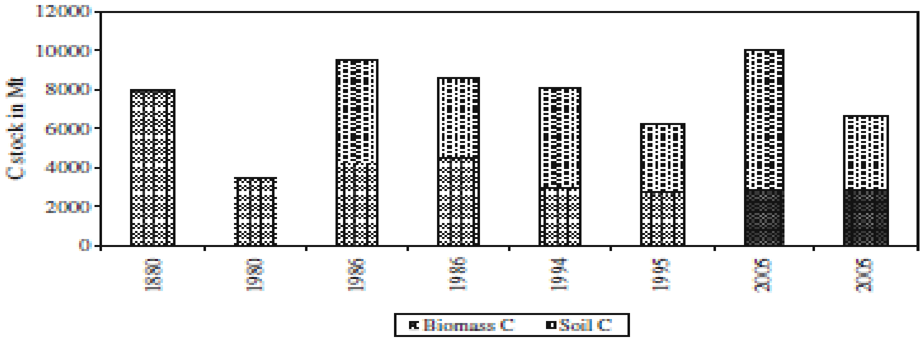


Fig. 3 Carbon stock estimates for Indian forests (Source: 1880—Richards and Flint 1994; 1980—Richards and Flint 1994; 1986—Ravindranath et al. 1997; 1986—Chhabra and Dadhwal 2004; 1994—Haripriya 2003; 1995—Kishwan et al. 2009, 2005—FAO 2005, 2005—Kishwan et al. 2009)

climate change scenarios, and (iii) vegetation types, NPP and carbon stocks as simulated by the dynamic model IBIS v.2 (Integrated Biosphere Simulator).

3.1 Vegetation model

The dynamic vegetation model IBIS is designed around a hierarchical, modular structure (Kucharik et al. 2000). The model is broken into four modules namely 1) the land surface module, 2) Vegetation phenology module, 3) Carbon balance module and 4) Vegetation dynamics module. These modules, though operating at different time steps, are integrated into a single physically consistent model that may be directly incorporated within AGCMs (Atmospheric General Circulation models). For example, IBIS is currently incorporated into two AGCMs namely GENESIS-IBIS (Foley et al. 2000) and CCM3-IBIS (Winter 2006). The state description of the model allows trees and grasses to experience different light and water regimes and competition for sunlight and soil moisture determines the geographic distribution of plant functional types and the relative dominance of trees and grasses, evergreen and deciduous phenologies, broadleaf and conifer leaf forms, and C3 and C4 photosynthetic pathways.

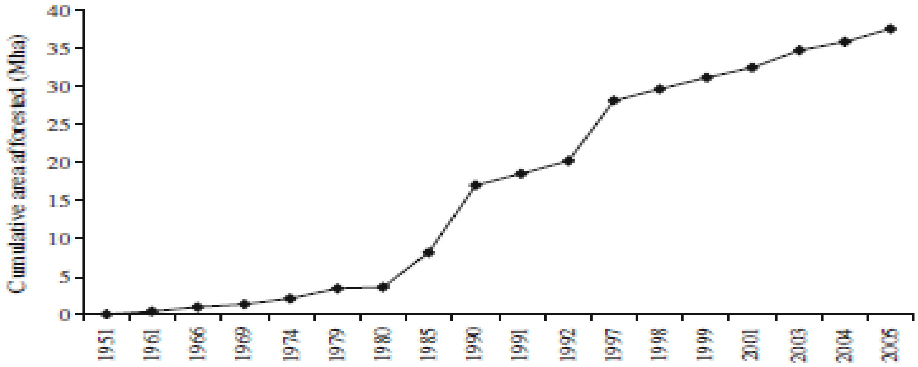


Fig. 4 Cumulative area afforested during 1951 to 2005

3.2 Input data

IBIS requires a range of input parameters including climatology as well as soil parameters. The main climatology parameters required by IBIS are: Monthly mean cloudiness (%), Monthly mean precipitation rate (mm/day), Monthly mean relative humidity (%), Monthly minimum, maximum and mean temperature (C) and wind speed (m/s). The main soil parameter required is the texture of soil (i.e percentage of sand, silt and clay). The model also requires topography information.

Observed climatology is obtained from CRU (New et al. 1999), while soil data was obtained from IGBP (IGBP 2000). For climate change projections, RCM outputs from Hadley centre model HadRM3 were used (Rupakumar et al. 2006). The climate variables for future scenarios were obtained using the method of anomalies. Briefly, this involved computing the difference between the projected values for a scenario and the control run of the HadRM3 model, and adding this difference to the value corresponding to the current climate as obtained from the CRU climatology. Climate Data Operators (CDO) software (Schulzweida and Kornblueh 2006) was used for the data editing and Climate Data Analysis Tool (CDAT) (Drach et al. 2007) for data processing and generation of various maps and plots.

3.3 Selection of forested grids

A digital forest map of India (FSI 2001) was used to determine the spatial location of all forested areas. This map was based on a high-resolution mapping (2.5′ by 2.5′), wherein the entire area of India was divided into over 165,000 grids. Out of these, 35,899 grids were marked as forested grids (along with the forest density and the forest type). Figure 5 shows the spatial location of these grids. Furthermore, these forest grids were classified into three categories as per forest density: 1) "Very dense forests" with crown density above 70%, 2) "Moderately dense forest" with crown density between 40% and 70%; 3) "Open forest" with crown density between 10% and 40%.

3.4 Scenarios of climate change

SRES scenario A2 (atmospheric CO_2 concentration reaches 740 ppm by 2085) is selected as one of the scenarios. However, since a more constrained emission pathway may emerge as a result of global mitigation actions, we also chose B2 scenario (575 ppm by 2085) in this study. We compare the results of these with the 'baseline' scenario, which represents the simulation using the 1961–91 observed climatology. 'Baseline' is also referred to as either 'reference' or 'control' case.

4 Model validation

We simulated the current vegetation pattern, NPP, biomass and soil carbon over India using the IBIS model driven by observed climatology from CRU (New et al. 1999). The validation of this baseline (or control) simulation is described below.

4.1 Vegetation distribution

Comparison of simulated vegetation cover with the observed vegetation map (Fig. 6) (Champion and Seth 1968) shows fair agreement. Many important observed vegetation

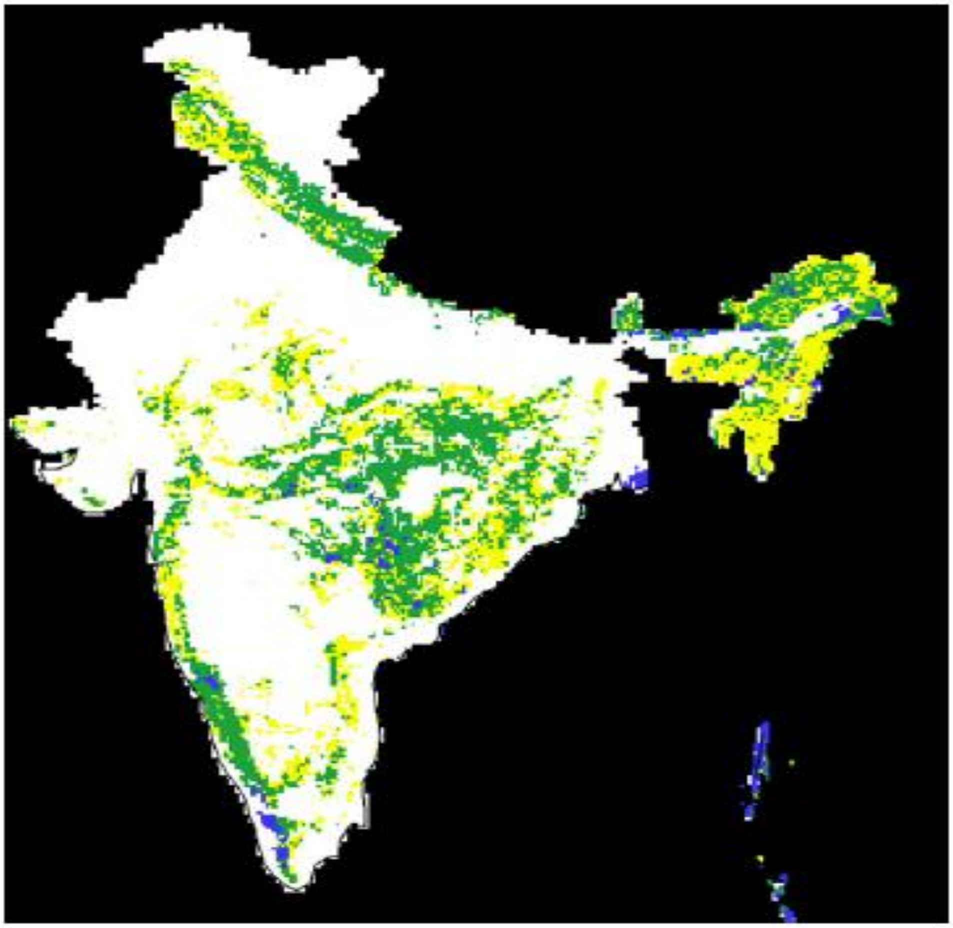
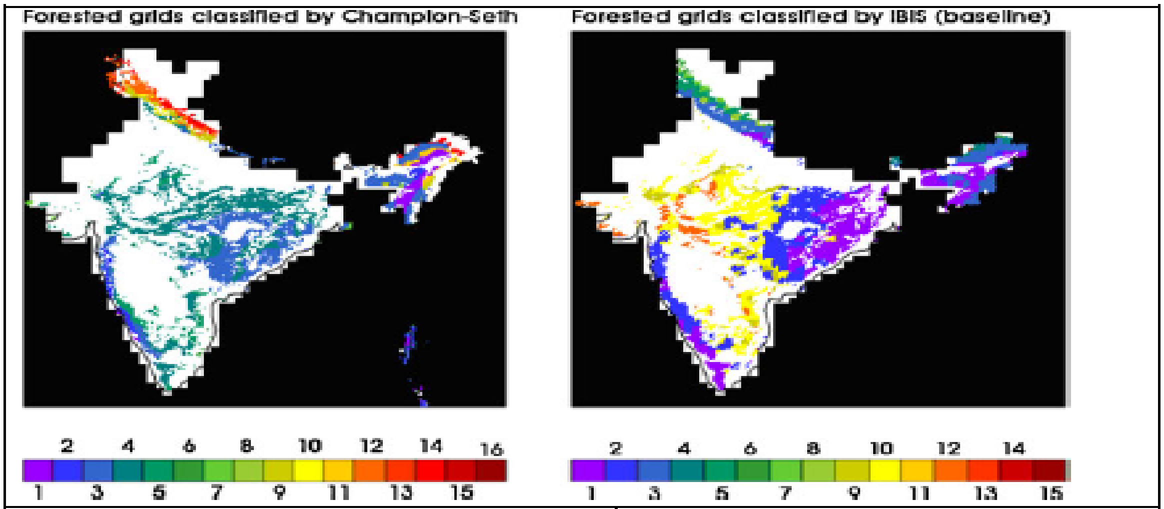


Fig. 5 The location of the 35,899 forest grid points (*coloured*) in India. Out of these, 4.3% of grid points (*blue*) were classified as "very dense forests", 54.9% (*green*) as "moderately dense forest" and 40.7% (*yellow*) as "open forests"

distribution patterns are reproduced in the simulation, including (1) the tropical evergreen forest vegetation in Western Ghats and North-east; 2) desert and thorny vegetation types in Western and south central parts, 3) tropical deciduous forests in most of its present day locations except parts of western Madhya Pradesh where the model simulates savanna and shrublands; 4) temperate evergreen conifer forests in Himalayas and higher elevations of North east.

IBIS simulates forests at about 70% of the FSI forest grids (FSI 2001). However it simulates savanna and shrublands over most grids in western Madhya Pradesh, Gujarat and Rajasthan whereas Champion and Seth (1968) classify these regions as forests. This anomaly of IBIS under-representing forests in the tropics is documented in previous studies (Kucharik et al. 2000; Cramer et al. 2001; Bonan et al. 2003) which find that IBIS has higher (than observed) grass coverage in the great plains, southern South America, Africa and India.



1.Tropical wet evergreen forests, 2.Tropical semi evergreen forests, 3.Tropical moist deciduous forest, 4.Tropical dry decidious forest, 5.Tropical thorny/scrub forests, 6.Tropical dry evergreen forest, 7.Litoral and swampy forest, 8.Subtropical broad -leaved hill forests, 9.Subtropical pine forests, 10.Sub-tropical dry evergreen forests, 11.Montane wet temperate forests, 12.Himalayan wet/ moist temperate forests, 13.Himalayan dry temperate forests, 14.Sub-alpine forests, 15.Moist alpine, 16.Dry alpine

1: tropical evergreen forest / woodland, 2: tropical deciduous forest / woodland, 3. temperate evergreen broadleaf forest / woodland, 4: temperate evergreen conifer forest / woodland, 5: temperate deciduous forest / woodland, 6: boreal evergreen forest / woodland, 7: boreal deciduous forest / woodland, 8: mixed forest / woodland, 9: savanna, 10: grassland / steppe, 11: dense shrubland, 12: open shrubland, 13: tundra, 14: desert, 15. polar desert / rock / ice

Fig. 6 Model simulated current vegetation distribution (*right*) compared with observed vegetation distribution (*left*, Champion and Seth 1968)

4.2 NPP

The remotely-sensed mean NPP data from satellites for the period 1982–2006 was obtained from Nemani et al. (2003) (as well as personal correspondence). It was regridded to a 0.5°× 0.5° format and the geographical region outside India was masked out. The correlation between this distribution and the NPP simulated by IBIS control case is estimated to be about 0.65, indicating fair agreement (Fig. 7). IBIS simulations of NPP (Mean: 424.0, Min: 7.0, max: 1374.0 g/m^2/year) show a reasonable match with satellite observations (Mean: 431.0, min: 0.0, max: 1195.0 g/m^2/year) over India. . It should be noted that simulated NPP represents the NPP of natural potential vegetation but observations represent NPP of current vegetation (including croplands).

4.3 Soil organic carbon

We compared the soil organic carbon data from IGBP (IGBP-DIS 1998) with the IBIS simulated soil carbon estimates for the control case (Fig. 8). We find that the mean from both the sources is approximately 5 kg/m^2 over India (mean of IBIS=5.0 kg/m^2 and mean of IGBP=4.7 kg/m^2). However, we find that the IBIS simulated spatial distributions (spatial standard deviation=4.27; Max=20.83; Min=0.13) to be substantially different from IGBP estimates (Standard deviation=1.33; Max=11; Min=1.8).

For a more detailed investigation, we selected a grid point in the Western Ghats. We selected this grid point as it is nearer to the field research centre operated by the Indian

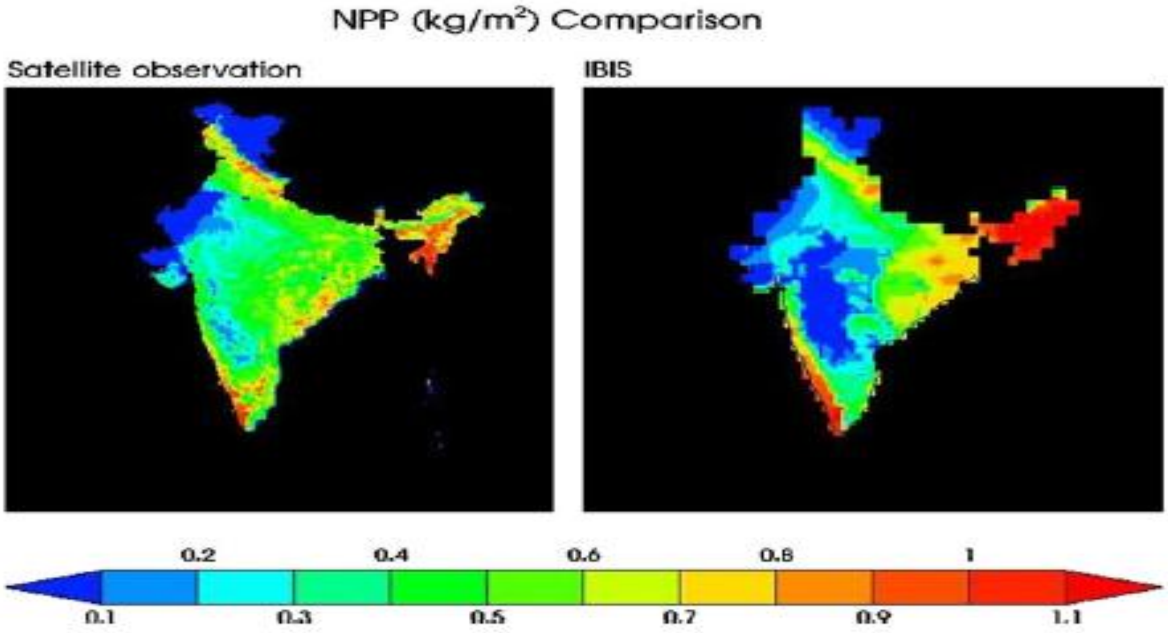


Fig. 7 Model simulated current NPP (kgC/m^2) compared with the remote-sensing-derived mean NPP data from 1982 to 2006

Institute of Science (IISc), Bangalore. Location of the grid can be seen in the map of India (inset of Fig. 9).

A total of 35 different locations were sampled in the Western Ghats out of which 15 sample locations were situated in forested areas and 20 were situated in non-forested areas. Sample sites are shown in Figs. 9 and 10. About 250 gms of soil samples were sampled

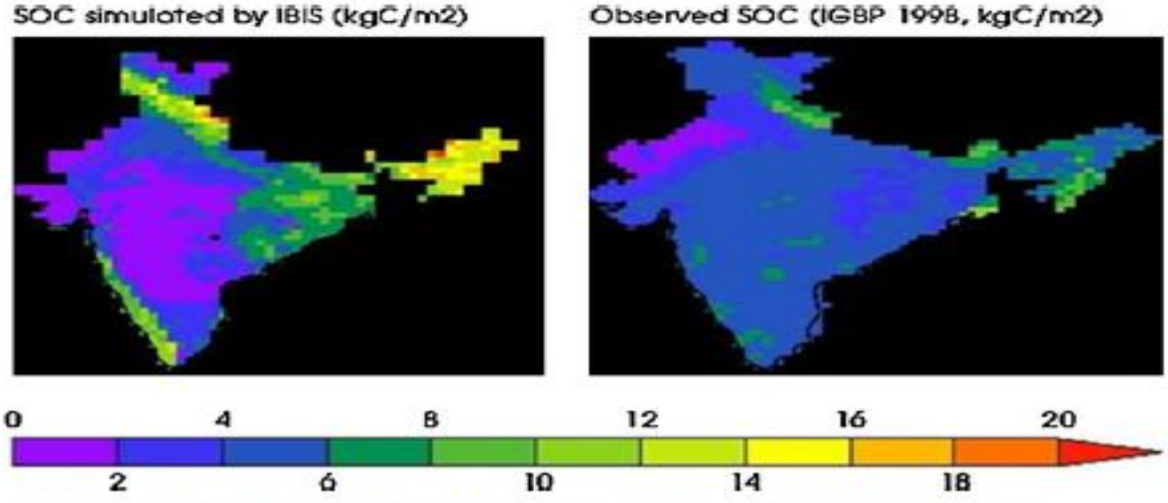


Fig. 8 Model simulated current SOC distribution compared with the observed SOC distribution

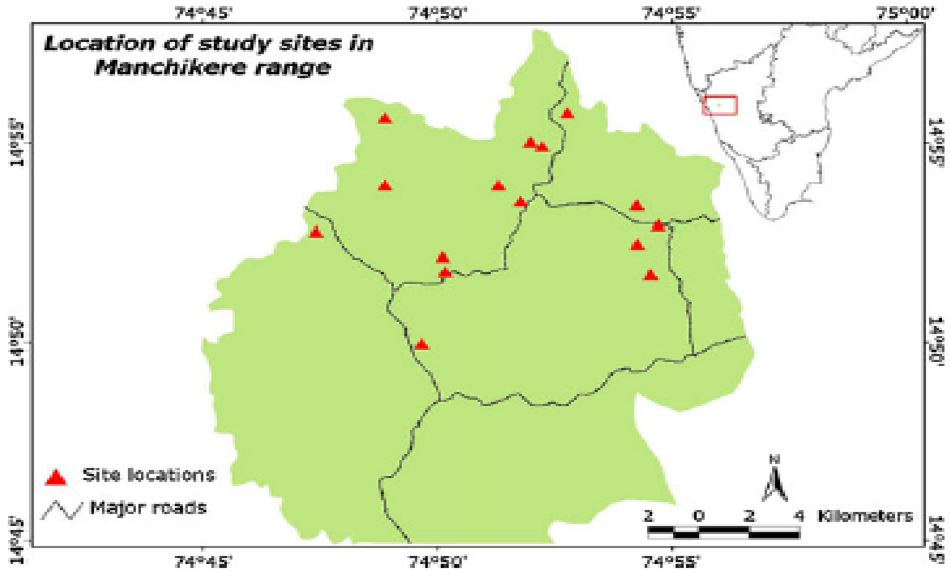


Fig. 9 Sample locations in forested sites

from two depth classes i.e. 0–15 cms and 15–30 cms. Soil organic carbon was analyzed using the Walkley and Black (1934) method.

Forested sites were found to have higher soil organic carbon with an average of 97 tonnes carbon per hectare (tC/ha) with a standard deviation (SD) of 19.8 tC/ha compared to non-forested areas with an average of 64 tC/ha (SD=27.2 tC/ha). The average soil organic carbon in the region is estimated to be 78.15 tC/ha (S.D=29.2 tC/ha) whereas IBIS simulates 89.13 tonnes C/ha for this particular grid. , Given the huge uncertainty involved with soil carbon estimation (Sudha et al. 2003), the model predictions appear to be reasonable.

Total carbon stocks For the control case (1975) IBIS simulated a total 3090 Mt of carbon in biomass over India while a review of published studies suggests a mean of 3386±989 Mt of carbon in biomass (Fig. 3). Further, IBIS simulations suggest a total of 4705 Mt of carbon in the form of SOC in the forested grids, while a review of published studies suggests a mean of 5,000±1464 Mt of SOC in Indian forests. SOC estimates are, in general, associated with larger uncertainty. In summary, IBIS simulates a total carbon stock (biomass plus SOC) of 7795 Mt of carbon for India while observational estimates suggest a mean of 8141±1705 Mt of carbon in Indian forests.

5 Impacts of climate change on forest types and extents

5.1 Changes in the distribution of forests

The vegetation distribution simulated by IBIS for baseline, A2 and B2 scenario in the forested grids are shown in Fig. 11. One can notice that there is an expansion of tropical

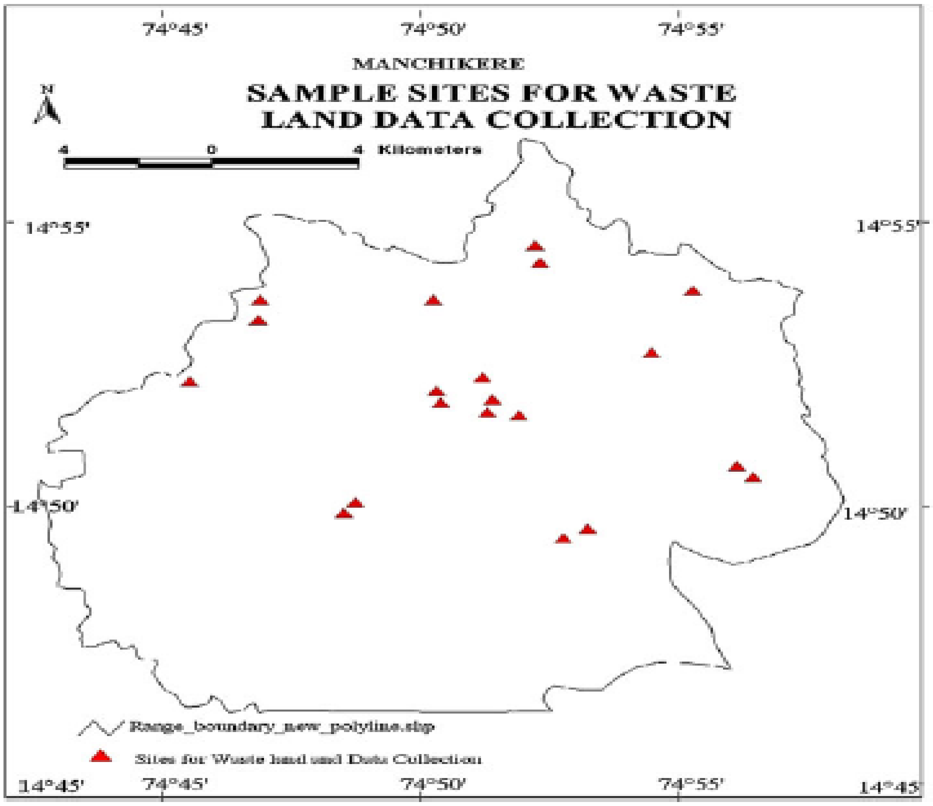


Fig. 10 Sample locations in Non-forest locations

evergreen forests (IBIS vegetation type 1) in eastern India plateau for both A2 and B2 scenarios. The same trend can be seen in the Western Ghats. It is interesting to note that there is almost no vegetation type change in the north-east. Further, there is a slight expansion of forests into the western part of central India. Overall, there is negligible difference between forest extents predicted for the future in the A2 and B2 scenarios except that forest expansion is higher into the western part of central India in the A2 scenario. This could be attributed to higher precipitation levels in A2 scenario relative to B2 in this region. One caveat to the expansion trend of forests (like tropical evergreen) is the assumption that forests are un-fragmented, and there is no dearth of seed-dispersing agents. In the real world, forests are fragmented, and, seed dispersal may not be efficient in the view of loss or reduction in number of dispersal agents due to human habitation pressures and climate change (Rosenzweig 1995). As the population of seed-dispersing agents may decline, predicted forest expansion is not guaranteed.

The vegetation change matrix corresponding to Fig. 11 (for both A2 and B2 scenario) is presented in Tables 1 and 2. One can notice from the table that the bulk of forest-type conversions are from tropical deciduous forests to tropical evergreen forests.

For further analysis, we consider the forested grid points obtained from Champion and Seth 1968 forest type classification (Fig. 2). Then, we identified grids where vegetation type

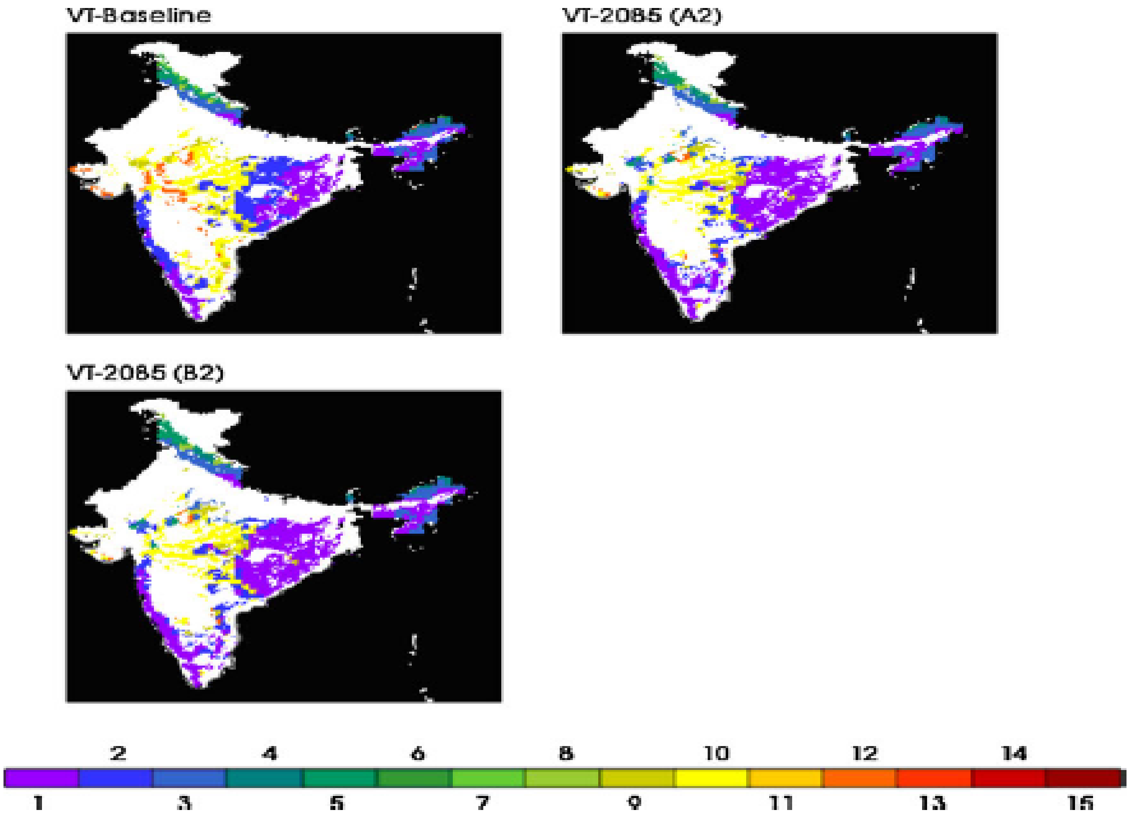


Fig. 11 Forest type distribution and extent simulated by IBIS for the baseline case and A2 and B2 scenarios. White areas represent non-forested grids. (VT—refers to Vegetation Types. The numbers refer to the following vegetation types 1: tropical evergreen forest / woodland, 2: tropical deciduous forest / woodland, 3. temperate evergreen broadleaf forest / woodland, 4: temperate evergreen conifer forest / woodland, 5: temperate deciduous forest / woodland, 6: boreal evergreen forest / woodland, 7: boreal deciduous forest / woodland, 8: mixed forest / woodland, 9: savanna, 10: grassland/ steppe, 11: dense shrubland, 12: open shrubland, 13: tundra, 14: desert, 15. polar desert / rock / ice)

(simulated by IBIS) is projected to change under A2 and B2 scenarios compared to baseline scenario (Fig. 12). Approximately 39 and 34% of forested grid are projected to experience vegetation type change under A2 and B2 climate scenarios, respectively. In agreement with earlier studies (Ravindranath et al. 2006), we too find a trend towards expansion of wetter forest types. Tropical dry deciduous forests currently constitute more than 40% of the Indian forested grids. Our analysis suggests that approximately 47 and 42% of these tropical dry deciduous grids undergo change under A2 and B2 climate change scenarios, respectively, as opposed to less than 16% grids for f tropical wet evergreen forests. Tropical moist forests, which constitute 20% of the grid points, appear to be relatively stable with only 38 and 34% of forested grids experiencing change under the two scenarios. However, tropical thorny scrub forest which constitutes 20% of the Indian forested area is projected to experience a larger change with majority of grids (more than 80%) undergoing change under A2 scenario and 50% grids experiencing change under the B2 scenario.

Table 1 Vegetation change matrix for A2 scenario. The table lists the number of grid points that changed from one IBIS vegetation type (in baseline) to another vegetation type (in 2085 for A2 scenario). For example, the number "6756" in 4th row and 3rd column denotes that 6756 forest grids changed from tropical deciduous forest (vegtype 2) to tropical evergreen forest (vegtype 1)

Changed from	Changed to														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	8143	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	6756	1675	0	0	0	0	0	0	0	0	0	0	0	0	0
3	0	0	4370	0	0	0	0	0	0	0	0	0	0	0	0
4	0	0	0	625	0	0	0	0	0	0	0	0	0	0	0
5	0	0	0	254	644	0	0	176	0	0	0	0	0	0	0
6	0	0	0	103	12	7	0	57	0	0	0	0	0	0	0
7	0	0	0	0	321	0	0	0	0	0	0	0	0	0	0
8	0	0	0	161	1	0	0	70	0	0	0	0	0	0	0
9	135	695	480	0	51	0	0	0	0	0	0	0	0	0	0
10	276	669	201	0	165	0	0	0	1075	3262	0	0	0	0	0
11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0	0	646	0	194	0	0	0
13	0	0	0	0	0	25	0	0	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Numbers 1–15 are IBIS vegetation types. These are: 1: tropical evergreen forest / woodland, 2: tropical deciduous forest / woodland, 3. temperate evergreen broadleaf forest / woodland, 4: temperate evergreen conifer forest / woodland, 5: temperate deciduous forest / woodland, 6: boreal evergreen forest / woodland, 7: boreal deciduous forest / woodland, 8: mixed forest / woodland, 9: savanna, 10: grassland / steppe, 11: dense shrubland, 12: open shrubland, 13: tundra, 14: desert, 15. polar desert / rock / ice

Table 2 Vegetation change matrix for B2 scenario. The table lists the number of grid points that changed from one IBIS vegetation type (in baseline) to another vegetation type (in 2085 for B2 scenario). For example, the number "6216" in 4th row and 3rd column denotes that 6216 forest grids changed from tropical deciduous forest (vegtype 2) to tropical evergreen forest (vegtype 1)

Changed from	Changed to														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	8041	102	0	0	0	0	0	0	0	0	0	0	0	0	0
2	6216	2215	0	0	0	0	0	0	0	0	0	0	0	0	0
3	0	0	4370	0	0	0	0	0	0	0	0	0	0	0	0
4	0	0	0	625	0	0	0	0	0	0	0	0	0	0	0
5	0	0	0	278	353	0	0	443	0	0	0	0	0	0	0
6	0	0	0	66	0	71	0	42	0	0	0	0	0	0	0
7	0	0	0	0	277	44	0	0	0	0	0	0	0	0	0
8	0	0	0	231	1	0	0	0	0	0	0	0	0	0	0
9	47	762	354	0	51	0	0	0	147	0	0	0	0	0	0
10	52	284	8	0	143	0	0	0	717	4398	0	46	0	0	0
11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0	0	581	0	259	0	0	0
13	0	0	0	0	0	25	0	0	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

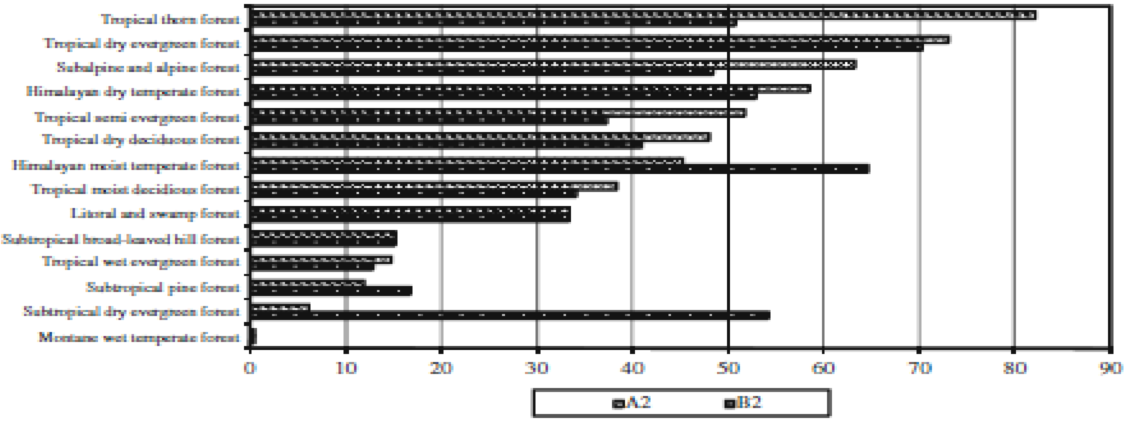


Fig. 12 Percentage of forest grids undergoing vegetation change by 2085 under A2 and B2 scenarios according to forest types

5.2 Impact on NPP

The NPP tends to increase over India (Fig. 13) for both A2 and B2 scenarios. It increases by an average of 66.5% by 2085 under A2 scenario and 49% by 2085 under the B2 scenario. Notably, increase is higher in the north-eastern part of India due to warmer and wetter climate predicated there.

Figure 14 shows the percent change in NPP under the A2 scenario compared to the baseline. While there is an increase in most places, the figure suggests that in central and western Indian forests NPP remains the same or increases only moderately and in some places even decreases by up to 12%. It must be noted that these areas already have a very low level of baseline NPP to start with (in most of cases, not exceeding more than 0.4 kg/m^2).

We analyzed the NPP change under A2 and B2 scenarios compared to the baseline scenario for forest grids classified according to Champion and Seth (Fig. 15). On an average, NPP increased by 67% and 49% under A2 and B2 scenarios, respectively, for these grids. Under A2 scenario, the Himalayan dry temperate forests and sub-alpine and alpine forests register maximum increase in NPP. Vegetation growth in these forests is limited by the lower temperatures, and hence increase in temperature (and precipitation) would favor NPP increase. The subtropical dry evergreen forests register lowest increase in NPP.

5.3 Impact on soil organic carbon (SOC)

A trend similar to NPP distribution can be observed for soil organic carbon (Fig. 16), which is to be expected as increased NPP is the primary driver of higher litter input to the soil. However, the quantum of increase compared to baseline in this case is lower: around 37% and 30%, for the A2 and B2 scenario respectively (averaged over whole of India). This increase is less due to the inertia of the SOC pool and increased soil respiration.

The SOC changes for A2 and B2 scenarios compared to baseline scenario for forested grids according to Champion and Seth 1968 forest type classification is presented in Fig. 17.

Tropical moist deciduous forests and sub-alpine and alpine forests are projected to have large (40–45%) increases in SOC. The increase in NPP results in augmented litter fall

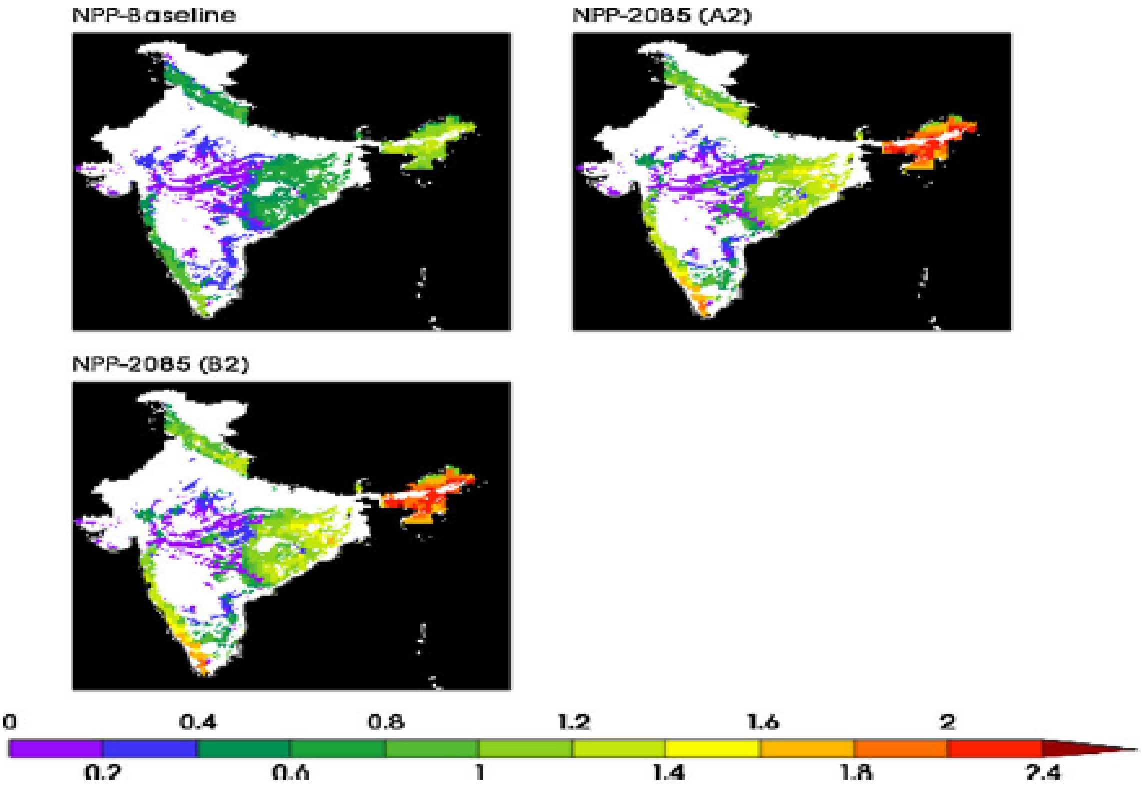


Fig. 13 NPP distribution (kgC/m^2) simulated by IBIS for the baseline case and A2 and B2 scenarios

which contributes to higher SOC. In contrast subtropical pine forests and Himalayan moist temperate forests have much smaller increases (20–30%) in SOC.

Our estimates for both NPP and SOC increase should be viewed with caution as IBIS, compared with other dynamic vegetation models, tends to simulate a fairly strong CO_2 fertilization effect (Cramer et al. 2001; McGuire et al. 2001). This can partly be explained by the fact that the nitrogen cycle and acclimation of soil microbiology to the higher temperatures are not explicitly taken into account in IBIS (Kirschbaum 2000; Tjoelker et al. 2001). It also does not simulate forest fires dynamically which are very common especially in dry deciduous forests of India (FAO 2001). IBIS does not simulate changed pest attack dynamics. Majority of forest species in India are susceptible to pest attack, and we have not included the impact of increased or decreased pest attack in a changed climate.

5.4 Implication at the state level

Statewise forest grid change estimates are provided in Table 3. Chattisgarh, Karnataka, Andhra Pradesh and Madhya Pradesh experience the largest percentage change in forested grids at 73 %, 67%, 62% and 49% respectively, under the A2 scenario while Northeastern states experience the least amount of changes in forested grids.

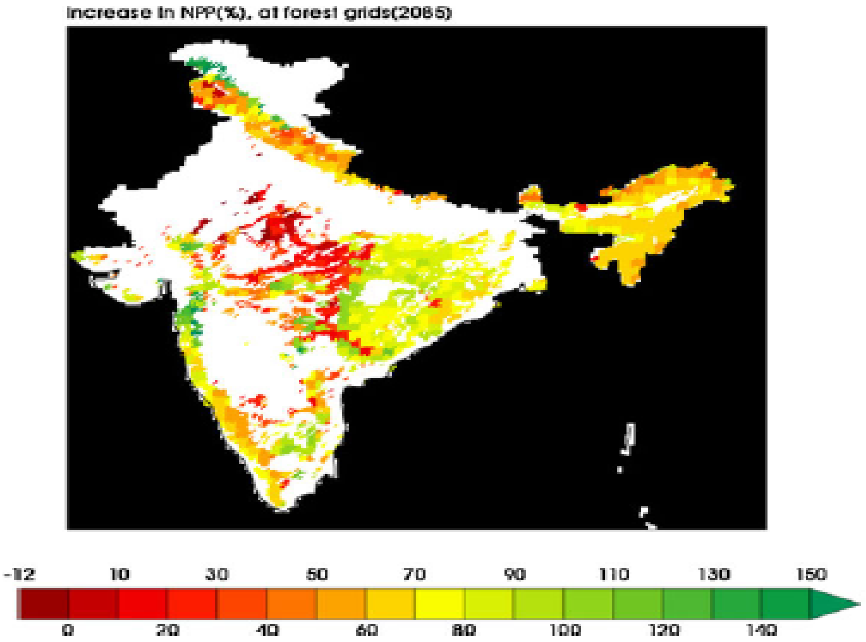


Fig. 14 The effect of climate change on the NPP of the forested grids by 2085 under A2 scenario. The values indicate percentage change in NPP compared to the baseline year

5.5 A vulnerability index for Indian forests

Forests in India are already subjected to multiple stresses including over extraction, insect outbreaks, live-stock grazing, forest fires and other anthropogenic pressures. Climate change will be an additional stress. Disturbed and fragmented forests and monoculture forests are likely to be more vulnerable to climate change (Rosenzweig 1995; Jandl et al.

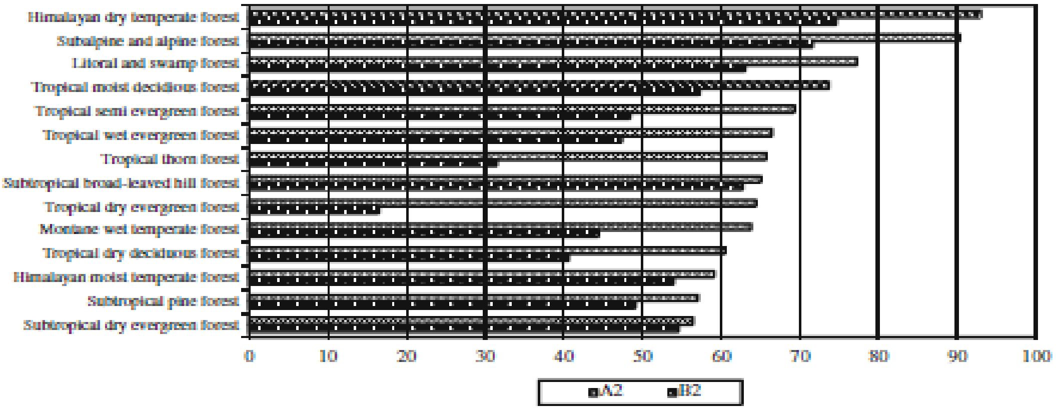


Fig. 15 Percentage change in NPP by 2085 for A2 and B2 scenarios compared to baseline (according to Champion and Seth 1968 classification)

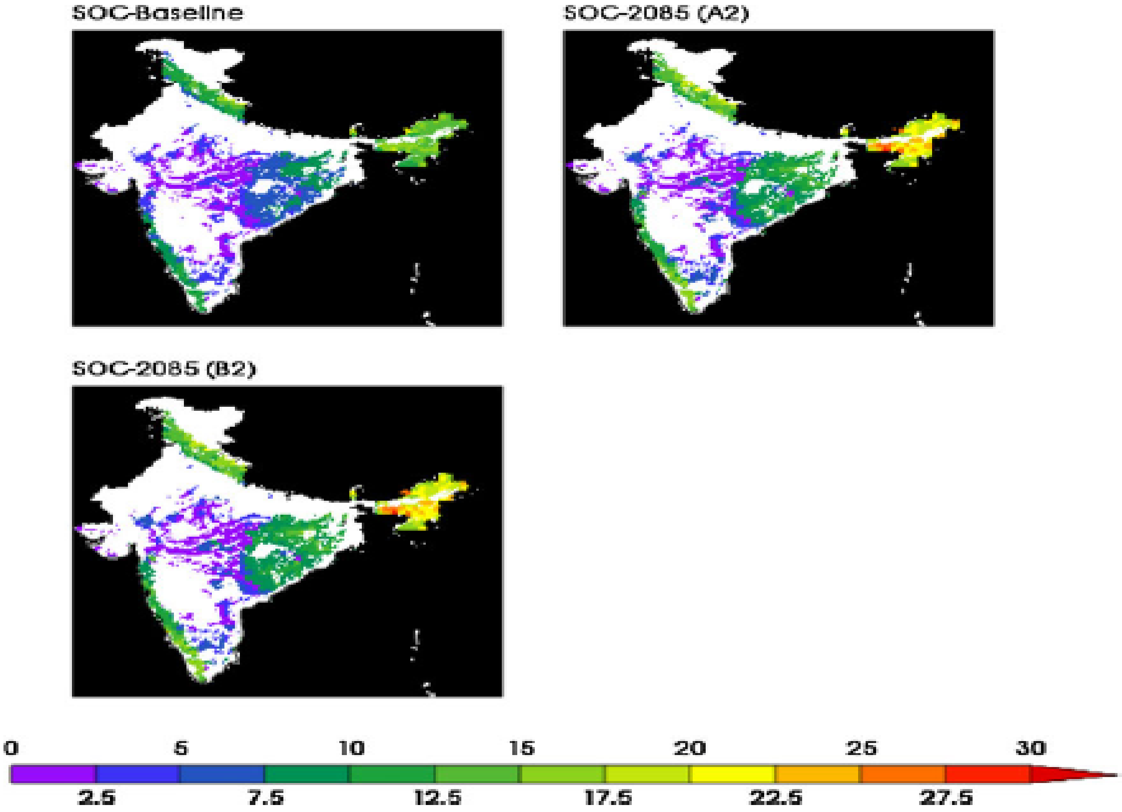


Fig. 16 Distribution of SOC (kgC/m^2) simulated by IBIS for the baseline case and A2 and B2 scenarios

2007). Therefore, we develop a vulnerability index and assess the vulnerability of different forest types and regions.

The various vulnerability index classes (Table 4) were defined by spatially combining information on forest diversity (monoculture versus natural forest), forest density (an indicator of degradation) and IBIS vegetation type change estimates for the forest grids under A2 scenario. For example, if a particular forest grid point had monoculture vegetation, a low forest density (or higher levels of degradation) and if there was a vegetation type shift in the future as predicted by IBIS, then this grid point is given the highest vulnerability Index of 7. The last row in Table 4 defines the "least vulnerability" scenario with no climate change. The distribution of this vulnerability index over the country is shown in Fig. 18.

From Table 4, one can notice that nearly 39% of forested grids are vulnerable to climate change in India.

- The forests in the central part of India, especially the north-western part of India are highly vulnerable. There are regions of vulnerability surrounded by non-vulnerable regions in that area.
- There are relatively few areas in the northeastern part of India that have a high vulnerability index. This low vulnerability index in this regions is because climate is

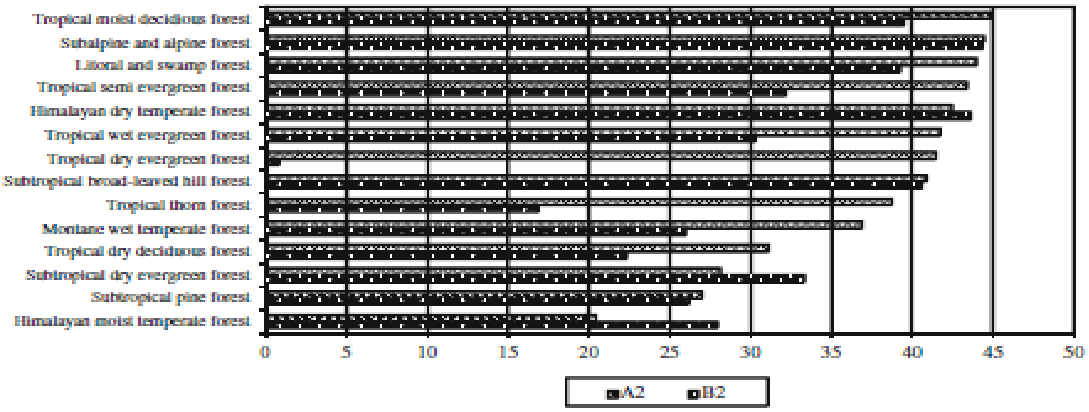


Fig. 17 Percentage change in SOC by 2085 for A2 and B2 scenarios compared to baseline

predicted to get hotter and wetter there, which is conducive to the existing vegetation types (such as tropical evergreen forests).

- A significant part of the Himalayan bio-diversity hotspot that stretches along the north-western part of India along the states of Punjab, Jammu and Kashmir and Himanchal Pradesh is projected to be highly vulnerable. This may be mostly attributed to the higher elevation of these regions. Our studies have shown that these regions will experience higher levels of warming.
- Northern and central parts of the Western Ghats seem to be vulnerable to climate change. Northern parts of the Western Ghats contain significant extent of open forests, which drive up the vulnerability score. High values of the index in the central part of

Table 3 Number of forested grid points projected to undergo change in different states

State name	Num. forest grids	Num. forest grids changed (A2)	% forest grids changed (A2)	Num. forest grids changed (B2)	% forest grids changed (B2)
Madhya Pradesh	4437	2183	49.20	1807	40.73
Arunachal Pradesh	3410	93	2.73	93	2.73
Chhattisgarh	3130	2292	73.23	2292	73.23
Andhra Pradesh	2588	1615	62.40	1191	46.02
Maharashtra	2338	1060	45.34	827	35.37
Orissa	2333	295	12.64	206	8.83
Karnataka	2004	1344	67.07	904	45.11
Jammu and Kashmir	1535	189	12.31	518	33.75
Assam	1247	12	0.96	12	0.96
Uttarakhand	1149	283	24.63	256	22.28
Others	10404	2573	24.73	2367	22.75

Table 4 Vulnerability Index for forested grid points in India

Forest diversity (monoculture vs. natural forest)	Forest crown density	Vegetation type change (IBIS projections)	Vulnerability Index	% of forest grids that fall into this vulnerability category (A2 scenario)
Yes	Low	Yes	7 (most vulnerable)	1.89
Yes	Medium	Yes	6	6.44
Yes	High	Yes	5	0.48
No	Low	Yes	4	11.61
No	Medium	Yes	3	18.16
No	High	Yes	2	0.68
Yes or No	Low or Medium or High	No	1 (least vulnerable)	60.75

the Ghats are likely caused by the negligible precipitation increase over there (with more than 3°C rise in temperature).Forests in the southern Western Ghats appear to be quite resilient as forests in this region are less fragmented, more diverse and they also support tropical wet evergreen forests which, according to IBIS simulations, are likely to remain stable.

6 Implications of climate impact assessment

We note that vulnerable forested grid points are spread across India. However, their concentration is higher in the upper Himalayan stretches, parts of central India, northern Western Ghats and Eastern Ghats. In contrast, northeastern forests, southern Western Ghats and the forested regions of eastern India are estimated to be least vulnerable.

6.1 Implications for afforestation and reforestation (A&R)

Currently, within the forested area of 69 Mha only 8.35 mha is categorized as very dense forest. More than 20 Mha of forest is monoculture and more than 28.8 mha of forests are fragmented (open forest) and have low tree density (FSI 2001; FSI 2009). Low tree density, low bio-diversity status as well as higher levels of fragmentation contribute to the vulnerability of these forests. It is very timely that Government of India under NAPCC (National Action Plan on Climate Change), has brought a proposal to afforest more than 6 Mha of degraded forested lands (Government of India 2008). We recommend that care should be taken to plant mixed species and planting should also be executed in such a way as to link the existing fragmented forests. Efforts should also be made to convert open forests to dense forests. Our analysis suggests that Western Ghats, though a bio-diversity hotspot, has fragmented forests in its northern parts. This makes these forests additionally vulnerable to climate change as well as to increased risk of fire and pest attack. Similarly, forests in parts of western as well as central India are fragmented and are having low bio-diversity. At the same time these are the regions which are likely to witness a high increase in temperature and either decline or marginal increase in rainfall.

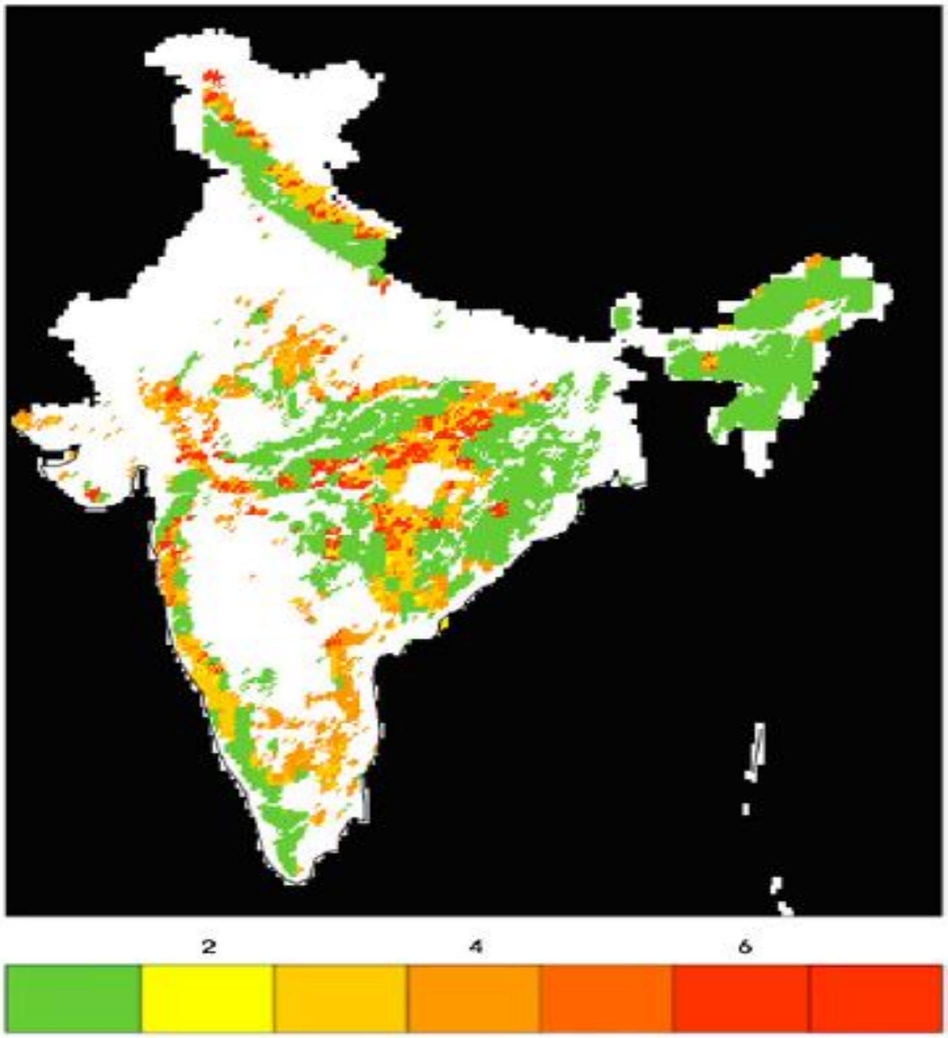


Fig. 18 Distribution of forest vulnerability index for A2 climate change scenario (for FSI forested grid points). Green colour indicates a vulnerability index of 1 (least vulnerable), while colours of yellow to red indicate increasing vulnerability with red indicating a vulnerability level of 7 (most vulnerable)

We notice that most of the mountainous forests (sub-alpine and alpine forest, the Himalayan dry temperate forest and the Himalayan moist temperate forests) are susceptible to the adverse effects of climate change (Fig. 12). This is because climate change is predicted to be larger for regions that have higher elevations. There is a need to explore win-win adaptation practices in such regions such as anticipatory plantations, sanitary harvest, and pest and fire management.

Forests are likely to benefit to a large extent (in terms of NPP) in the northern parts of Western Ghats and the eastern parts of India, while they are relatively adversely affected in western and central India (Fig. 14). This means that afforestation, reforestation and forest management in northern Western Ghats and eastern India may experience carbon sequestration benefits. Hence, in these regions, a species-mix that maximizes carbon sequestration should be planted. On the other hand, in the forests of western and central India, hardy species which are resilient to increased temperature and drought risk should be planted and care should be taken to further increase forest resilience. This may be achieved by planting mixed species, linking up forest fragmentations, devising effective pest and fire management strategies and carrying out anticipatory plantation activities.

6.2 Implication for forest conservation and REDD+

Northeastern forests, southern Western Ghats and Forests of eastern India are estimated to be least vulnerable. This is on account of their high biodiversity, low fragmentation, high tree density as well as low rates of vegetation change (as these regions experience lower levels of temperature increase and gain substantially in terms of precipitation). The resulting low vegetation vulnerability makes these regions especially suitable for reduced deforestation and forest conservation projects such as REDD+ (UNFCCC 2009). For example, northeastern India which has more than 80% of land area classified as forests is currently under severe pressure of deforestation. This region witnesses the highest rate of deforestation in India (65% of total deforestation in India over the period of 2005–2007), mainly due to encroachment and shifting cultivation (FSI 2009). Over the period 2005–2007, according to the latest FSI (2009), 201 km^2 in Nagaland, 119 km^2 in Arunachal Pradesh, 100 km^2 in Tripura and 66 km^2 in Assam were deforested. Given that the ecosystem in this region appears robust in the face of climate change, it is desirable to create REDD+ projects in this area to combat deforestation and resulting loss of flora.

7 Uncertainties, model and data limitations

There are a few notable limitations in this study. IBIS tends to simulate a fairly strong CO_2 fertilization effect (Cramer et al. 2001; McGuire et al. 2001) because IBIS does not have representation for nitrogen and other nutrient cycles (Cramer et al. 2001). It is known to over-predict grasslands (Bonan et al. 2003).

IBIS model, in its current form, does not include a dynamic fire module (Foley et al. 1996). It does not account for changes in pest attack in a changed climate. We believe that many of these limitations of the model have led to the overestimation of future NPP and SOC gains. Climate projections are currently not available in probabilistic terms, which currently limit us from presenting a probability based forest dynamics scenario for India.

There is uncertainty in climate projections, particularly in precipitation at down-scaled regional levels. Land-use change and other anthropogenic influences are not represented in the model projections. Effects of Afforestation and regeneration (e.g. on abandoned croplands or wastelands) on climate are also not taken into account.

Finally, due to lack of regional model predictions for short (2025) and medium term (2050), we could not provide policy relevant recommendations for short and medium periods. However, it is important to recognize the likely trends in the impacts, adopt win-win adaptation strategies and expand research programs to reduce uncertainties in climate projections and impacts of climate change in the forest sector.

Acknowledgements Research for this publication was conducted under the project "Impact of climate change on tropical forest ecosystems and biodiversity in India", funded by the Royal Norwegian Embassy, in collaboration with CICERO, Oslo. We thank the Royal Norwegian Embassy and CICERO for their support. We thank IITM, Pune, and in particular K Krishna Kumar and Savita Patwardhan for providing HadRM3 climate projections under the NATCOM project. Rajiv K. Chaturvedi would also like to acknowledge the support provided by CSIR in the form of research fellowship during his studentship at Centre for Ecological Sciences. Raman Sukumar acknowledges the BP Pal National Environment Fellowship from Govt. of India.

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Mitig Adapt Strateg Glob Change
DOI 10.1007/s11027-015-9659-7

ORIGINAL ARTICLE

Assessment of inherent vulnerability of forests at landscape level: a case study from Western Ghats in India

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Received: 6 August 2014 / Accepted: 27 April 2015

Abstract Assessment of vulnerability is an important step in building long-term resilience in the forestry sector. The objective of this paper is to present a methodological approach to assess inherent vulnerability of forests at landscape level. The approach involves use of vulnerability indicators, the pairwise comparison method, and geographic information system (GIS) tools. We apply this approach to assess the inherent vulnerability of forests of the Western Ghats Karnataka (WGK) landscape, which is a part of the Western Ghats biodiversity hotspot in India. Four vulnerability indicators, namely biological richness, disturbance index, canopy cover, and slope, are selected. We find that forests in 30, 36, 19, and 15 % grid points in this region show low, medium, high, and very high inherent vulnerability, respectively. The forest showing high and very high inherent vulnerability are mostly dry deciduous forests and plantations located largely on the eastern side of the landscape. We also find that canopy cover is one of the key indicators that determine the inherent vulnerability of forests, and natural

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forests are inherently less vulnerable than man-made plantations. Spatial assessment of inherent vulnerability of forests at landscape level is particularly useful for developing strategies to build resilience to current stressors and climate change in future.

Keywords Forest · Indicators · Inherent vulnerability · Plantation · Resilience · Vulnerability assessment

1 Introduction

Forests are a vital global resource with large implications for global biodiversity (Myers et al. 2000), distribution of fresh water (Ellison et al. 2012), and carbon cycle. However, during the twenty-first century, forest ecosystems could become vulnerable to climate and non-climate stressors (IPCC 2014). Exposure and vulnerability are key determinants of such risk and reducing vulnerability and increasing resilience are important risk management approaches (IPCC 2012). To deal with the risks to forests, assessment of vulnerability to identify the drivers of vulnerability is a critical pre-requisite (Murthy et al. 2011; Ribot 2011).

The concept of vulnerability and its assessment can be operationalized either prior to (starting-point approach) or after (end-point approach) the occurrence of a hazard. The starting-point approach to assess vulnerability considers vulnerability to be "something that exists within systems independently of external hazards" (Brooks 2003, p. 4). Brooks (2003, p. 4) further argues that "for vulnerability arising purely from the inherent properties of non-human systems or systems for which the term 'social' is not appropriate the term 'inherent vulnerability' might be used." Forest ecosystems are biophysical systems and are characterized by a host of compositional (e.g., species diversity), structural (e.g., canopy cover density), and process-based (e.g., photosynthesis) inherent properties. These inherent properties make an undisturbed forest resilient. Conversely, in case of a disturbed forest, these properties are degraded and determine the propensity of forest to suffer adverse effects. Inherent vulnerability thus represents the extent by which the compositional and structural attributes and functionality of a forest are degraded as compared to undisturbed forests. It further provides a measure for lack of current potential to counter and prevent harm in future. Application of the concept of inherent vulnerability is useful to understand the factors that enhance such propensity of a forest ecosystem (Sharma et al. 2015). In our opinion, the manageability of forest ecosystems in anticipation of climate change begins with the assessment of inherent vulnerability and improves by addressing the current sources of vulnerability.

Vulnerability assessment studies exclusively for forests at landscape level are lacking; the available studies combine forestry sector along with several other sectors at landscape level (Wang et al. 2008) or regional scale (Lindner et al. 2010; Metzger et al. 2006). In this study, we develop a tool to assess inherent vulnerability of forests for risk management under current climate. The choice of assessment at landscape level is guided by the understanding that to preserve forests, the whole landscape should be considered as a conservation unit (Niemelä 1999; Haila and Kouki 1994). In the present study, landscape is understood as an area composed of adjacent and interacting ecosystems that are related because of geology, landforms, soils, climate, biota, and human influences. Furthermore, landscape level in forestry planning and practices stands for "the appropriate spatial or temporal scale for planning, analysis, and improvement of management activities to achieve ecosystem management objectives" (Price 2008). The following are the specific objectives of the study.

(a) To develop a methodological approach to assess inherent vulnerability of forests at landscape level.
(b) To apply the methodological approach for assessment of the inherent vulnerability of forests in Western Ghats Karnataka (WGK) landscape.

1.1 The Western Ghats Karnataka landscape

WGK landscape is a global biodiversity hotspot (Myers et al. 2000) located along the western coast in peninsular India and is spread across six states. This 1500-km-long (between 8° N and 21° N latitude) and 48 km (minimum) to 210 km (maximum) wide (between 72° E and 78° E longitude) landscape meets the water needs of about 245 million people (GOI 2011). The topographical heterogeneity in the WG landscape is highlighted by the altitudinal variation from sea level to about 2675 m above sea level. Humid and tropical climate dominates the landscape and the main soil types found are red, lateritic, black, and humid soils (Subramanyam and Nayar 1974). About 60 % of WGK landscape falls in Karnataka state (WGK landscape), which constitutes the vulnerability assessment area for the present case study. Of the 38 natural heritage sites identified by the United Nations Educational, Scientific and Cultural Organization (UNESCO) 10 sites are in WGK landscape in Karnataka state. The WGK landscape is characterized by high species endemicity, high rainfall gradient (7500 to 600 mm per year across the landscape from west to east), distinct 6-month-long wet season (June–November), altitudinal variation of about 1100 m, designated wildlife protected areas (WPA) spreading over 15 % of the forest area, and a human population density of <100 person/km^2 in forest dominated areas (GOI 2011).

1.2 Delineating the boundary of the WGK landscape

WGK landscape spreads between 11° and 16° N latitude and 74° and 77° E longitude. The boundary of the WGK landscape was obtained in geographic information system (GIS) format from the Karnataka Forest Department (KFD). Identification and delineation of WGK landscape by KFD is based on considerations of geological features, contiguity of forests, socio-cultural perception by the communities, and identification of Western Ghats area for implementation of government schemes in the past. The total area of the landscape is 4.479 Mha of which 2.609 Mha (58 %) is under forest cover.

1.3 The forest types in WGK landscape

Four major tropical forest types, namely wet evergreen (EG), semi-evergreen (SEG), moist deciduous (MD) and dry deciduous (DD) forests, and man-made plantations (PL), are found in WGK landscape. The wet evergreen forests have multiple canopy layers with species such as *Dipeterocarpus alatus*, *Vateria indica*, *Canarium strictum*, and *Mesua ferrea* in the top canopy; *Albizzia odoratissima* and *Artocarpus lakoocha* in the middle canopy; and *Limonica acidissima* and *Vitex negundo* in the understory. Placed between wet evergreen and moist deciduous, the semi-evergreen forests host evergreen as well as deciduous forest species. The common species found in these forests are *Dipterocarpus indicus* and *Hopea parviflora*. In the moist deciduous forests, the species remain deciduous only for a short time during March and April. The prominent species found in these forests include *Dalbergia latifolia*, *Tectona grandis*, *Terminalia paniculata*, and *Anogeises latifolia*. The undergrowth in these forests consists of bamboo in open patches and canes on wet ground. The dry deciduous forests in the Western Ghats are located on the eastern side in the rain shadow region and host species such as *Terminalia tomentosa*, *Lagerstromia lanceolata*, *Phyllanthus emblica*, and *Cassia fistula*. In the plantation forests, Teak (*Tectona grandis*), Acacia (*Acacia auriculiformis*, *Acacia hybrid*, etc), Eucalyptus (*Eucalyptus grandis*, *Eucalyptus citriodora*, etc), Casuariana (*Casuariana equisetifolia*), and Silver Oak (*Greviliea robusta*) species are found.

2 Methods and materials

The conceptual framework to understand and assess the inherent vulnerability of forests in the context of WGK landscape is presented in Fig. 1. The purpose of assessing the inherent vulnerability of forests of the WGK landscape is to conserve the forests and the forest ecosystem services in the long term.

The following steps are used in the assessment.

Step 1: Stratification of the forests in the landscape

Forests within WGK landscape differ in terms of forest-type, status of biodiversity, and the extent of disturbance, and thus their inherent vulnerability is expected to be different. The assessment and analysis of inherent vulnerability in the present study is carried out for different forest types and for two canopy cover density classes (open forests having <40 % and dense forests having >40 % canopy cover density).

Step 2: Selection of indicators

The framework for selection of vulnerability indicators for WGK landscape is presented in Fig. 2. The choice of vulnerability indicators is narrowed down by invoking expert judgment to quantifiable variables pertaining to biodiversity, physical structure of forests, and the factors of disturbance. The purpose of the

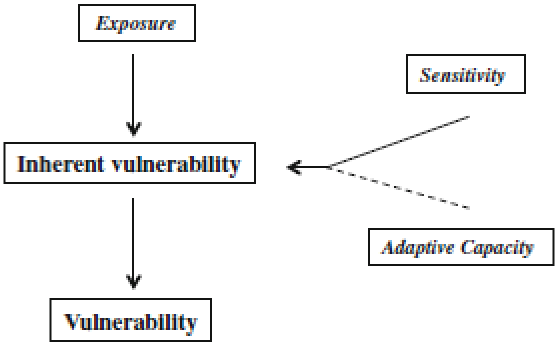

Fig. 1 Conceptual model adopted for assessing the inherent vulnerability of forests in the Western Ghats Karnataka (WGK) landscape. Sensitivity and adaptive capacity are internal properties of a system and determine the inherent vulnerability. Inherent vulnerability of a system is directly proportional to sensitivity and inversely proportional to adaptive capacity. *Dashed line* indicates reduction in inherent vulnerability owing to adaptive capacity of a system. A system with lower inherent vulnerability is likely to be more resilient

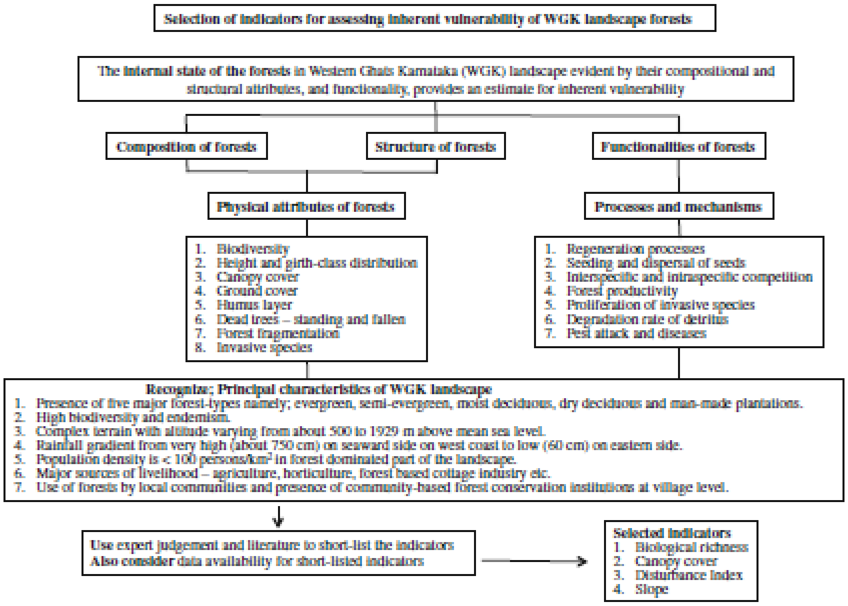

Fig. 2 Framework for identification of indicators for assessment of inherent vulnerability of forests at landscape level. Inherent vulnerability of a forest system is estimated by assessment of its internal state, which is determined by the composition and structure of a forest and the status of ecological processes. The framework combines information about forests and the factors influencing forests in the landscape and employs expert judgment to identify the indicators

assessment, the principal characteristics of the landscape pertaining to climate, geology, forest types, anthropogenic pressures on forests, forest management, and the constraints with respect to availability of data on the indicators are considered in the expert judgment. Often, the lack of data becomes the deciding factor in selection of vulnerability indicators. Four vulnerability indicators, namely biological richness, canopy cover, disturbance index, and slope, are identified for assessment.

Step 3: Indicator weights

To develop weights for the indicators, pairwise comparison method (PCM) was used (Wang et al. 2008). Ten experts and researchers independently assigned weights using PCM technique (Saaty 2008). Arithmetic mean of indicators weights assigned by the experts and researchers was calculated and adopted. The weights assigned to the indicators are presented in Section 4.

Step 4: Placing the landscape onto a regular grid

The boundary of the landscape is marked and the landscape area is divided into area grids of 2.5′ × 2.5′ size (approximately 18.66 km^2). There are 2400 grid points in the landscape. The forest types map for the landscape was obtained from the Karnataka Forest Department. Using GIS technique, the landscape area was stratified into five strata, namely wet evergreen forests (EG), semi-evergreen forests (SEG), moist deciduous forests (MD), dry deciduous forests (DD), and man-made forestry plantations (PL).

Step 5: Classification of forest grid points under a particular forest-type

A grid point having forest area (area with >10 % tree canopy cover) is classified as forest-grid. Out of a total number of 2400 grid points in the WGK landscape, 2372 are forest grid points, and the remaining 28 are non-forest points. A forest grid point is classified under a forest-type that constitutes majority of the forest area.

Step 6: Estimation of vulnerability value at a grid point

The details of the indicator values and their categorization in different vulnerability classes, the sources of data, and the measured variables are provided in Table 1. The range of estimated value for an indicator is first clustered into low, medium, and high vulnerability classes. For example, the value of biological richness (BR) obtained from the database of Indian Institute of Remote Sensing (IIRS) varies between 2 and 91 with biological richness increasing from 2 to 91. This dataset classifies BR values into four classes namely low (2–33), medium (34–49), high (50–69), and very high (70–91) BR. In the present study, we have considered only three BR classes by merging high and very high BR classes into one class and termed it as high BR class (50–91). As vulnerability varies inversely with the BR, the vulnerability class values of 1 (low), 2 (medium), and 3 (high) are assigned for BR range values of 50–91, 34–49, and 2–33, respectively. The vulnerability value (*VV*) for a grid point is obtained in three

Table 1 Details on the indicators selected for assessment of inherent vulnerability of Western Ghats Karnataka (WGK) landscape forests

Indicator values and vulnerability classes for the WGK landscape

Indicator	Range of indicator value (vulnerability class) (indicator measure value assigned)	Source of indicator values	Indicator measurable
Biological richness	Biodiversity richness value a. 50–91 (low) (1) b. 34–49 (medium) (2) c. 2–33 (high) (3)	Indian Institute of Remote Sensing (IIRS) data set available as part of Biodiversity Information System (BIS) at www.bis.iirs.gov.in.	Area-weighted average biodiversity richness value
Disturbance Index	Disturbance Index value a. <18 (low) (1) b. 19–23 (medium) (2) c. 24–72 (high) (3)	As above	Area-weighted average Disturbance Index value
Canopy cover	Canopy cover percentage a. >70 (low) (1) b. 40–70 (medium) (2) c. 10–40 (high) (3)	Forest Survey of India (FSI) data set on forest canopy cover	Area-weighted average cover density
Slope	Ground slope in degree a. <5 (low) (1) b. 5–15 (medium) (2) c. >15 (high) (3)	Georeferenced contour layer obtained from Karnataka Forest Department (KFD)	Area-weighted average slope using 50 m interval contours

The indicator data sources are the national level data bases generated by the agencies of the government in India. High indicator values for biological richness and canopy cover indicate low vulnerability, while high indicator values for disturbance index and slope indicate high vulnerability. Value of an indicator at a grid point is calculated as the area-weighted average for an indicator obtained by using the indicator values for all the pixels falling within that grid point steps. In the first step, area-weighted vulnerability-class value (*VCV*) for an indicator for a grid point is obtained as sum of the products of the proportion of forest area under different vulnerability classes and the corresponding vulnerability-class values (3-high, 2-medium, and 1-low vulnerability). In the second step, *VCV* is multiplied by weight (W_i) to obtain vulnerability due to an indicator. Finally, the vulnerability value at a grid point (VV_j) is obtained by adding the vulnerability values for all the indicators.

Step 1: $VCH_{ij}=(P_{ij1}\times 1+P_{ij2}\times 2+P_{ij3}\times 3)$
Step 2: $VV_{ij}=(VCV_{ij}\times W_i)$
Step 3: $VV_j=\sum_{i=1}^{4}(VV_{ij})$

VCV_{ij} is the vulnerability class value for *i*th indicator in *j*th grid point; P_{ij1}, P_{ij2}, and P_{ij3} are the proportions of the area of a grid point under vulnerability classes 1, 2, and 3 for *i*th indicator in *j*th grid point; W_i is weight for *i*th indicator; VV_{ij} is vulnerability value for *i*th indicator in *j*th grid point; VV_j is vulnerability value for *j*th grid point.

Step 7: Developing inherent vulnerability profile

To develop the spatial profile of inherent vulnerability, the vulnerability values for forest grid points are subjected to cluster analysis inbuilt in the Arch GIS 10 software. Four vulnerability classes namely low, medium, high, and very high vulnerability are identified. The profile of inherent vulnerability is presented in Fig. 3.

3 Summary description of indicators

Four indicators, namely biological richness, disturbance index, canopy cover, and slope, are selected to assess the inherent vulnerability of the forests of WGK landscape.

3.1 Biological richness

The dataset for biological richness (and disturbance index) indicator is obtained from the Indian Institute of Remote Sensing (IIRS), a Government of India agency. This dataset hosted by IIRS is part of Biodiversity Information System (BIS) available at www.bis.iirs.gov.in. The biological richness (BR) indicator is a composite of five parameters, namely species richness (SR), ecosystem uniqueness (EQ), terrain complexity (TC), biodiversity value (BV), and disturbance index (DI) (Roy et al. 2012). BR takes into account factors of ecology, geology, economic value, usefulness to stakeholders, and disturbances and indicates the present status of the species diversity as well as the habitats. It provides a measure of potential for hosting biodiversity (Roy et al. 2012). Therefore, by using the information about BR, it is the loss in potential of a habitat to be biologically richer that is estimated to assess inherent vulnerability. Thus, in this study, a lower value of BR is considered to represent lower adaptive capacity of forests or conversely higher vulnerability. Accordingly, the following vulnerability classes have been identified for different BR value classes in the WGK landscape: low vulnerability (BR value 50–91), medium vulnerability (BR value 34–49), and high vulnerability (BR value 2–33) (Table 1).

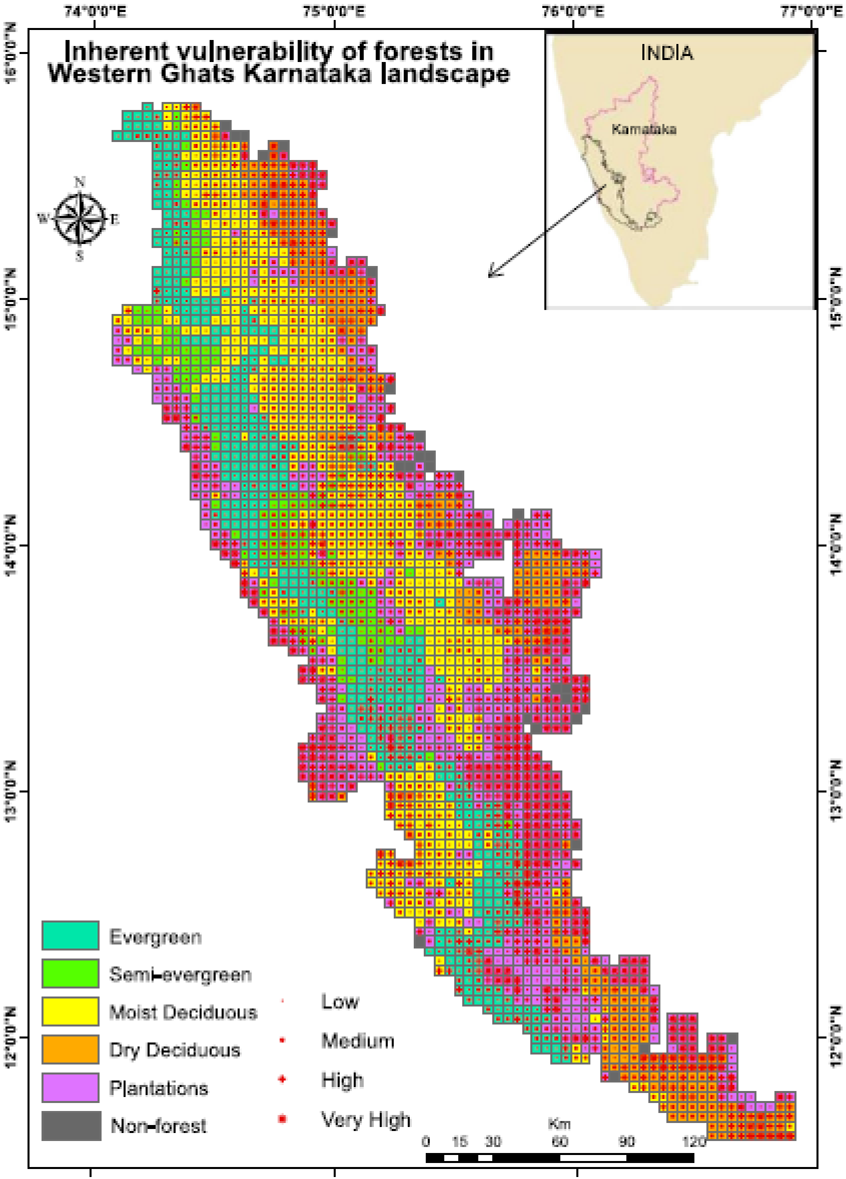

Fig. 3 Distribution of inherent vulnerability in Western Ghats Karnataka (WGK) landscape according to forest types. Inherent vulnerability in the landscape is shown in low, medium, high, and very high vulnerability classes. Generally, forest grid points with high and very high inherent vulnerability are located in plantation forests, and in the dry deciduous forests on the eastern side in the landscape

3.2 Disturbance index

The spatial dataset for DI is also part of Biodiversity Information System (BIS) dataset. DI is composed of five variables, namely fragmentation (F), porosity (P), interspersion (I), juxtaposition (J), and biotic disturbance (BD) (Roy et al. 2012). DI combines the current spatial structure of forests and ground-based disturbance indicators such as status of invasion, regeneration, and low girth class (Roy et al. 2012). Furthermore, DI is one of the five components of BR. DI is included as part of BR to account for the "level of stress on the biologically rich areas" (Roy et al. 2012). However, the implications of DI for forest vulnerability are more and arise from the compromised status of the resilience building attributes of forests such as complex forest structure and forest contiguity. DI represents these forest attributes through porosity, interspersion, juxtaposition, and forest fragmentation. Since BR and DI account for different aspects of vulnerability—BR accounts for vulnerability due to loss of species richness and the potential of a habitat, and DI accounts for the change in the spatial structural elements and fragmentation of forests—DI is also selected as an independent indicator. The IIRS data computes the DI values in the range 0–72 and classifies in four classes, namely very high (29–72), high (24–28), medium (19–23), and low (<18) disturbance (Roy et al. 2012). In the present study, the high and very high DI classes have been merged and three classes indicating low (DI value: <18), medium (DI value: 19–23), and high (DI value: 24–72) vulnerability are used as vulnerability increases with disturbance (Table 1).

3.3 Canopy cover

The canopy cover indicator provides a measure for forest area covered by tree canopy, which determines the microclimate under a forest. Kauffman and Uhl (1990) have reported that a 50 % reduction in canopy cover in Amazonian forests increased average temperature by 10 °C and decreased relative humidity by 35 %. Thinning of canopy cover can therefore drastically alter the conditions of light, temperature, moisture, and wind in a forest and thereby can have severe implications for forest resilience. These changes can potentially mediate or trigger other changes in a forest ecosystem such as increased inter-species competition. Thinning of canopy cover is therefore an important indicator of forest vulnerability.

The spatial data on canopy cover was obtained from Forest Survey of India (FSI), a Government of India agency. The three canopy cover classes (open, moderately dense, and very dense forests correspond to 10–40, 40–70, and >70 % canopy density, respectively) used by the FSI for reporting the status and quality of forests have been adopted for categorizing canopy cover in different vulnerability classes. In the present study, the canopy cover classes with 10–40, 40–70, and >70 % canopy density have been identified with high, medium, and low vulnerability classes, respectively (Table 1).

3.4 Slope

Forests located on steep slopes are inherently more vulnerable from landslides and soil erosion than those located on gentle slopes. WGK landscape has undulating terrain that frequently rises and transforms into mountain-valley system with steep slopes. The steep slopes combined with heavy monsoon rainfall, network of roads, and anthropogenic pressure add to the vulnerability of forests. Furthermore, terrain complexity, a component of BR indicator, accounts for variability of terrain and thereby the habitat heterogeneity but not for the propensity of the habitat to erosive forces of water and wind. Slope is thus selected as a vulnerability indicator. The spatial pattern of slope at 50-m contour-interval was obtained from the Karnataka Forest Department. The slope classification values of <5, 5–15, and >15° indicating gentle, strong, and steep slope classes are used to represent low, medium, and high vulnerability (Wang et al. 2008; FSI 2002).

4 Results and discussion

The spatial data on forest types obtained from the Karnataka Forest Department shows the area under different forest types: evergreen—0.58 Mha, semi-evergreen—0.24 Mha, moist deciduous—0.76 Mha, dry deciduous—0.31 Mha, and plantations—0.72 Mha.

4.1 Distribution of the forest area

Break-up of forest area into forest types is presented in Table 2. Out of the 2372 forest grid points in the landscape, it is found that 64 % have more than 1000 ha (i.e., at least 53 % of the total geographical area is under tree canopy cover) and only 8 % forest grid points have <100 ha of the total geographical area under forest cover. There are no grid points that have <100 ha forest cover in case of semi-evergreen forests. For plantation forest, 18 % (138 out of 751) grid points have <100 ha under forest cover. Furthermore, 74 % (138 out of 187) grid points having forest area <100 ha are plantation grid points and in remaining 26 % natural forests are majority forest-type. Generally, the number of grid points having low forest cover (i.e. <100 ha of the area under forest cover) in case of natural forest is significantly less compared to plantation forests. Majority of the plantation forests are located in the eastern and western fringe of the landscape. These areas are under severe anthropogenic pressure.

All the 2372 forest grid points have been considered for assessment. Very few grid points (<5 %) have <50 ha forest area and 76 % of these have forest area between 10 and 50 ha. Considering all the forest grid points irrespective of the extent of forest area at a grid point is necessary because the purpose of assessment is to identify the forest grid points under different vulnerability classes.

Table 2 Forest grid points in different area classes according to forest types

Forest-types	Number of grids with forest area (ha)							
	<5	5–10	10–50	50–100	100–500	500–1000	1000–1500	>1500
Evergreen	2	2	4	5	15	28	168	232
Semi evergreen	0	0	0	0	4	41	74	40
Moist deciduous	3	0	2	8	48	85	233	298
Dry deciduous	2	0	11	10	72	80	64	90
Plantations	8	11	72	47	170	122	227	94
Total	15	13	89	70	309	356	766	754

Majority of the low forest cover (<100 ha) grid points are contributed by man-made plantation forests. Natural forest grid points have higher proportion of area under forest cover

4.2 "Open" versus "dense" canopy forests in the landscape

Factors such as soil depth, moisture regime, and climate in WGK landscape are favorable to high vegetative productivity and dense forest canopy. However, over a period of time, human activities in the landscape such as cultivation of cash crops (e.g., coffee), expansion of agriculture, housing and road network, forest biomass harvesting, cattle grazing, forest fire, and mining activities have had adverse implications for forest canopy cover. In the present study, forests having <40 % canopy cover density have been considered as open forests (FSI 2011). Such forests are characterized by high disturbance, low stocking, and higher abundance of invasive species, and as a consequence are likely to have lower resilience and higher inherent vulnerability. Forests with >40 % canopy cover density have been considered as dense forests. Of the 2372 forest grid points, 702 (30 %) have average canopy cover of less than 40 % and 1670 (70 %) have average canopy cover of more than 40 % (Table 3) in the landscape. Considering forest types, it is observed that evergreen forest grid points have least percentage (7 %) with <40 % canopy cover followed by semi-evergreen (9 %), moist deciduous (23 %), dry deciduous (40 %), and plantations (48 %).

4.3 The vulnerability indicators and indicator weights

Inherent vulnerability has been assessed by aggregating four vulnerability indicators, namely biological richness (BR), disturbance index (DI), canopy cover (CC), and slope (S). The weights for the indicators are BR-0.552, DI-0.266, CC-0.123, and S-0.059.

4.4 Segregating forest grid points in different inherent vulnerability classes

The vulnerability values for forest grid points in the landscape are estimated between 1.06 and 2.90. This range of grid point vulnerability values are segregated under four cluster-groups using Jenks natural breaks classification method, which defines data clusters by minimizing variance within a cluster and maximizing it between clusters. Accordingly, the forest grid

Table 3 Number and percentage of forest grid points having open (<40 % density) and dense (>40 % density) canopy cover according to forest types

Forest-types	Forest area (ha)	Total grids		Grids with <40 % canopy cover		Grids with >40 % canopy cover	
		Number	Percent	Number	Percent	Number	Percent
Evergreen	584,500	456	19.22	32	7.02	424	92.98
Semi evergreen	240,200	159	6.70	15	9.43	144	90.57
Moist deciduous	760,200	677	28.54	158	23.34	519	76.66
Dry deciduous	306,300	329	13.87	133	40.43	196	59.57
Plantations	718,000	751	31.66	364	48.47	387	51.53
Total	2,609,200	2372		702		1670	
Non-Forest	30,800	28					

Approximately 68 and 32 % grid points have natural and plantation forests, respectively. Compared to plantations, natural forests have higher percentage of grid points under dense canopy cover points are clustered under low (1.06–1.44), medium (1.44–1.87), high (1.87–2.40), and very high (2.40–2.90) inherent vulnerability classes.

4.5 Profile of inherent vulnerability in the landscape

Out of the 2372 forest grid points in the landscape, 30, 36, 19, and 15 % grid points are assessed in low, medium, high, and very high inherent vulnerability classes, respectively. The spatial distribution of inherent vulnerability in the landscape is shown spatially in Fig. 3. Generally, high and very high vulnerability grid points are located toward the fringes of the landscape in dry deciduous forests and plantations. While for evergreen, semi-evergreen, and moist deciduous forests, the percentage of grids with high and very high inherent vulnerability is less than 14 %; in the case of dry deciduous forests and plantations, this percentage is 47 and 65 %, respectively (Table 4). The grid points having higher inherent vulnerability are located mainly on the eastern side of the landscape, which predominantly hosts dry deciduous forests and plantations. The higher inherent vulnerability of dry deciduous forests and plantations could be attributed to the following reasons. (1) Because of the more gentle terrain on the eastern side the forests are more accessible and have higher anthropogenic pressure. (2) The forests on eastern side have lower productivity because of less rainfall. (3) In the dry deciduous belt, plantations have been raised because such forests could not regenerate due to unrelenting anthropogenic pressure and these areas were in various stages of degradation. The results suggest that plantation forests are more vulnerable than natural forests in the WGK landscape (Thompson et al. 2009).

Among the natural forest types, semi-evergreen forests are least vulnerable as no semi-evergreen forest grid point is assessed in very high inherent vulnerability class and the total percentage of grid points with high and very high inherent vulnerability for this forest-type is the lowest (11 %) (Table 4). The evergreen forest-type has a total of 12 % grid points under high and very high inherent vulnerability classes. Under evergreen and semi-evergreen forest types, 88 and 89 % grid points, respectively, are under (combined) low and medium inherent vulnerability classes. The moist deciduous forests are placed in between evergreen and semi-evergreen on one side and dry deciduous and plantation forests on the other with 35, 51, 12, and 2 % of grid points in low, medium, high, and very high inherent vulnerability, respectively. Among natural forest-types, dry deciduous forests have highest inherent vulnerability in WGK landscape.

Table 4 Percentage of forest grid points in low, medium, high, and very high inherent vulnerability classes according to forest types. Plantation forests show higher inherent vulnerability than natural forest-types

Forest-type	Inherent vulnerability (percent grid points)			
	Very high	High	Medium	Low
Evergreen	2.85	8.99	25.44	62.72
Semi evergreen	0.00	10.69	35.85	53.46
Moist deciduous	1.92	11.82	51.26	35.01
Dry deciduous	10.64	36.78	48.63	3.95
Plantations	40.35	24.50	22.24	12.92

4.6 Forest degradation and inherent vulnerability

The ecological carrying capacity of the WGK landscape is sufficient to host dense canopy forests (GOI 2011) and any thinning of canopy cover to lower stocking is considered a sign of disturbance. Thus, forests with <40 % canopy cover have been considered as degraded forests. In this study, we consider forests having >40 % canopy cover density as resilient.

The distribution of high and very high inherent vulnerability grid points in open canopy and dense canopy cover categories shows that while 60 % forest grid points have high and very high inherent vulnerability in open forests, only 23 % dense forest grid points are under these classes. As against 9 % grid points in low inherent vulnerability class for open canopy forests, there are 39 % such grid points in dense canopy cover forests. This demonstrates that degraded forests with more open canopy cover have higher inherent vulnerability compared to those with denser canopy. Thus, it could be inferred that canopy cover is one of the most important contributing factors for the inherent vulnerability of forests in WGK landscape.

For evergreen, semi-evergreen, and moist deciduous forest-types, about 30 % grid points are in high and very high inherent vulnerability classes when the canopy is open. However, only about 10 % of the grid points show high and very high inherent vulnerability for these forest-types when the canopy cover is dense. The combined proportion of high and very high inherent vulnerability grid points, between open and dense canopy covers within a forest-type, is found to be 4:1 for semi-evergreen, 3:1 for moist deciduous, 2.7:1 for evergreen, 2.3:1 for dry deciduous, and 1.28:1 for plantations. This suggests that, with other factors remaining constant, the sensitivity of inherent vulnerability to canopy cover change is maximum in case of semi-evergreen forests and minimum for plantation forests. Compared to man-made plantation forests, the inherent vulnerability of natural forest-types is markedly more sensitive to canopy cover.

4.7 Inherent vulnerability and forest management

The term inherent vulnerability of forests relates to the loss in capacity of forests to resist or adapt to change. Such capacity depends on forest resilience, which is strongly tied to biodiversity (Thompson et al. 2009). Therefore, the factors that impact the status of biodiversity must be addressed to ensure resilience and adaptability of forests. Climate change is likely to bring additional stress to the forests of WGK landscape (Chaturvedi et al. 2011). Such additional climate stress may have implications for inherent vulnerability through exacerbated impacts of non-climate stressors. It is therefore useful to identify the current non-climate stressors and address them to secure resilience against future stressors including climate change. The present study in WGK landscape has addressed the following questions.

(a) What is the status and distribution of inherent vulnerability in WGK Landscape?
(b) How does inherent vulnerability in the landscape vary among forest-types?

Such information is useful for decision-making and has vital implications for forest management in the WGK landscape in following respects. First, it helps by identifying vulnerable forest areas of critical conservation importance such as wildlife corridors, special habitats, and areas of exceptional biological richness. Second, it prompts forest management to probe the site-specific sources of vulnerability and to design specific management response to address such vulnerabilities. Third, such information is necessary to justify the demand of forest management for resource allocation. Fourth, in the local socio-political context, such information could improve the understanding and connect of the leadership and stakeholders with the risks and thereby promote action for taking up adaptive forest management.

We have identified the location and canopy cover dependence of inherent vulnerability in the WGK landscape forests. Furthermore, because of their socioeconomic and ecological importance, all the remnant forests in this landscape should be conserved and networked to maintain the functionality of the landscape as one ecological unit. However, resource limitations necessitate prioritization of areas for management and hence areas having high and very high inherent vulnerability identified by the present study could provide guidance in this regard.

Our study also finds higher inherent vulnerability in dry deciduous and plantation forests located on the eastern side in the landscape. Participatory forest management involving local communities could be initiated and strengthened in such areas to deal with the vulnerability driven by anthropogenic pressure (Sharma et al. 2015). Community involvement would facilitate addressing the inherent vulnerability and thereby enhance forest adaptability under current climate as well as future climate. Such a process can also help in evolving a balanced policy approach with respect to development vis-à-vis forest conservation. For the forest areas of conservation importance (such as wildlife protected areas or those part of wildlife corridors) showing medium or higher inherent vulnerability, vulnerability assessments at local scale are required to identify the specific vulnerability source mechanisms to initiate appropriate vulnerability reduction actions. Periodic assessment of inherent vulnerability would help in identification of new factors that drive inherent vulnerability and could guide revision of forest restoration/adaptation plans (Füssel and Klein 2006; Sharma et al. 2013). Spatial distribution of inherent vulnerability in the landscape confirms the location-specific nature of vulnerability.

4.8 Applicability of assessment methodology

The approach adopted to understand and assess inherent vulnerability in the present study is consistent with that adopted in the latest assessment report of intergovernmental panel on climate change, which considers vulnerability according to starting-point approach in the risk assessment framework for decision-making (IPCC 2014). Assessment of inherent vulnerability is a precursor step, the outcome of which informs the process of developing management strategies for resource conservation. Thus to manage the risk to global forest resources, it is useful to assess inherent vulnerability and evolve informed management strategies for reducing it. Assessment of inherent vulnerability of forests gains importance as an insurance approach for long-term forest conservation under climate change (Sharma et al. 2013; Thompson et al. 2009). It is a "low or no regret" approach, as it would potentially yield net ecological and social benefits whether or not there is climate change.

To our knowledge, the present case study is the first attempt to assess inherent vulnerability of forests at landscape level. The case study involves a typical high-biodiversity high human-pressure tropical forest system. However, we believe that the methodological approach adopted in the case study has universal applicability in other climatic zones including sub-tropical and temperate zones.

5 Conclusions

Use of vulnerability indicators, pairwise comparison method (PCM), and GIS tools is a novel approach in forestry sector to assess inherent vulnerability at landscape level. Application of this methodological approach in the WGK landscape shows that 30, 36, 19, and 15 % forest grid points in the landscape have low, medium, high, and very high inherent vulnerability, respectively. Forests having high and very high inherent vulnerability are located largely toward the eastern boundary of the landscape in dry deciduous forests and plantations. Among the various forest-types found in the landscape, the inherent vulnerability varies in the following order: semi-evergreen<evergreen< moist deciduous<dry deciduous forests<plantation forests. We find that the biodiversity rich natural forests are less vulnerable than man-made plantation forests. Inherent vulnerability of forests is found to depend on canopy cover: forests with open canopy cover (<40 %) have higher inherent vulnerability compared to those with dense canopy cover (>40 %) in the landscape. The spatial profile of inherent vulnerability of forests in the WGK landscape shows that the forests in the central and southern part of the landscape have comparatively higher inherent vulnerability. The significance of inherent vulnerability assessment lies in its potential for reducing the risk under changing climate by addressing the current non-climate sources of vulnerability.

In conclusion, the present case study demonstrates the utility of our methodological approach, which is generic and can be applied to other forest landscapes by appropriate selection of vulnerability indicators and their weights. The methodology and the case study would add to the capacity of forest managers to assess the inherent vulnerability of forests at landscape level to address the risks under climate change.

Acknowledgments We thank the Norwegian Research Council and Center for International Climate and Environmental Research (CICERO) Oslo, Norway for supporting the research project on "Climate change and forests". We thank Karnataka Forest Department (KFD, Bangalore), Forest Survey of India (FSI, Dehradun) and Indian Institute of Remote Sensing (IIRS, Dehradun) for providing spatial data on indicators. RKC would like to thank the Ministry of Environment and Forests, Government of India for supporting this study in the form of National Environmental Sciences Fellowship.

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Nat Clim Chang. Author manuscript; available in PMC 2017 December 01.

Published in final edited form as:
Nat Clim Chang. 2017 June ; 7: 395–402. doi:10.1038/nclimate3303.

Forest disturbances under climate change

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Abstract

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Author contributions

R.S. and C.P.O.R. initiated the research. R.S. and D.T. designed the study, with feedback from all authors during workshops in Vienna, Austria (April 2015) and Novi Sad, Serbia (November 2015). G.V., D.A., P.M., C.P.O.R. and R.S. reviewed the fire literature. D.M.-B., M.Petr and V.T. reviewed the drought literature. J.W., M.J.L., M.F. and T.N. reviewed the wind literature. D.T. and T.N. reviewed the snow and ice literature. M.K., D.T., M.J.L., M.S. and J.W. reviewed the literature on insects. M.Peltoniemi, J.H. and M.Petr reviewed the literature on pathogens. R.S. conducted the analyses. All authors contributed to writing and revising the manuscript.

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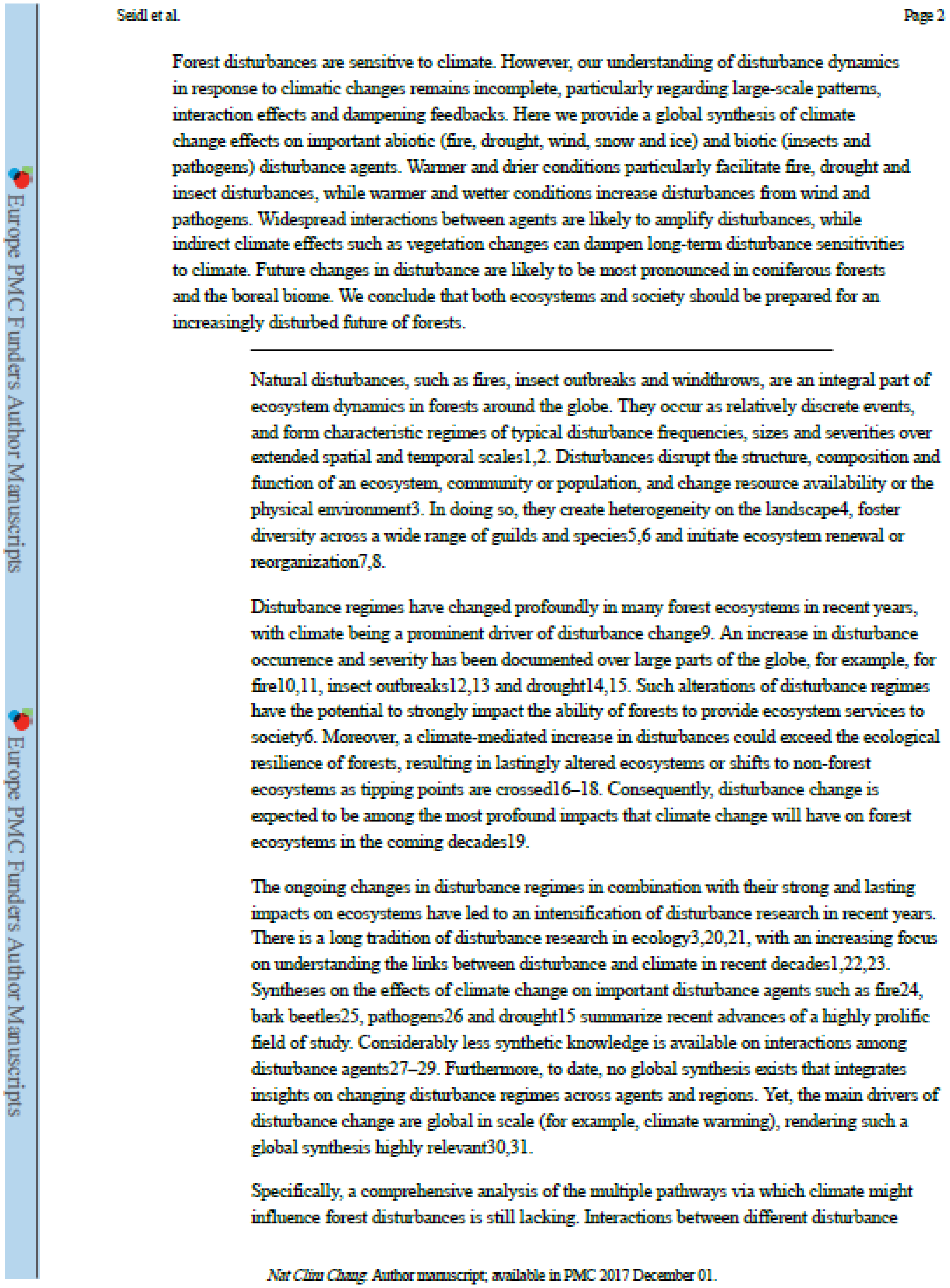
Competing financial interests

The authors declare no competing financial interests.



Forest disturbances are sensitive to climate. However, our understanding of disturbance dynamics in response to climatic changes remains incomplete, particularly regarding large-scale patterns, interaction effects and dampening feedbacks. Here we provide a global synthesis of climate change effects on important abiotic (fire, drought, wind, snow and ice) and biotic (insects and pathogens) disturbance agents. Warmer and drier conditions particularly facilitate fire, drought and insect disturbances, while warmer and wetter conditions increase disturbances from wind and pathogens. Widespread interactions between agents are likely to amplify disturbances, while indirect climate effects such as vegetation changes can dampen long-term disturbance sensitivities to climate. Future changes in disturbance are likely to be most pronounced in coniferous forests and the boreal biome. We conclude that both ecosystems and society should be prepared for an increasingly disturbed future of forests.

Natural disturbances, such as fires, insect outbreaks and windthrows, are an integral part of ecosystem dynamics in forests around the globe. They occur as relatively discrete events, and form characteristic regimes of typical disturbance frequencies, sizes and severities over extended spatial and temporal scales[1,2]. Disturbances disrupt the structure, composition and function of an ecosystem, community or population, and change resource availability or the physical environment[3]. In doing so, they create heterogeneity on the landscape[4], foster diversity across a wide range of guilds and species[5,6] and initiate ecosystem renewal or reorganization[7,8].

Disturbance regimes have changed profoundly in many forest ecosystems in recent years, with climate being a prominent driver of disturbance change[9]. An increase in disturbance occurrence and severity has been documented over large parts of the globe, for example, for fire[10,11], insect outbreaks[12,13] and drought[14,15]. Such alterations of disturbance regimes have the potential to strongly impact the ability of forests to provide ecosystem services to society[6]. Moreover, a climate-mediated increase in disturbances could exceed the ecological resilience of forests, resulting in lastingly altered ecosystems or shifts to non-forest ecosystems as tipping points are crossed[16–18]. Consequently, disturbance change is expected to be among the most profound impacts that climate change will have on forest ecosystems in the coming decades[19].

The ongoing changes in disturbance regimes in combination with their strong and lasting impacts on ecosystems have led to an intensification of disturbance research in recent years. There is a long tradition of disturbance research in ecology[3,20,21], with an increasing focus on understanding the links between disturbance and climate in recent decades[1,22,23]. Syntheses on the effects of climate change on important disturbance agents such as fire[24], bark beetles[25], pathogens[26] and drought[15] summarize recent advances of a highly prolific field of study. Considerably less synthetic knowledge is available on interactions among disturbance agents[27–29]. Furthermore, to date, no global synthesis exists that integrates insights on changing disturbance regimes across agents and regions. Yet, the main drivers of disturbance change are global in scale (for example, climate warming), rendering such a global synthesis highly relevant[30,31].

Specifically, a comprehensive analysis of the multiple pathways via which climate might influence forest disturbances is still lacking. Interactions between different disturbance agents can, for instance, result in strong and nonlinear effects of climate change on disturbance activity32. In contrast, climate-mediated vegetation changes can dampen the climate sensitivity of disturbances33. Many assessments of disturbance responses to climate change are currently neglecting such complex effect pathways34,35. More commonly still, the effects of changing disturbance regimes are disregarded entirely in analyses of future forest development36,37 and studies quantifying the climate change mitigation potential of forest ecosystems38, potentially inducing significant bias39,40.

Here we review the current understanding of forest disturbances under climate change, focusing on naturally occurring agents of disturbance. Specifically, we synthesize the existing knowledge of how climate change may affect disturbance regimes via direct, indirect and interaction effects. We reviewed the disturbance literature published from 1990 onwards, applying a consistent analysis framework over a diverse set of major forest disturbance agents, including four abiotic (fire, drought, wind, as well as snow and ice) and two biotic agents (insects and pathogens). We compiled evidence for climate effects from all biomes and continents, and analysed it in a qualitative modelling framework. We tested the hypothesis that climate change will considerably increase forest disturbance activity at the global scale, and specifically that positive, amplifying effects of climate change on disturbances dominate negative, dampening effects.

Literature review and analysis

We screened the literature for peer-reviewed English-language papers addressing the climate sensitivity of forest disturbances (that is, a change in disturbance in response to a change in climate). Due to conceptual advances in disturbance ecology in the 1980s3,21 and the increasing availability of climate scenario data and remotely sensed information, we chose to focus our analysis on research emerging from 1990 onwards. Material was selected by searching for our six focal disturbance agents (fire, drought, wind, snow and ice, insects, and pathogens) or applicable aliases (for example, bark beetles or defoliators for the insects category), in combination with the terms climate and/or climatic change in the title, abstract and/or key words of published papers. In the context of drought, it is important to note that here we applied an ecological definition rather than a meteorological one, that is, we focused on events of severe water limitation that affect ecosystem structure and functioning, and thus fall under the definition of ecological disturbance. After initially screening the abstracts of several thousands of papers, studies not directly addressing climatic controls of disturbances (for example, work describing disturbance patterns but not their climatic drivers) and those unrelated to the subject matter (for example, work on insect species that are reproducing in dead trees and are thus not acting as a disturbance agent) were excluded, and 674 papers were selected for detailed review. As individual papers frequently contained evidence for more than one climatic effect on disturbances, 1,669 observations were extracted from the selected papers (see Supplementary Text as well as Supplementary Table 1 and Supplementary Figs 1 and 2). We conducted an in-depth uncertainty analysis of the information synthesized from the literature, assessing how well the data corresponded with the variable of interest in our analysis (that is, disturbance activity and changes therein) and evaluating the methodological rigour applied in its generation (see Supplementary Text and Supplementary Figs 3–5). We subsequently omitted information that we deemed to be a poor proxy for disturbance change or of limited methodological rigour, resulting in 1,621 observations available for analysis (Supplementary Dataset 1).

We applied a common analysis scheme to all reviewed papers. For each paper we recorded meta-data on study location, methodological approach (empirical, experimental or simulation-based) and the disturbance agent(s) studied. We distinguished direct, indirect and interaction effects of climate change41–43 on disturbances in our analysis of the literature. Direct effects were defined as the unmediated impacts of climate variables on disturbance processes. Examples included changes in the frequency or severity of wind events and drought periods, changes in lightning activity or climate-mediated changes in the metabolic rates of pests and pathogens. Indirect effects were defined as changes in the disturbance regime through climate effects on vegetation and other ecosystem processes not directly related to disturbances. Prominent processes considered here are climate-mediated changes in the tree population and community composition, and include an alteration of the disturbance susceptibility through a change in tree species composition, size, density (for example, fuel available for burning) and distribution, as well as changes in tree-level vulnerability (for example, changes in soil anchorage of trees against wind due to variation in soil frost). Interaction effects were defined as linked or compounding relationships between disturbance agents27, such as an increased risk of bark beetle outbreaks resulting from wind disturbance (creating large amounts of effectively defenceless breeding material supporting the build-up of beetle populations) or drought (weakening tree defences against beetles). Only interactions between the six agents investigated here were considered explicitly.

To characterize the climate sensitivity of disturbances, we first collated the evidence for direct, indirect and interaction effects of climate change for each of the six disturbance agents studied. We screened the information for key climatic drivers of disturbances, and analysed their variation over biomes. As an auxiliary variable, we determined the response time of the ecosystem (that is, the time needed to respond to a respective change in a climate driver) on an ordinal scale. Subsequently, we synthesized the literature regarding potential future changes in the disturbance regime. This analysis was conducted at two levels. First, the sign of the climate effect (positive, more disturbance; negative, less disturbance) in response to changes in the respective climate variable(s) was assessed. Interaction effects were grouped by directionality (links between individual agents) and also analysed for the sign of the interaction. This information was synthesized qualitatively, scrutinizing whether amplifying or dampening climate change impacts prevail for each disturbance agent (Supplementary Fig. 6). We conducted this analysis separately for two broad trajectories of change: (1) warmer and wetter conditions, which assume an increase in both indicators of the thermal environment and water availability (for example, warmer temperatures, higher levels of precipitation and soil moisture, or lower levels of water deficit and drought indices); and (2) warmer and drier conditions, with an opposite direction of change for indicators of water availability under warming temperatures (see Supplementary Text for details). Second, we calculated a relative effect size (disturbance change in response to future climate change relative to baseline climate conditions, with a value of one indicating no change) across all the potential future climate conditions studied in the literature. Relative effect sizes were tested against the null hypothesis of no change in disturbance as a result of climate change using Wilcoxon signed rank sum tests. All analyses were conducted using the R language and environment for statistical computing44, specifically employing the packages 'circlize'45 and 'fsmb'46.

Pathways of climate influence

We found evidence for a substantial influence of climate on disturbances via all three scrutinized pathways, that is, direct, indirect and interaction effects. More than half of the observations reported in the literature related to direct climate effects (57.1%), which were the most prominent pathway of climate influence for all analysed agents except insects (Fig. 1). Direct effects were found to be particularly pronounced for abiotic agents: abiotic disturbances are often the direct consequence of climatic extremes, and are thus highly sensitive to changes in their occurrence, intensity and duration (Table 1). Furthermore, 25.0% of the analysed observations reported indirect effects of climate change on disturbances. Climate-mediated changes in forest structure and composition were particularly relevant in the context of wind disturbance. Also interactions between disturbance agents are well documented in the analysed literature (17.9% of the overall observations). For insects, for instance, 40.8% of the reported effects were associated with disturbance interactions. Links between abiotic (influencing agent) and biotic (influenced agent) disturbances were found to be particularly strong (Fig. 2a). The large majority of the recorded interaction effects were positive or predominately positive (71.0%), indicating an amplification of disturbance as a result of the interaction between agents. In particular, disturbances by drought and wind strongly facilitate the activity of other disturbance agents, such as insects and fire (Fig. 2b and Supplementary Table 2). Overall, only 16.2% of the studies on disturbance interactions reported a negative or predominately negative (that is, dampening) effect between interacting disturbance agents.

Climate drivers and response times

The climatic drivers of disturbances varied strongly with agent and region. However, temperature-related variables were the most prominent climatic drivers reported in the forest disturbance literature (42.0%). Water availability was a second important climatic influence on disturbance regimes (37.9%). The importance of temperature-related variables on the disturbance regime increased with latitude and was highest in the boreal biome (Supplementary Fig. 9). Conversely, the importance of water availability decreased with latitude and was highest in the tropics. In addition to temperature and water availability, a wide range of other climate-related variables were associated with disturbance change, ranging from wind speed and atmospheric moisture content to snow pack and atmospheric CO_2 concentration.

The response times of the disturbance regime to changes in the climate system varied widely, ranging from annual to centennial scales. Response times were clearly related to the type of climate effect, with disturbance interactions constituting the fastest responding pathway and indirect effects being the slowest (Supplementary Fig. 10). For interaction effects, the analysed literature reports a response time of <6 years in 81.0% of the reviewed cases, and only 9.0% of the studied interaction effects have a response time of >25 years.

For indirect effects, only 38.6% of the systems responded within the first five years of the respective climatic forcing, while 44.6% of the responses took >25 years.

Potential future disturbance change

At the global scale, our analysis suggests that disturbances from five out of the six analysed agents are likely to increase in a warming world. The exception was disturbances from snow and ice, which are likely to decrease in the future, especially under warmer and drier conditions (Supplementary Figs 7 and 11). For warmer and drier future conditions, the large majority of studies suggested an increase in fires (82.4% of the observations), drought (74.2%) and insect activity (78.4%) (Fig. 3). Under warmer and wetter conditions, the evidence for increased activity from these disturbance agents was significantly reduced (55.0%, 51.2% and 65.3%, respectively). Wetter conditions were found to particularly foster wind disturbance (expected to increase in 89.1% of the cases) and pathogen activity (69.0%). Indirect climate effects were dampening the overall climate sensitivity of the system more often than direct climate effects (Supplementary Table 2 and Supplementary Figs 7 and 8), although no significant differences in effect sizes were found (Supplementary Fig. 13). Interaction effects were largely amplifying climate sensitivity (Fig. 2).

Across all scenarios considered in the analysed literature, the ratio between disturbances under future climate to disturbances under baseline conditions was significantly positive ($P < 0.05$). The exception was disturbances from snow and ice, which decreased significantly (median effect size of 0.345 over all studies and climate change scenarios; see Supplementary Fig. 11). Disturbances from all other agents increased under future climate change, with median effect sizes of between 1.34 and 1.51. Climate-related disturbance effects were positive across all biomes ($P < 0.001$) and moderately increased with latitude (Supplementary Fig. 12), with the highest values reported for the boreal zone (1.71). Furthermore, coniferous forests had a significantly higher future disturbance effect size than broadleaved and mixed forest types (Supplementary Fig. 14). Also, longer response times of disturbances to climate change were associated with increased effect sizes (Supplementary Fig. 15).

Discussion and conclusion

We found strong support for the hypothesis that climate change could markedly modify future forest disturbance regimes at the global scale. Our analysis of the global forest disturbance literature suggests that disturbances from fire, insects and pathogens in particular are likely to increase in a warming world (regardless of changes in water availability). These agents and their interactions currently dominate disturbance regimes in many forests of the world, and will probably gain further importance globally in the coming decades. Future changes of disturbances caused by other agents, such as drought, wind and snow, will be strongly contingent on changes in water availability, which can be expected to vary more strongly locally and intra-annually than temperature changes. Wind disturbance, for instance, which is currently the most important disturbance agent in Europe40, is expected to respond more strongly to changes in precipitation (and the corresponding changes in tree soil anchorage and tree growth) than to warming temperatures (compare Fig.

3). Yet the most influential climate variable determining wind disturbance remains the frequency and intensity of strong winds, for which current and future trends remain inconclusive47,48. In general, our global summary of the climate sensitivity of forest disturbance regimes suggests that the recently observed increases in disturbance activity10,40,49 are likely to continue in the coming decades as climate warms further50,51.

Our synthesis of effect pathways showed that direct climate effects were by far the most prominently reported impact in the analysed literature. This underlines the importance of climatic drivers as inciting factors of tree mortality, and highlights the strong dependence of developmental rates of biotic disturbance agents on climatic conditions26,35. However, the prominence of direct effects in the literature may at least partially result from the fact that they are easier to study and isolate (for example, in laboratory experiments52) than indirect and interaction effects. Publication bias might thus result in an overestimation of the importance of direct effects relative to indirect and interaction effects in our analysis.

Indirect effects, mediated by climate-related changes in vegetation structure and composition, were most frequently reported for wind disturbance, but were documented in the literature for all six studied disturbance agents. They are slower than climate effects via direct and interaction pathways, with response times frequently in the range of several decades. Also, indirect effects are often dampening disturbance increases (Supplementary Table 2 and Supplementary Figs 7 and 8), for example, when trees susceptible to an increasingly aggressive insect pest are outcompeted by individuals or species better adapted to warmer climates, ultimately resulting in a system less vulnerable to disturbances33,53. A second important class of dampening indirect effects occur when a previous disturbance event lowers the probability for subsequent disturbances by the same agent, for example, through a disturbance-induced alteration of forest structure or the depletion of the resource a disturbance agent depends on54–56. The temporal mismatch observed between direct and indirect effects (Supplementary Fig. 10) suggests that disturbances will probably increase further in the coming decades, as dampening effects of changes in forest structure and composition take effect only with considerable delay. Here it has to be noted that our estimate of response times to climatic changes is necessarily truncated by the observation periods of the underlying studies. It might thus be biased against longterm effects8 and underestimate the full temporal extent of climate effects on disturbances.

Evidence for potential changes in disturbance interactions was found for all six investigated agents. In this context, it is noteworthy that the large majority of the interaction effects reported in the literature are positive, that is, they amplify disturbance activity. We showed that interactions are especially important for the dynamics of biotic disturbance agents. As an increasing disturbance activity under climate change also means an increasing propensity for disturbance interactions, biotic agents could be particularly prone to further intensification via the influence of other disturbance agents29,57. This is of growing concern, as amplification of disturbances through interactions could also increase the potential for the exceedance of ecological thresholds and tipping points27,58.

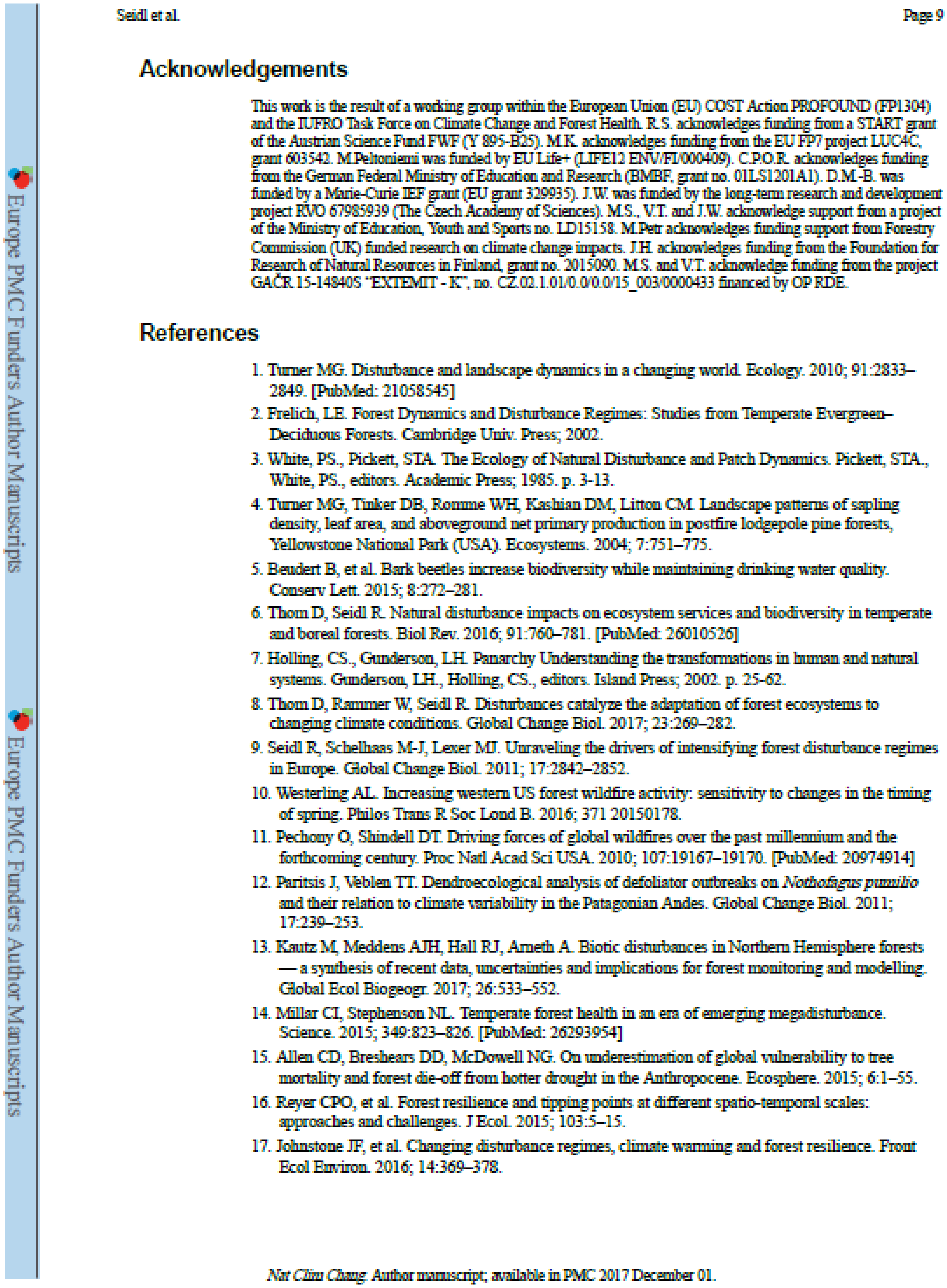
In particular, the indirect and interaction effects of climate change on disturbance regimes need to be better understood to comprehensively assess future trajectories of disturbance in a changing world. The complexity of disturbance interactions complicates predictions of future forest change, and highlights the need for further research comprising multiple interacting disturbance agents and larger spatiotemporal scales. Dynamic vegetation models are prime tools for this domain of inquiry59. Simulation models are able to consistently track vegetation–disturbance feedbacks over time frames of decades to centuries33,60 and allow controlled experiments to isolate the effects of interactions between different agents32,60. However, many current disturbance models either do not explicitly consider vegetation processes, or disturbance agents are simulated in isolation, neglecting potential interaction effects. Future work should thus focus on integrating disturbance and vegetation dynamics in models, to address the complex interrelations between climate, vegetation and disturbance61,62. Furthermore, long-term ecological observations and dedicated experimentation are needed to improve our understanding of changing disturbance regimes, and provide the data needed for parameterizing and evaluating the above-mentioned simulation models59.

Our analysis revealed a strong bias of the literature towards agents such as fire, drought, insects and pathogens, as well as ecosystems located in North America and Europe (Supplementary Table 1 and Supplementary Fig. 1). However, climate change is a global phenomenon, affecting forests in all regions of the world. To obtain a more comprehensive understanding of the global patterns of disturbance change, considerable knowledge gaps on the climate sensitivity of disturbance regimes need to be filled. It remains unclear, for instance, whether the increasing effect of future climate change with latitude reported here (Supplementary Fig. 9) is the result of an increased exposure of boreal forests to climate change in combination with naturally lower tree species diversity, or whether it is simply the effect of a publication bias towards these ecosystems. Furthermore, the fact that disturbance research is currently focused on a limited number of agents could be increasingly problematic in the future, as agents that were of little regional relevance in the past could gain importance under changing climatic conditions. In this regard, it should be noted that invasive alien pests63,64 were not in the focus of our analysis, but are likely to contribute considerably to future changes in disturbance regimes.

Climate-induced changes in disturbance regimes are a major challenge for the sustainable provisioning of ecosystem services to society6,14. Our finding of prominent indirect effects suggests that forest management can actively modulate the climate sensitivity of disturbance regimes via modifying forest structure and composition. However, mitigating the direct effects of a changing climate through management will be rarely possible, which suggests that future management will need to find ways of coping with disturbance change. A promising approach in this regard is to foster the resilience of forests to changing disturbance regimes, enabling their recovery from and adaptation to disturbances17,65, to ensure a continuous provisioning of ecosystem services18 and, ultimately, prepare both ecosystems and society for an increasingly disturbed future of forests.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.



Acknowledgements

This work is the result of a working group within the European Union (EU) COST Action PROFOUND (FP1304) and the IUFRO Task Force on Climate Change and Forest Health. R.S. acknowledges funding from a START grant of the Austrian Science Fund FWF (Y 895-B25). M.K. acknowledges funding from the EU FP7 project LUC4C, grant 603542. M.Peltoniemi was funded by EU Life+ (LIFE12 ENV/FI/000409). C.P.O.R. acknowledges funding from the German Federal Ministry of Education and Research (BMBF, grant no. 01LS1201A1). D.M.-B. was funded by a Marie-Curie IEF grant (EU grant 329935). J.W. was funded by the long-term research and development project RVO 67985939 (The Czech Academy of Sciences). M.S., V.T. and J.W. acknowledge support from a project of the Ministry of Education, Youth and Sports no. LD15158. M.Petr acknowledges funding support from Forestry Commission (UK) funded research on climate change impacts. J.H. acknowledges funding from the Foundation for Research of Natural Resources in Finland, grant no. 2015090. M.S. and V.T. acknowledge funding from the project GAČR 15-14840S "EXTEMIT - K", no. CZ.02.1.01/0.0/0.0/15_003/0000433 financed by OP RDE.

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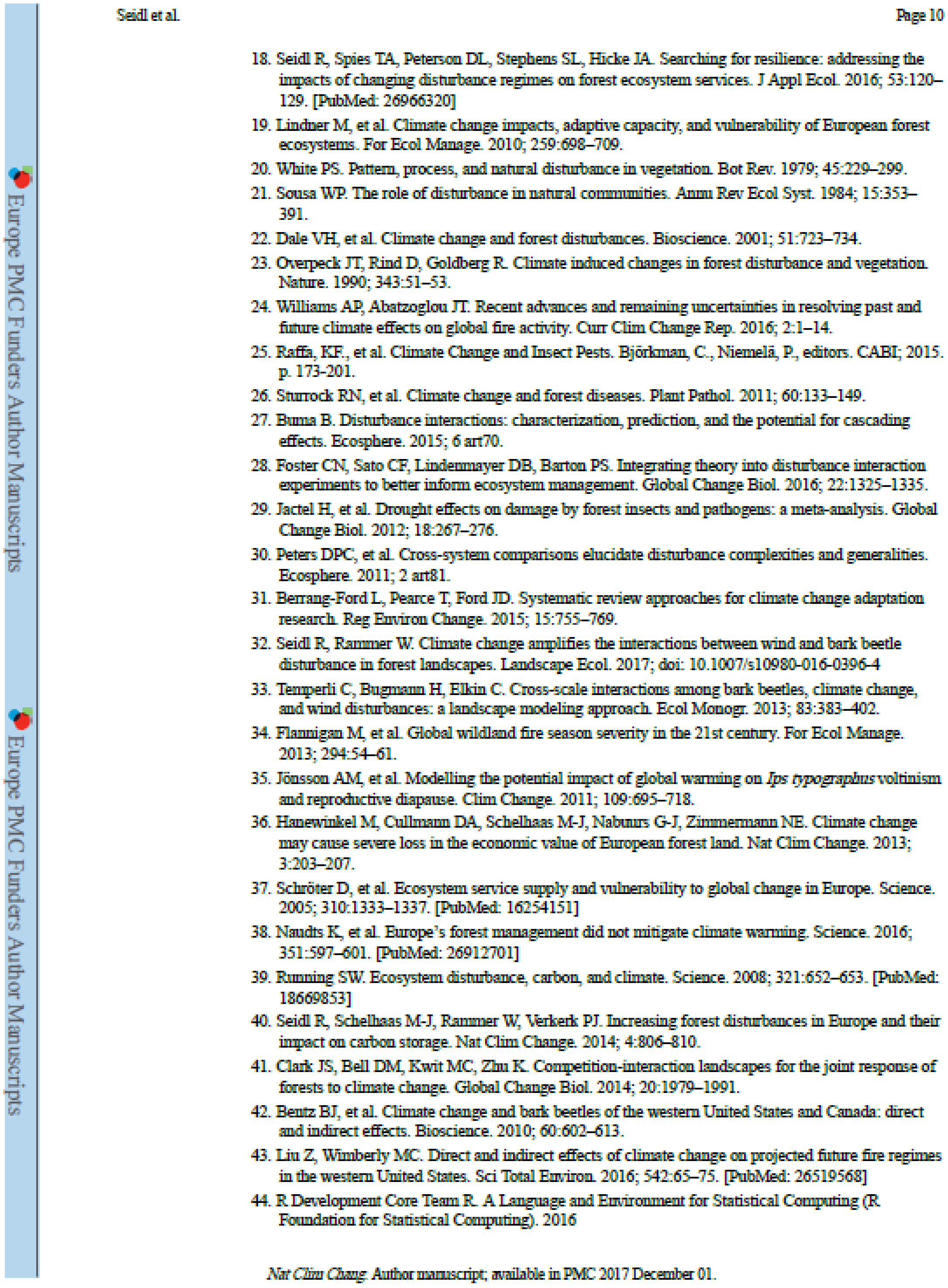

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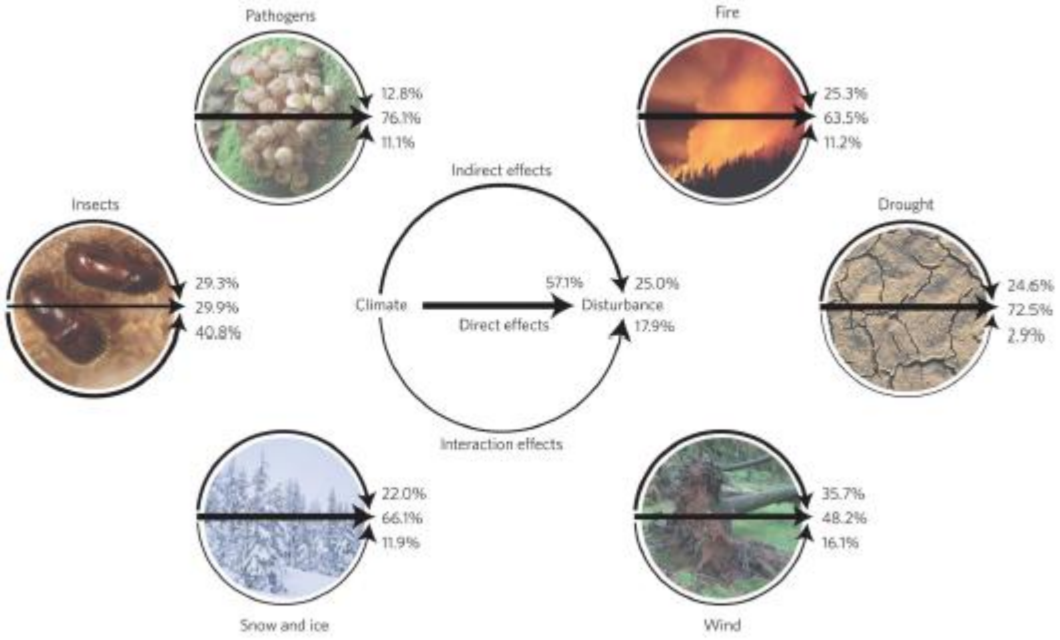

Figure 1. Distribution of evidence for direct, indirect and interaction effects of climate change on forest disturbance agents in the reviewed literature.

For every agent, arrow widths and percentages indicate the relative prominence of the respective effect as expressed by the number of observations extracted from the analysed literature supporting it. The central panel displays the aggregate result over all disturbance agents. Direct effects are unmediated impacts of climate on disturbance processes, while indirect effects describe a climate influence on disturbances through effects on vegetation and other ecosystem processes. Interaction effects refer to the focal agent being influenced by other disturbance agents. Image credits: David R. Frazier Photolibrary/Alamy Stock Photo (fire); PhotoDisc/Getty Images/Don Farrell (drought); Chris Warham/Alamy Stock Photo (wind); Royalty-Free/Corbis (snow and ice); Nigel Cattlin/Alamy Stock Photo (insects); and Naturepix/Alamy Stock Photo (pathogens).

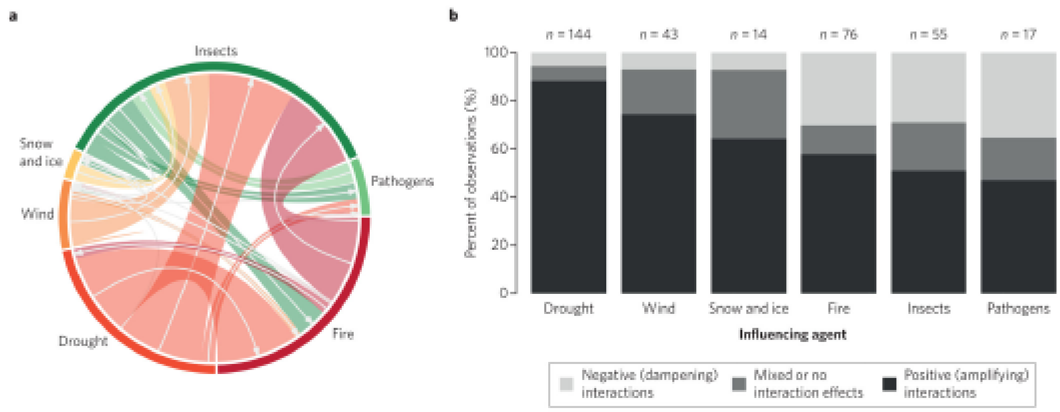

Figure 2. Interactions between forest disturbance agents.

a, The sector size in the outer circle indicates the distribution of interactions over agents, while the flows through the centre of the circle illustrate the relative importance of interactions between individual agents (as measured by the number of observations reporting on the respective interaction). Arrows point from the influencing agent to the agent being influenced by the interaction. b, Sign of the interaction effect induced by the influencing agent on the influenced agent. *n*, number of observations.

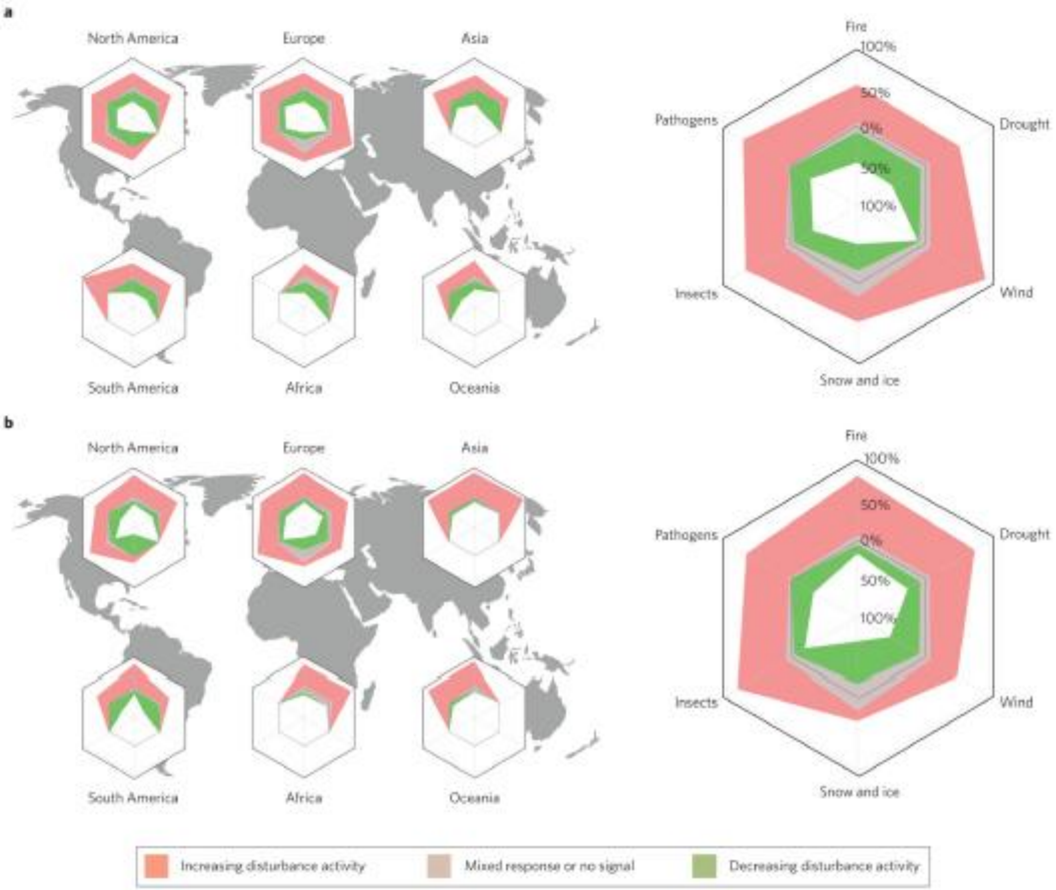

Figure 3. Global disturbance response to changing temperature and water availability.
a,b, Radar surfaces indicate the distribution of evidence (% of observations) for increasing or decreasing disturbance activity under warmer and wetter (a) as well as warmer and drier (b) climate conditions. The large radar plots to the right summarize the responses over all continents. Disturbance agents with less than four observations were omitted in the analysis. Only direct and indirect climate effects are considered here. More details on the qualitative modelling applied can be found in the Supplementary Information.

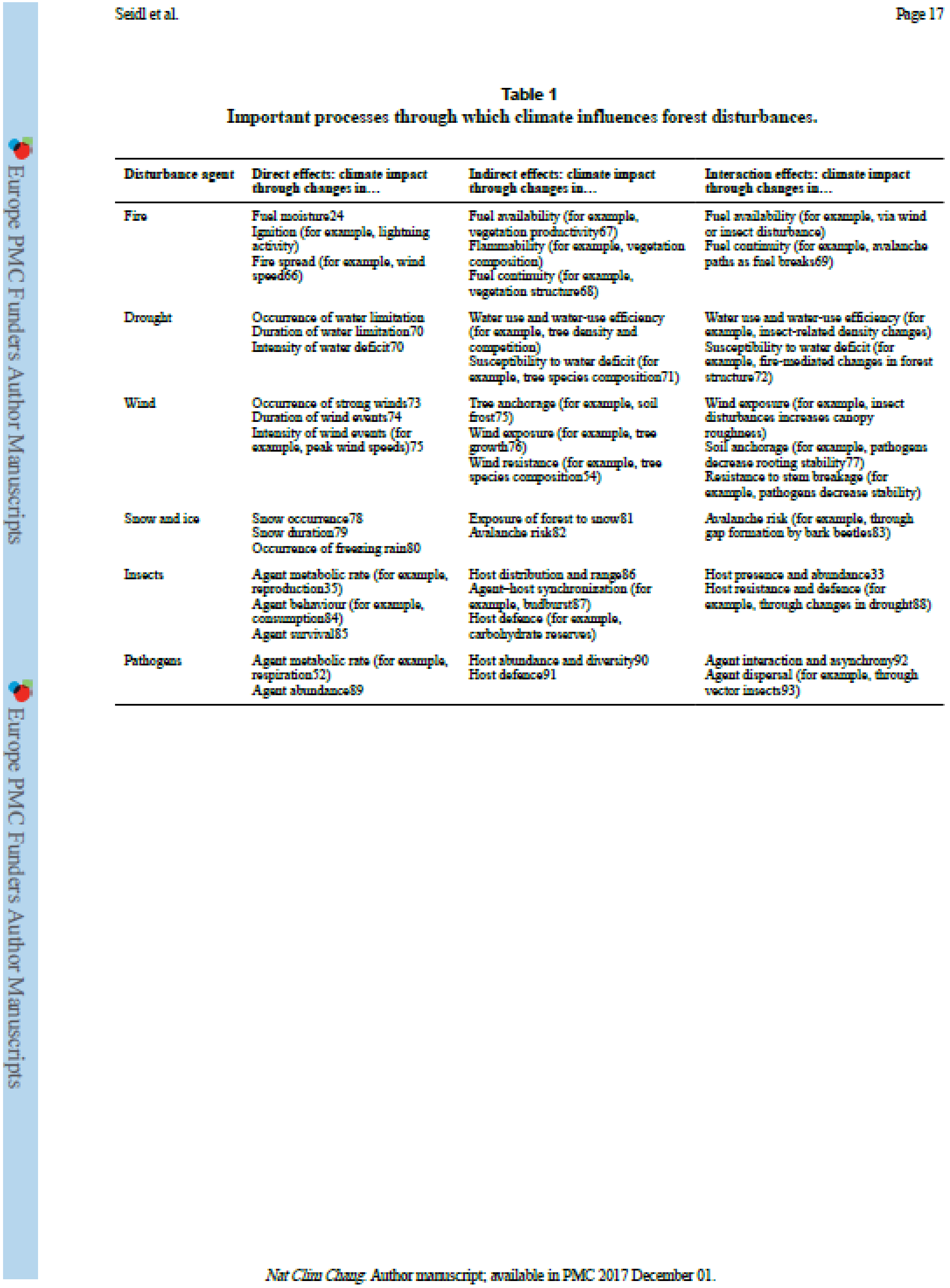

Table 1

Important processes through which climate influences forest disturbances.

Disturbance agent	Direct effects: climate impact through changes in…	Indirect effects: climate impact through changes in…	Interaction effects: climate impact through changes in…
Fire	Fuel moisture24 Ignition (for example, lightning activity) Fire spread (for example, wind speed66)	Fuel availability (for example, vegetation productivity67) Flammability (for example, vegetation composition) Fuel continuity (for example, vegetation structure68)	Fuel availability (for example, via wind or insect disturbance) Fuel continuity (for example, avalanche paths as fuel breaks69)
Drought	Occurrence of water limitation Duration of water limitation70 Intensity of water deficit70	Water use and water-use efficiency (for example, tree density and competition) Susceptibility to water deficit (for example, tree species composition71)	Water use and water-use efficiency (for example, insect-related density changes) Susceptibility to water deficit (for example, fire-mediated changes in forest structure72)
Wind	Occurrence of strong winds73 Duration of wind events74 Intensity of wind events (for example, peak wind speeds)75	Tree anchorage (for example, soil frost75) Wind exposure (for example, tree growth76) Wind resistance (for example, tree species composition54)	Wind exposure (for example, insect disturbances increases canopy roughness) Soil anchorage (for example, pathogens decrease rooting stability77) Resistance to stem breakage (for example, pathogens decrease stability)
Snow and ice	Snow occurrence78 Snow duration79 Occurrence of freezing rain80	Exposure of forest to snow81 Avalanche risk82	Avalanche risk (for example, through gap formation by bark beetles83)
Insects	Agent metabolic rate (for example, reproduction35) Agent behaviour (for example, consumption84) Agent survival85	Host distribution and range86 Agent–host synchronization (for example, budburst87) Host defence (for example, carbohydrate reserves)	Host presence and abundance33 Host resistance and defence (for example, through changes in drought88)
Pathogens	Agent metabolic rate (for example, respiration52) Agent abundance89	Host abundance and diversity90 Host defence91	Agent interaction and asynchrony92 Agent dispersal (for example, through vector insects93)

Tree Improvement and Biotechnological Strategies for Climate Resilience

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Summary

Changing climate and increases in biotic and abiotic pressures will economically and ecologically affect forests and plantations. Climate change manifestations include spatial and temporal change in temperature, rainfall pattern, wind speed, humidity and related elements. These parameters directly or indirectly contribute to adaptive genetic variation in survival, shoot phenology, growth rate, drought and frost hardness, morphology and physiology. Information on climate change effects in temperate and boreal trees and adaptation to climate are well documented, whereas, in tropical trees such information is very limited. Tree improvement and biotechnological strategies recommended include the following: (i) Conservation and maintenance of genetic diversity, where the genetic variations for adaptive traits will be recorded to understand the genetic basis of adaptation. Conventional breeding requires identification of genetic variability to various stress tolerance within a species or among sexually compatible species and introducing these unique features into identified genotypes (ii) Assisted migration and assisted gene flow, where seed zones and tree breeding regions will be delineated to translocate the propagules of pre-adapted populations. Genetic variations across latitudes and altitudes need to be assessed to guide the assisted gene flow. Composite seed sources from multiple provenances are recommended to increase diversity and buffer against future climate uncertainty. Genomic explorations are carried out to reveal local adaptation at gene level, which facilitates movement of germplasm across geographical gradients. (iii) Marker assisted selection for adaptive traits such as biotic and abiotic stress tolerance and growth through phenotype-environment associations and phenotype-genotype-environment associations. Complementing the traditional approach of trait improvement, Quantitative Trait Loci (QTL) analysis is an important component of tree improvement strategy, where correlation between DNA markers and adaptive traits will allow breeders and geneticists to hasten the development stress tolerant genotypes. (iv) Genetic modification for adaptive traits to enhance the tolerance level of pests and diseases, salt and drought by introducing stress-inducible genes into the genome of target species.

Introduction

Climate change poses a major threat to all life forms. Forest trees, being climate dependent perennial species, are vulnerable to climate changes. The long life span and generation time exhibited by several forest trees places them in a precarious position when changes in their growing environment occur rapidly. The environmental challenges associated with climate change include increased incidences of drought, heat, fire, floods, insect pest and pathogen pressure, change in growing seasons and forest fragmentation. This adversely affects both natural and managed forests, limiting survival, growth and reproductive fitness (Dai 2013). The pressure on water and nutrient foraging and increased disease and pest infestations will economically and ecologically affect forests and tree plantations. Unlike breeding of annual crops, trees require several seasons of vegetative and reproductive phases to select or identify best performing individuals for a defined utility. During these cycles, trees are susceptible to the rapidly changing environmental conditions. Although increase in atmospheric CO_2 concentration may stimulate photosynthesis and plant growth, but climate change side effects will not compensate the general reduction of productivity (Rustad et al. 2011). Low rainfall and increased temperatures are already contributing to spreading of desertification, mostly in arid and semi-arid regions, and the situation is expected to worsen in the near future. Therefore, it is imperative to develop and implement new strategies for improving forest productivity.

In India, the climate change can amplify the impact on the plantations due to poor soil conditions, water availability, the magnitude of air, water quality and faster urbanization and industrialization. When compared to other sectors, introduction of advanced technologies in forestry sector is not adequate; as a result the forest ecosystem becomes more vulnerable to climate change effects. Although lot of importance is given to tree planting considering the advantages of forests, very less knowledge available about the species requirements and its environmental interactions. Along with exotics, native tree species plays major role in combating the climate change issues, as these species are naturally selected for various climatic conditions of the local environments. In the recent days, there are studies and recommendations at the clonal level on the suitability of the clones for matching the clones to specific site conditions.

The most important strategy for forest climate adaption is identification and planting of well-suited tree species in a phased manner. At the same time, diverse climate resilient species, well-adapted to future conditions needs to be maintained. It is also critical to preserve within species diversity for a more stable forest plantations with resilient populations. These activities need to be given at most importance as it will take few decades to shift the normal routine planting programmes to climate resilient tree species.

Current selections focus on the vigorous growth of the trees on the present day climatic factors and not envisaging climatic conditions of the future. Right trees need to be selected considering the factors that may influence performance in the future. The basic information available on the tolerances and responses of a species is frequently incomplete, adding uncertainty to decision-making (Sjoman and Nielsen, 2010).

According to Harris et al. (1999), selection is a compromise among proposed function of the plant and its adaptation to the site. Miller (1997) proposed a species selection model that included site factors like environmental and silvicultural constraints, social factors like aesthetics, functions and disservices and economic factors like cost of plant, establishment and maintenance. Sæbø et al. (2005) considered climate adaptation as primary selection criteria in addition to growth and pest resistance for street and park trees. Yang (2009) evaluated the potential effects of climate change on the biology of pests in Philadelphia, Pennsylvania, as well as the suitability of tree species to future predicted climatic condition.

Plantation forestry is the source of industrially important products such as paper pulp, timber, fuel wood, biofuel and charcoal. Plantations reduce pressure on natural forests and provide ecosystem services, while contributing to economic growth and livelihood opportunities. These plantations are continuously subjected to various challenges posed by climatic conditions and associated threats, regardless of their contribution to mitigate climate change. Under such conditions, productivity of plantations decrease significantly due to change in phenology, increased challenges from native and exotic pests, enhanced salinity/acidity/alkalinity and reduced rainfall, soil fertility and water availability. Evidences are mounting on climate change risks of drought and heat induced mortality in forests trees (Allen et al. 2010). With burgeoning human population and increase demand for food production, plantations are likely to be pushed to the marginal areas in the near future. Additionally, the requirement of wood is on rise necessitating optimal productivity from traditionally un-cultivable land. At this juncture, development of appropriate adaptation strategies in response to these challenges will require a comprehensive approach. Various technologies from the fields of tree improvement, breeding and biotechnology have an important role to play in mitigating the impending climate change.

Strategies for breeding climate resilient trees

Trees are in continuous interaction with below and above ground environments and over the period, trees adapt to changes in climate. Such adaptations acquired are imprinted through epigenetic modifications in the tree genome. The general strategy used by tree breeders to alleviate the effect of climatic variation is by using seed zones and breeding regions which ensures seedlings are well adapted to their planting environments. (Gray et al. 2016). It has been argued that breeding for adaptive traits can be a long term goal in genetic improvement programs, while delineation of breeding zones and deployment of planting material from relatively homogenous local environments can ensure sustainable productivity and reproductive fitness in the face of climatic changes (Mijnsbrugge et al. 2010). The strong linkage between climate and genetic differentiation has been reported from several tree species and a study in *Pinus contorta* has demonstrated that local populations are significantly climate resilient when compared to introduce populations and hence can be a short term adaptive measure (Gray et al. 2016). Recently climate based provisional seed zone delineation based on minimum temperature and aridity index was conducted in Mexico (Castellanos-Acuña et al. 2018), which recommended moving seed sources from warm, dry locations towards currently wetter and cooler planting sites, to compensate for climate change that has already occurred and is expected to continue for the next decades. Such climate based seed zone system allows practitioners to match seed procurement regions with planting regions under observed and anticipated climate change.

Insect outbreaks due to climate change are significant disturbances in forests ecosystems. Mountain pine beetle infestation in western North America is a classic example of pine forest devastation due to increase in temperature. Ponderosa pine (*Pinus ponderosa*) and lodgepole pine (*Pinus contorta*) are the suitable hosts for this insect. It developed adaptive seasonality, synchronous emergence of adults from host trees at an appropriate time, to overwhelm tree defenses. Recently, a strategy for selection on growth rates over time was proposed to control the insect pest by selecting fast (at juvenile stage) and slow (mature stage) growing genotypes thus maintaining genetic diversity for growth rate in pine populations instead of fast growing families (de la Mata et al. 2017). Including pest resistance traits in the breeding programs may contribute to a sustainable protection. Warming climate is thought to be a major cause of epidemic outbreaks of native diseases and pests that are causing relatively new and catastrophic problems; recent examples include spruce bark beetle damage in Finland (Neuvonen and Viiri 2017) and *Larix* defoliaters in China (Fan and Bräuning 2017).

Biotechnological applications in forestry has been mainly focused on improving productivity, monitoring diversity status at ecosystem and landscape levels and reducing vulnerability to biotic and abiotic pressures. One of the main contribution of this technology was in energy saving, waste reduction and remediation of toxic chemicals by using microbial enzymes in pulping process (Ahuja et al. 2004). However, these applications of biotechnological tools are limited to six genera (*Pinus, Populus, Eucalyptus, Picea, Quercus* and *Acacia*) (FAO, 2010), mostly of temperate origin. Use of markers (DNA based and biochemical) in operational plantation management is an area where the technology has expanded over decades and three major areas were identified like genetic fingerprinting suitable for less intensively managed plantations; markers tagging industrially relevant traits for intensively managed commercial plantations and the third area includes the most sophisticated group of technologies like genomics approaches and genetic modification of targeted traits (FAO, 2010; Gartland et al. 2013).

Maintenance of genetic diversity

In trees, the extent of genetic diversity determines the ecosystem integrity, evolutionary capacity, adaptability and economic potential of the species. Knowledge on genetic diversity is important for planning breeding strategies and provides a basis for improving the management of genetic resources in forest tree species (Graudal et al. 2014). Long-term breeding is aimed at achieving a balance between continuous genetic gains and maintenance of adequate levels of genetic variation. High levels of heterozygosity in the population have been repeatedly shown to confer resistance to environmental change.

Climatic conditions mainly temperature determine the genetic differentiation and evolution of locally adapted population (Linhart and Grant 1996) and temperature is the key parameter governing natural selection and adaptive genetic variation as documented in conifers (Gray et al. 2016; Thomson and Parker, 2008) and *Eucalyptus* (Merchant et al. 2006). Adaptation and phenological plasticity in trees with response to temperature presents strong differences between species.

Landscape genomics determines the relationship between genetic and environmental heterogeneity in populations and is a powerful tool for discovery of genes underlying complex patterns of adaptation in forest ecosystems. In *Acacia koa*, an endemic species to Hawaiian Islands, a strong association between genetic structure and mean annual rainfall was detected, despite that genome level association studies predicted changing rainfall pattern may lead to genetic offsets or maladapted population (Gugger et al. 2017). Similarly, In *E. melliodora*, a foundation species of a critically endangered community in Australia, landscape genomic model revealed that seed can be sourced broadly across the landscape, providing ample diversity for adaptation to environmental change (Supple et al. 2017). Such knowledge on genetic changes due to climate change would help in devising seed transfer guidelines across various ecological zones of a species distribution. Such vulnerable geographic regions demand transfer of seed material from pre-adapted germplasm. Recently, key considerations for planning genomic assessment and monitoring of locally adaptive variation to inform species conservation has been identified (Flanagan et al. 2017).

Assisted gene flow to mitigate climatic influence

The immediate response to environmental challenges is migration and changing spatial boundaries. Existing models predict long-distance migration by seed dispersal in trees at 100–200 m yr^{-1} (Nathan et al. 2011), which is much slower than the temperature change rates across geographical gradients. This was reported for temperate broad-leaf and mixed forests of North America, where the expected migration rate predicted was 350 m yr^{-1} (Loarie et al. 2009) suggesting that trees would need to migrate at 10 times the present rate to keep up with their suitable habitats. This is further impeded by landscape fragmentation (Pearson and Dawson

2005), indicating that integrated interventions are required to develop stress adapted trees to improve forest lands and commercial plantations.

Transfer of seeds from such pre-adapted individuals or transfer of seeds within existing species range is considered to be one of the effective tools in climate resilient tree generation. This type of human assisted movement of plants is known as assisted gene flow (AGF). It will facilitate planted forests adaptation, where these planting stock will have the capacity to maintain production and fitness in a changing climate. Genecology, defined as knowledge on relationships between genetic variation of natural populations and their geographic (native environment) variations, would be the prerequisite for assisted gene flow to facilitate rapid adaptation of species to climate change. In temperate and boreal forest species including *Abeis*, *Pinus*, *Picea*, *Quercus* and *Populus* sufficient knowledge and rich history of research is available to initiate managed translocation within the species range across climate gradients (Aitken and Bemmels 2015).

It is suggested that along with conventional strategies like within and between population variation in phenotypic traits, height and girth, comprehensive understanding on clinal variations, cold and drought hardiness, variation in adaptive and neutral genetic markers at population level, genomic scans, along with well designed provenance trials are essential for translocation of species and generation of climate resilient trees. Aitken and Bemmels (2015) had listed several recommendations for AGF of forest trees, after synthesizing the broad knowledge that has accrued on local adaptation over the past several centuries. Local adaptation involves alleles that are beneficial in one environment and neutral elsewhere, hence, understanding the genetic basis of adaptation to climate is of paramount importance for preserving and managing genetic diversity. Studies of adaptive traits in temperate forest trees revealed the presence of clinal variation in phenotypes, as well as genetic differentiation among populations, suggesting that local adaptation is present in trees (Kramer et al. 2017). In conifers, considerable amount of research was carried out to characterize the genomic basis of adaptation to local climate. Such studies provided an important resource for breeding and conservation genetics in a changing climate.

Markers assisted selection for adaptive traits

Marker Assisted Selection (MAS) is one of the methods for a successful breeding for adaptive traits, which relies on the identification of Quantitative Trait Loci (QTL) linked molecular markers associated with traits of interest. In the past decades, few studies have been conducted to map genes or QTL associated to drought tolerance in Conifers (Moran et al. 2017), *Populus* (Viger et al. 2016), *Eucalyptus* (Mora et al. 2017; Sumathi et al. 2018), *Quercus* (Brendel et al. 2008) and salt tolerance in *Salix* (Zhang et al. 2017) and *Eucalyptus* (Subashini 2017). Genetic basis of elevated CO_2 was studied in *P. trichocarpa* x *P. deltoides* and 3 genomic regions in 6 different linkage groups were recognized to determine above ground growth and root growth response (Rae et al. 2007). However, till date, conversion of marker-QTL information to breeding programs is highly limited mainly due to dependence of the QTL effects on genetic background and environment.

The new genomic approaches like Next Generation Sequencing (NGS) allow massive discovery of molecular markers to obtain ultra-high density genetic maps, which are very useful to precisely locate genomic regions governing the trait. Moreover, Single Nucleotide Polymorphisms (SNPs) generated through NGS can be used in high-throughput genotyping platforms, which permit the simultaneous analysis of many markers and many individuals. Presently, it is possible to move from the exploration of recent recombination through the analysis bi-parental mapping populations to the Genome-Wide Association (GWA) studies, which use the natural diversity to identify genetic loci associated with phenotypic trait variation and provides better resolution.

Foliar and floral budburst timing is an important component of the fitness of trees. Chilling and forcing temperature requirements are key traits determining a tree's response of the date of foliar budburst to temperature. In Sitka spruce (*Picea sitchensis*), association mapping for quantitative trait variation in bud set timing and autumn cold hardiness was analyzed with SNPs and associations were detected in several candidate genes, which cumulatively explained 28 and 34% of the phenotypic variance in cold hardiness and bud set, respectively (Holliday et al. 2010). The genetic basis of adaptation to climate using mean annual temperature and total annual precipitation in *Picea glauca* was explored through association genetics and found that 43 genes are most important for adaptation to climate which involves genes related to development, metabolism, and stress response and most of them were related to bud set phenology (Hornoy et al. 2015). By analysing the provenance trials of European beech (*Fagus sylvatica*) established in the year 1995 over a wide geographic and climatic range in Europe, Kramer et al (2017) concluded that adaptive differences exist between provenances in the critical chilling and forcing requirements triggering budburst and they show plastic response to local environmental conditions. In a recent report, several genomic regions that strongly influenced cold hardiness in Douglas-fir was documented (Vangestel, 2018). Similarly, numerous structural, functional and regulatory genes were identified by analysing the transcriptome, small RNA, and degradome for drought-responsiveness in *Paulownia* which is expected to provide new direction for drought tolerance breeding (Zhao et al. 2018).

Genetic modification for adaptive traits

In the last three decades, genetic transformation has become an indispensible tool in gene discovery programs. In trees, transgenics is considered as an efficient alternate for introgression of essential traits, since conventional breeding is slow due to long generation time; high background polymorphism and outcrossing nature of most trees (Busov et al. 2005).

Robust transformation systems are reported in trees from Populus (Busov et al. 2005; Han et al. 2013; Maheshwari and Kovalchuk, 2016); Eucalyptus (Matsunaga et al. 2012; Prakash and Gurumurthi, 2009; de Alcantara *et al.* 2011) and conifers (Tang and Newton, 2003; Malabadi and Nataraja, 2007; Pijut et al. 2007). The study is limited to few genera and traits like wood formation, biomass enhancement and tolerance to pest and disease. Studies on adaptive trait introgression are few due to limited genomic knowledge, inefficient regeneration/transformation systems in species relevant to tropical ecosystems and regulatory issues in conducting field trials.

In *E. camaldulensis*, *CodA* from *Arthrobacter globiformis* was ectopically expressed and the transgenic lines showed tolerance to high salinity and temperature (Yamada- Watanabe et al. 2003). Similarly, uptake of inorganic phosphate in acidic soil was achieved through heterologous expression of mitochondrial citrate synthetase gene into *E. grandis* × *E. urophylla* (Kawasu et al. 2003). In subsequent studies, drought enhanced drought tolerance was demonstrated in transgenics expressing the transcription factor *DREB1*(Kondo et al. 2003; Ishige et al. 2004) while freezing tolerance was imparted by ectopic expression of *EguCBF1a/b* in Eucalyptus hybrids (Navarro et al. 2010).

In *Populus simonii* × *Populus nigra*, over-expression of ERF76 enhanced salinity tolerance in transgenic line (Yao et al. 2016). In recent reports, expression of Arabidopsis stress tolerant genes AtSRK2C and AtGolS2 enhanced abiotic stress tolerance in transgenic *P. tremula* × *tremuloides* (Yu et al. 2017), while expression of PtDRS1 enhanced both drought and salinity in transgenic hybrid poplar (Mohammadi et al. 2018). Poplar transgenics expressing the ABA signaling receptors, PtPYRL1 and PtPYRL5 significantly enhanced tolerance to drought, osmotic and cold stresses (Yu et al. 2017). Further, expression of effector genes in hybrid poplar revealed tolerance to multiple-stresses including drought, salinity, water logging and insect tolerance (Su et al. 2011).

Tree improvement strategies to combat climate change

The following are the major t**ree improvement strategies to combat climate change**

- **Identification of promising tree species:** Economically important tree species are grown widely by farmers and other planting agencies to meet the raw material demand of industries. A number of native tree species are being planted by forest department in government estates. Similarly, various tree species are being identified for planting in urban areas for the purpose of shade and better climatic conditions. No specific emphasis is given for climate change and need to have a resilient tree species. Available native trees need to be relooked and identified for various end uses and can be grown with altered climatic conditions.
- **Delineation of common habitats and their characteristics with reference to climatic conditions:** These are unique agroclimatic conditions presently available, wherein specific cropping pattern is present according to the climatic conditions and suitability of the tree species in those areas. A detailed study would help to identify the extend of climatic variation that the species withstand, the possibilities to continue with the existing tree species in these agroclimatic conditions and the vulnerability of the existing tree species in the changed climatic scenario.

- **Selection of Plus trees that are resilient to climate change:** Characters that are related to economic importance is given priority while selecting the trees. The economic importance of the characters varies depending on the species and the selection criteria are fixed depending on the end use. Even within a species, the selection criteria changes while selecting for timber and fruits. However, pest and disease are considered for every end use. Similarly, relevant parameters for climate change resilience need to be considered while selecting plus trees.
- **Collection of germplasm of resilient tree species with wide range of variability:** A wide germplasm is essential for every tree breeding program, although only a part of the germplasm is largely exploited for commercial cultivation. The climate change scenario is not explicit and the test conducted in expected change in scenario is also not complete. Hence, a wide germplasm is required for actual testing of the germplasm during the changed climatic conditions.
- **Study the physiological and biochemical adaptations of selected tree species:** Studies have been carried out on the physiological and biochemical mechanisms of the tree species with reference to various environmental conditions. Detailed studies would help us to identify the possible physiological and biochemical characters that are to be considered while selection trees for the changed climatic conditions.
- **Study the genotype and environmental interactions:** Genotype into environmental interaction studies have been conducted in many species. However, these studies have been conducted under the prevalent environmental conditions. Studies are meagre in the expected changed climatic conditions. These are studies the reveals that the climate itself changes due to cultivation of adopted tree species. GxE interaction studies in the expected altered climatic conditions would be a key area for finding the climate resilient tree species.
- **Testing of selected plus trees under extreme climatic conditions:** Most stable genotypes would be the better climate resilient trees to combat with the climate change situations. Conducting the GxE studies in the extreme climatic conditions of the present day would help us to find the extremely stable genotypes for future.

Conclusion

Forests of the future will require more resilient trees than those of the past and trees that are more resistant to temperature extremes, impacts like drought, diseases and insects need to be generated to keep the land healthy and productive. Combination of various approaches of breeding and biotechnology would pave way for production of climate resilient tree crops. Change in genetic composition of forest stands, increased diversity by altering species consortium are inevitable in developing forest trees adapted to changing climates and environments. Most of the climate change related information generated is from temperate tree species while tropical trees need special attention in this aspect.

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Genetic Improvement and Genomic Approaches to Breed Climate-Resilient Trees

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Introduction

Shifts and changes in temperature and precipitation patterns associated with global climate change are likely to influence large areas of natural forests and forest plantations. Climate change can potentially influence the frequency, duration, and severity of drought, flooding, pest, and heat-wave events in forest ecosystems. Combined with abiotic threats, emergence of new biotic agents is also a major concern for foresters. In temperate forest ecosystems, warmer winters can encourage pests, both native and invasive, to expand rapidly and affect areas more quickly and extensively, while more extreme weather patterns and episodic forest events are likely to increase the intensity of wildfires in the tropics. Thus a variety of threats, most importantly insect and disease infestation, will increase the risk that forest trees could experience either population-level extirpation or species-level extinction.

Other milder consequences of climate change on forests may include reduced growth or promoting a shift in some native and cultivated ranges of species. Species distribution models predict a wholesale redistribution of trees in the next century due to climate change. Although tree species can naturally migrate, they do so slowly, averaging less than one-half of a kilometer per year (for subtropical and temperate conifers). Some climate models predict that trees would need to migrate at 10 times this rate to keep up with suitable habitats. Hence the tree populations would be maladaptive in a rapidly changing climate and it is necessary to correct these through targeted planting. Typically in temperate forest ecosystems, on an average about half million saplings are planted every year, and it is essential to control the genetic composition to them to be adaptive to the rapidly changing climate. Therefore, alternative sources of seed for immediate deployment to address climate change are needed.

Planting stress-adapted trees can improve the health of all forest types, including commercial plantations and non-commercial natural forestlands. Adaptation strategy could be to select and breed commercial species for optimum biomass production for the expected future climate. Developing such next-generation trees that can withstand climatic and pest threats needs an integrated approach considering above issues.

In this short summary we present evidence for climate-change-driven increased tree mortality across globe, highlight a frame work that can possibly be adopted to prioritize the species / traits for tree breeding, review common garden experiments that show some leads on the strategy to improve tree species as well as touch upon genomic approaches for tree breeding to cope with climate change effects.

Is There Evidence to Suggest Climate Induced Forest Tree Mortality is on the Rise?

By reviewing over 150 global references, Allen *et al*., (2010) have recently documented 88 examples of forest mortality that were driven by the climatic water / heat stress. The examples range from modest but significant local increases in background tree mortality rates to climate-driven episodes of regional-scale forest die-off. Examples from each of the wooded continents that collectively span diverse forest types and climatic zones were given. Although examples from North America, Europe, and Australia were comprehensive, mainland Asia and Russia were under-represented in this review. Further, events of tree mortality have increased with a jump in 1998 and particularly in 2003-2004.

Climate-induced tree mortality and forest die-off is relatively well documented for North America (Allen *et al*., 2010). Drought and warmth across western North America in the last decade have led to extensive insect outbreaks and mortality in many forest types throughout the region, affecting >20 million ha and many tree species since 1997 from Alaska to Mexico. Examples of forest die-off range from >1 million ha of multiple spruce species in Alaska and >10 million ha of *Pinus contorta* in British Columbia to drought-induced *Populus tremuloides* mortality across a million hectares in Saskatchewan and Alberta. In the southwestern U.S., die-off of *Pinus edulis* on over a million hectares was specifically linked to ‘‘global-change-type drought’’. In the eastern portion of the continent, declines and increased mortality among oaks, particularly in the red oak family, have been reported from Missouri to South Carolina in relation to multi-year and seasonal droughts in the 1980s–2000s (Allen *et al*., 2010).

There are many more examples that have gone unnoticed because of poor documentation and reporting. It is very essential that such an attempt be done in the Indian context by reviewing a large number of gray literature.

Vulnerability Assessment of Tree Species to Climate Change

Priority setting frameworks are becoming increasingly important when climate changes are rapid although capacity / resources / time to conserve are less. Species vulnerability assessments allow managers to allocate limited resources to the management of those species that are most threatened. By considering trait data of 339 native tree species and predictions of expected climate change pressure, Potter *et al*., (2017) have prioritized and tree species for conservation, monitoring, management and restoration across United States and Alaska. About 43 tree species were identified to be most sensitive and had high exposure to potential climate change effects.

Understanding the adaptive genetic potential of forest tree populations is crucial for evaluating their risk to climate change. Intensive efforts have been implemented to assess the diversity of ecologically important traits and their underlying genes by combining genomic and more traditional approaches. The traits that have received the most attention are apical bud phenology, drought resistance and resistance to pests. The integration of functional traits into vulnerability assessments is a promising approach to quantitatively capture differences in species sensitivity and adaptive capacity to climate change, allowing the refinement of tree species distribution models.

Aubin *et al*., (2016) have identified such functional traits that help in drought resistance, coping with fire and in migration to be focused while breeding. Traits that help in drought resistance include: 1. Rooting depth 2. Stomatal sensitivity 3. Leaf mass 4. Xylum conductance 5. Xylum recovery capacity. Traits that help in cope with fire regime include: 1. Bark thickness 2. Leaf an bark flammability 3. Seed dispersal ability and 4. Resprouting ability. Traits that help in dispersal to newer areas following a climate change include 1. Ecological amplitude 2. Age at sexual maturity 3. Seed and pollen dispersal abilities 4. Bud burst timing.

Assessing the extent of genetic variations for and developing simpler protocol to measure the above functional traits in tropical trees of India is one of the major tangential goal of a modern tree improvement programme.

Common Garden Experiments to Arrive at Tree Selection Strategy for Climate adaptation

Common garden experiment is essentially a plantation in which tree populations corresponding to different geographical origins (provenances) are compared using statistical designs. Such experiments yield good information on the level of genetic variation at a phenotypic level and on genetic differentiation among natural populations. In a comprehensive regional case study, Gray *et al*., (2016) have tested over 1800 families and provenances of lodgepole pine (*Pinus contorta* Dougl.) across six breeding regions of Canada, to assess genotype x environment interactions, and show how this information allows the development of a regional climate change adaptation strategy. The results indicated that local populations perform well, but that some transfer opportunities do exist. With the exception of the highest elevation populations, the general assumption guiding seed transfer policy, ''local seed is best for reforestation" appears largely valid for most of the lodgepole pine breeding programs in Alberta. Hence the seed transfers suggested were minimum in geographic range. They also found that some breeding regions could be amalgamated based on the observation of high positive correlation of population performance and very low genotype by environment interactions. They also showed that a large portion of the genetic variation resides within breeding populations, and therefore an alternate adaptation strategy could be the selection of families within breeding regions to enhance resilience to climate change.

MacLachlan *et al*., (2017) argue that as climates shift, breeding zones are no longer optimal seed deployment zones because base populations are becoming dissociated from their historical climatic optima. In response, climate-based seed transfer (CBST) policies incorporating assisted gene flow (AGF) are being adopted to pre-emptively match reforestation seedlots with future climates, but their implementation requires accurate knowledge of genetic variation in climatically adaptive traits. They compared 105 natural stand and 20 selectively bred lodgepole pine seedlots from Alberta and British Columbia grown in a common garden of 2200 seedlings. The effects of selection on phenotypic variation and climatic associations among breeding zones were assessed for growth, phenology and cold hardiness. They found substantial differences between natural and selected seedlings in growth traits, but timing of growth initiation was unaffected, growth cessation was delayed slightly (average 4 days, range 0.7 days to 10 days), and cold injury was slightly greater (average 2.5%, range 7% to 11%) in selected seedlings. Clearly, selection, breeding and progeny testing combined produced taller lodgepole pine seedlings that are not adaptively compromised relative to their natural seedling counterparts. Selective breeding produces genotypes that achieve increased height growth and maintain climate adaptation, rather than reconstituting genotypes similar to populations adapted to warmer climates.

The above two cited case studies point to different strategies to select trees for climate resilience. The first one emphasizes on the naturally selected local seeds for adaptations with little or no seed transfers; while the latter points to the requirement of fresh selections based on the progeny tests and climate-based seed transfer. However, in India with a lack of strict restrictions on seed transfers, it may too difficult to achieve climate-based seed transfer. Even for economically most important species such as teak, the seed transfers are un regulated and un documented in India since the last two centuries, resulting in admixtures of natural populations and plantations raised from seeds of unknown origin. It is now time to achieve some level of discipline in seed transfers and a have seed transfer policy in place for the country.

The Role of Hybridization in Forest Management and Conservation under Climate Change

Hybridization is broadly defined as the successful mating between individuals from two populations, or groups of populations, that are differentiated on the basis of one or more heritable. A hybrid zone refers to an area in which genetically distinct parental individuals form hybrids of mixed ancestry, often resulting in genetic clines from one parental genotype to the other across a variety of spatial contexts. Zones of mixed ancestry are important sources of novel recombinant genotypes, in which hybrids are considered the raw material of evolution and a source of functional novelty. Thus, hybrid zones are important sources of genetic variation for examining the mechanisms that underlie evolution in natural environments.

Hybrid zones are valuable sources of genetic variation across a shifting landscape. With the increasing availability of genomic tools, high-throughput phenotyping, and association with a wealth of climatic data; forest hybrid zones are primed to address fundamental questions in speciation, conservation, and community ecology under changing environments. The mechanisms influencing species divergence, particularly the relative contribution of environmental and non-environmental barriers to reproduction remains an area that has not garnered much attention in forest trees. However, integrating genomic tools, provenance tests, and experimental crosses holds great promise for teasing apart the mechanisms contributing to species barriers, their frequency and the extent of the incompatibilities (Janes and Jill, 2017).

New Directions for Tree Breeding and Genomics

Tree breeders today live in a rapidly changing world faced with climate change and need to create completely new forest (/unknown?) products to cope with the climate change. White *et al*. (2014) have proposed three philosophical ideas for ‘‘Breeding for Value in a Changing World’’ *viz*.:

(1) adopt a robust philosophy that aims to ensure maximum value produced per ha even in a future world that will be quite different;
(2) embrace technology at every phase in the tree improvement process; and

(3) encourage interdisciplinary teams of scientists to solve complex problems that require expertise ranging from molecular to landscape scales.

Putting resources toward restarting or increasing the capacities of tree breeding programs can accelerate development of stress-adapted tree species and enhance deployment decisions by:

- Increasing capacity to predict adaptability of improved selections in various environments, *i.e.*, genetic x environment interaction;
- Promoting understanding of tree species and forest physiology to enhance tree resilience;
- Advancing novel ways to perform early screening and field testing for pest-resistance traits, an important challenge in non-commercial and commercial tree species;
- Providing institutional support for maintenance and archiving of longterm studies essential for understanding forest interactions with climate and pests; and

Common garden experiments can be informative in breeding for climate change, but their power is dependent on the number of different test environments, the duration of the tests and the genetic diversity of experimental populations. In addition, it is logistically challenging, costly and time consuming to extract the full value of information from these resources. These limitations impose a practical constraint on how much information can realistically be obtained through common gardens in the timeframe needed by resource managers.

An alternative to the common garden approach is to estimate adaptive genetic potential on the basis of information from DNA sequences and other genetic marker information from population samples. This approach involves estimating population genetic parameters, such as measures of nucleotide diversity and divergence, and performing tests for departure from neutrality. Genomics is a foundational science for developing stress-adapted trees. It provides information and tools for accelerating tree breeding, discovering genes useful for genetic enhancement, and improving deployment and conservation decisions.

Molecular population genetics and landscape genomics approaches are just beginning to be applied to forest tree populations, and the practical application of this work will be the development of diagnostic tools, database and geographical information system (GIS)-based tools to facilitate the management, conservation and restoration of forest tree populations. Neale and Kramer (2011) have highlighted the following five priority research areas for genomics research in forest trees. First, acquiring reference genome sequences for many genera of tree species which is a necessary step for cataloguing the largely unknown diversity of tropical tree species. Second, greater attention to be payed to the ecological functions of trees in terrestrial ecosystems since the trees are major drivers of terrestrial biodiversity. Third, next generation sequencing technologies should be used for assessing adaptive differentiation and species divergence in natural populations. Genome-scanning approaches will allow the identification and localization of the genomic regions that are responsible for the maintenance of phenotypic species differentiation. Fourth, there must be a greater investment in genome database resources, particularly construction of geo-referenced databases of genomic diversity data that will in the long term allow the inference of the main ecological drivers of genomic and phenotypic diversity in natural ecosystems. Fifth, development of improved phenotyping technologies, though forest trees are difficult to phenotype. Geneticists will need to work more closely with physiologists, ecologists and engineers to develop informative, precise and standardized high-throughput phenotyping technologies.

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Evolutionary Applications
Open Access
Evolutionary Applications ISSN 1752-4571

REVIEW AND SYNTHESES

Time to get moving: assisted gene flow of forest trees

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Keywords
assisted migration, climate change, ecological genetics, forest policy, genetic clines, local adaptation, provenance, temperate species.

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Received: 20 March 2015
Accepted: 22 June 2015

doi:10.1111/eva.12293

Abstract

Geographic variation in trees has been investigated since the mid-18th century. Similar patterns of clinal variation have been observed along latitudinal and elevational gradients in common garden experiments for many temperate and boreal species. These studies convinced forest managers that a 'local is best' seed source policy was usually safest for reforestation. In recent decades, experimental design, phenotyping methods, climatic data and statistical analyses have improved greatly and refined but not radically changed knowledge of clines. The maintenance of local adaptation despite high gene flow suggests selection for local adaptation to climate is strong. Concerns over maladaptation resulting from climate change have motivated many new genecological and population genomics studies; however, few jurisdictions have implemented assisted gene flow (AGF), the translocation of pre-adapted individuals to facilitate adaptation of planted forests to climate change. Here, we provide evidence that temperate tree species show clines along climatic gradients sufficiently similar for average patterns or climate models to guide AGF in the absence of species-specific knowledge. Composite provenancing of multiple seed sources can be used to increase diversity and buffer against future climate uncertainty. New knowledge will continue to refine and improve AGF as climates warm further.

Introduction

Long-lived, largely undomesticated and slow to reach reproductive maturity, forest trees have never been ideal genetic subjects. As a result, genetic knowledge of trees has lagged behind that of agricultural crops and model organisms. However, one area in which knowledge of genetic variation within forest trees has led many other life forms for over two centuries is genecology, the study of relationships between natural populations and their native environments. The economic importance of trees for wood and fibre combined with their ecological importance as foundation species motivated scientists to characterize geographic variation as a prerequisite for deciding what to plant where. The synchronization of growth and dormancy timing of trees with their local climate was recognized early on to be a prerequisite for successful reforestation and led to a general practice of using locally collected seed for reforestation. A rapidly warming global climate is now disrupting adaptation of local populations, and the long, historically appropriate conservative tradition of 'local is best' has been slow to evolve to address this new challenge.

The future health and productivity of tree populations will depend on the match between genotypes and new environments. Contemporary scientists are addressing these questions using traditional common garden approaches, as well as new phenotyping and genomic methods, to assess capacity for adaptation to new climates and inform 'assisted gene flow' (AGF), the managed translocation of individuals within the current species range to facilitate rapid adaptation to climate change (Aitken and Whitlock 2013) (Fig. 1). Here, we argue that we already have sufficient knowledge from a rich history of research to initiate AGF of temperate and boreal forest trees. We do not extend our analysis or recommendations to tropical species as there are fewer data available on local adaptation and the ecological context differs greatly.

Göte Turesson (1923) coined the term genecology and defined it as 'race ecology', the study of 'hereditary variation in relation to habitat', emphasizing the ecological rather than genetic content of the definition. The current

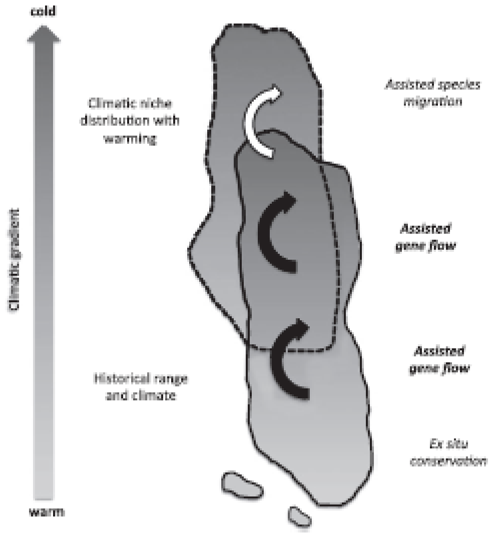

Figure 1 Schematic diagram of management options for reforestation and restoration in a changing climate. While this illustrates the northward movement of individuals, assisted gene flow may also occur along elevational or longitudinal climatic gradients.

use of genecology is largely synonymous with the more widely used term ecological genetics, although Langlet (1971) argued Turesson intended for the former to emphasize ecology, while the latter emphasizes genetics. Genecology is used frequently by many forest geneticists; most other botanists use ecological genetics, perhaps because genecology autocorrects in most software to a branch of gender-specific medicine. The French term 'provenance' has long been used in forestry to describe the place of origin of genetic material and is often used interchangeably with population, the interbreeding individuals of a species at a location. In this study, we will use genecology and provenance to honour a long and rich tradition in forest biology.

Here, we review the history of genecological research in forest trees, emphasizing the relationships between populations and climate. We then highlight advances in genecology and other relevant fields in recent decades; summarize key findings from population genetics and genomics relevant to local adaptation; present data on the concordance of genetic clines among tree species in western North America; and discuss the implications for managing tree populations in a rapidly warming world. This study builds on recent reviews and syntheses by the senior author (Box 1) and others describing the range of potential responses of forest trees to climate change and the factors controlling them (Aitken et al. 2008); the potential for evolutionary and plastic responses to climate change in trees (Alberto et al. 2013) and plants in general (Franks et al. 2014); and the genetic risks and benefits of AGF (Aitken and Whitlock 2013).

Early studies of geographic variation in forest trees

Scientists have studied relationships between tree populations and environmental characteristics of their provenances in common garden experiments for over 250 years, long before Clausen et al. (1940, 1948) conducted their much-cited reciprocal transplant experiments in California with the herbaceous perennial *Achillea millefolium* and other species. Olof Langlet (1971) compiled a detailed history of genecology, and this brief historical summary is largely derived from his work.

The need to grow trees for timber, particularly for shipbuilding, drove pioneers in forest genetics to seek optimal seed sources for planting. H.L. Duhamel du Monceau, the Inspector-General of the French Navy and a forest botanist, grew Scots pine (*Pinus sylvestris*) from Central Europe, Russia, Scotland and the Baltic region on his estate in the 1740s and 1750s, but the results were never published (Langlet 1971). Around the same time, North American tree species were being evaluated for use in Europe, and von Wagenheim (1787) emphasized the importance of considering provenance climate and soils within the native range when selecting seed sources for either montane or lowland German planting sites. The need for naval timber also motivated Patrick Matthew's (1831) little-known book *On Naval Timber and Arboriculture*, in the appendix of which he published a theory of natural selection 28 years before Charles Darwin.

Pierre Philippe André de Vilmorin repeated the earlier work of Duhamel in France in the 1820s, establishing a provenance study of Scots pine on his own estate that included seed collections from across Europe and Russia comprising all previously described varieties and closely related species. Vilmorin (1862, in Langlet 1971) was the first to recognize the continuous nature of intraspecific variation among populations across geographic areas and environmental gradients, rather than distinct taxonomic or morphological varieties that might be described if only populations at the ends of these gradients were sampled. This work was highly influential in European forestry.

Charles Darwin was a keen observer of tree biology among other things. In *On the Origin of Species*, he referenced William Hooker's study of Himalayan pines and rhododendrons collected from provenances at different elevations and observed they "possess different constitutional powers of resisting cold" when grown at Kew Gardens in London (Darwin 1859). Darwin also recognized the high lifetime fecundity of long-lived trees, and the great wide ranges and continuous distributions generally have lower F_{ST} estimates and higher Q_{ST} estimates than species with smaller or fragmented ranges (Alberto et al. 2013).

Cold and drought hardiness

Cold and drought hardiness are important traits reflecting adaptation to abiotic stresses, but they are difficult to assess in field tests, as damage from extreme weather events occurs sporadically, and injury or mortality can be difficult to attribute to the correct agent. Methods have been developed to phenotype seedlings for cold hardiness, drought hardiness and phenology in common garden experiments in controlled nursery or growth chamber environments (St Clair and Howe 2007; K.J. Liepe, A. Hamann, P. Smets, C.R. Fitzpatrick and S.N. Aitken, unpublished data). Methods have also been developed to screen for resistance to specific insects and diseases, but these are host and pest specific and beyond the scope of this review.

To be well adapted to local temperatures, trees need to be able to utilize the available frost-free period and grow competitively as long as other environmental conditions remain favourable for growth, yet cease growth and develop cold hardiness in response to lengthening nights before damaging fall frosts occur (Fig. 2). In a warming world, cold hardiness may remain an important trait as disruptions to seasonal thermal cues can result in unseasonal growth, especially in late winter and spring (Harrington and Gould 2015). Fall cold hardiness and bud set phenology show strong population differentiation and strong clines along provenance thermal gradients, and less phenotypic plasticity than spring events (Howe et al. 2004; Savolainen et al. 2007; Alberto et al. 2013). Height growth cessation and bud set in temperate and boreal trees can be triggered by photoperiod, temperature cues or endogenous factors, depending on the species (Cooke et al. 2012), and drought or other stresses can result in earlier cessation (Howe et al. 2004). Winter and spring cold hardiness and bud flush phenology show weaker and more variable patterns of variation among populations and show strong plasticity in response to variation in chilling and heat sum accumulation (Duputié et al. 2015; Harrington and Gould 2015). Provenance variation in growth often reflects a direct tradeoff with cold hardiness and frost-free growing season length (Langlet 1971; Howe et al. 2004; Savolainen et al. 2007). The development of methods for artificial freeze testing of large numbers of detached shoot or leaf samples from common garden experiments has improved phenotyping of cold hardiness (e.g. Aitken and Adams 1996; Hannerz et al. 1999). Not all phenological clines necessarily evolve from avoidance of cold injury: Soularue and Kremer (2014) showed through population simulations that non-adaptive clines in reproductive phenology can evolve along environmental gradients as a result of selection for overlapping flowering periods in populations in different environments.

Clines in growth rate in provenance trials are often more strongly correlated with provenance temperature regimes than with annual or seasonal precipitation variables for many temperate and boreal species (Rehfeldt et al. 1999; St Clair et al. 2005; Wang et al. 2006; K.J. Liepe, A. Hamann, P. Smets, C.R. Fitzpatrick and S.N. Aitken, unpublished data) (also see 'Shared patterns of adaptive variation' section below). While interspecific variation in drought tolerance is high, drought-related phenotypic traits generally show weaker population differentiation than temperature-related traits (McDowell et al. 2008; Alberto et al. 2013). Drought hardiness has become a greater concern than it was historically, as climate change is having uncertain and variable effects on precipitation patterns, and drought-related mortality in natural forests due to hydraulic failure or carbon starvation has increased (McDowell et al. 2008; Allen et al. 2010; Chmura et al. 2011). As rising temperatures create greater evapotranspirational demands, traits related to water use are also receiving more attention. However, drought hardiness is challenging to phenotype due to the complexity of responses to low water availability, including physiological and morphological mechanisms of drought avoidance or tolerance, and potential phenotypic effects of drought including growth reductions, injury or mortality. Many species are quite drought tolerant later in the growing season and acclimate following drought exposure (Kozlowski and Pallardy 2002), but exposure to drought earlier can result in injury or premature growth cessation. It is not clear the extent to which greater water-use efficiency due to higher CO_2 concentrations will compensate for temperature-related increases in drought stress (Chmura et al. 2011). Finally, predictions for changes to precipitation regimes from global circulation models vary more than temperature predictions, and so greater uncertainty exists around future water availability than future temperatures. Planting forests with high genetic diversity, including seedlings from warmer, drier populations, should provide some buffering against this uncertainty as long as sites remain within a species' bioclimatic niche.

Population variation in adaptive and neutral genetic markers

While genecological studies suggest divergent selection on phenotypic traits for local adaptation to climate must be relatively strong (Howe et al. 2004; Savolainen et al. 2007; Alberto et al. 2013), population genetic studies suggest gene flow is high, as most widespread species show weak-to-moderate population differentiation (F_{ST}) for selectively focus on phenotypic variation in common garden experiments for characterizing patterns of local adaptation as few comprehensive population genomic studies are available at this time.

Using common gardens to predict responses to climate change

The use of provenance variation to adapt tree populations to climate change is not a new idea. Over 20 years ago, when the threat of climate change to biodiversity was emerging, Ledig and Kitzmiller (1992) were the first to recognize the potential for AGF:

> ‘If global warming materializes as projected, natural or artificial regeneration of forests with local seed sources will become increasingly difficult. However, global warming is far from a certainty and predictions of its magnitude and timing vary at least twofold. In the face of such uncertainty, reforestation strategies should emphasize conservation, diversification, and broader deployment of species, seed sources, and families. Planting programs may have to deploy non-local seed sources, imported from further south or from lower elevations, which necessitates a system for conserving native gene pools in seed banks or clone banks’.

Mátyás (1994) anticipated the value of provenance trials as climate change experiments that could predict evolutionary responses to climate change and identify pre-adapted provenances for future climates, by substituting spatial climatic variation for temporal variation (although provenance trials have some limitations; Aitken et al. 2008; Franks et al. 2014). Mátyás also argued for selecting and breeding genotypes that performed well over a wide range of climates, and investigating what genetic mechanisms produced phenotypes with broad climatic stability and consistent productivity. Twenty years later, we still have little idea why some provenances are productive over a wide range of climates, while others have a relatively narrow productive niche (e.g. Wang et al. 2006).

The first comprehensive analysis of provenance trial data for predicting the response of populations to climate was by Rehfeldt et al. (1999). They analysed 20-year growth data from the Illingworth lodgepole pine provenance trial in British Columbia, an incomplete reciprocal transplant experiment with 118 provenances and 60 test sites. Response functions describing individual population growth as a function of individual climatic variables at test sites were fit using a quadratic regression approach. It is worth noting that 45% of the response functions were not significant at $P < 0.1$, indicating that local adaptation to climate is not always detectable, and that there is a lot of unexplained site-to-site environmental variation in performance at a given temperature or moisture regime (also see supp. figures in this study). Wang et al. (2006) re-analysed the Illingworth trial using improved climatic data and a new approach for anchoring response functions of populations based on extrapolations of niche margins from transfer functions. Better matching of lodgepole pine populations to new climates was projected to yield 10–35% more wood than *status quo* local seed use as in the shorter term, growth was projected to increase over historic levels due to warming of cold-limited environments, but then decrease farther into the future as warmer sites become more heat and drought limited. The same data were used by Wang et al. (2010) to develop the universal response function (URF) approach, integrating the climatic effects of provenance and planting site in a single model, and to facilitate selection of the best seed sources for projected future climates for a given planting environment. While comprehensive field provenance trials can provide excellent knowledge for designing species-specific AGF strategies, few species have such comprehensive studies for scientists to

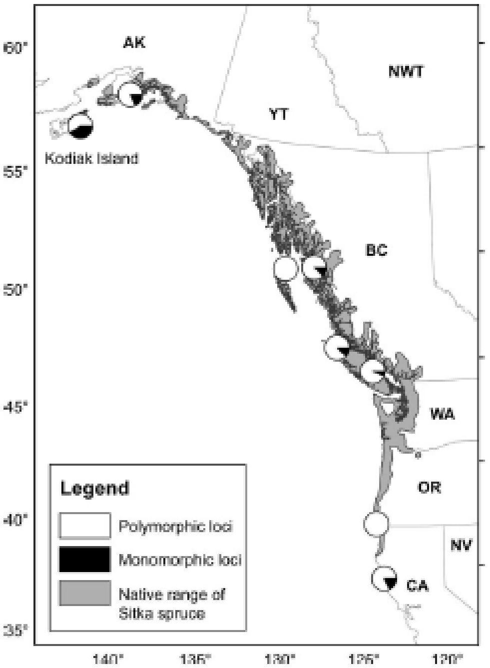

Figure 3 Map of *Picea sitchensis* showing the proportion of 17 putatively adaptive SNPs found to be associated with fall cold hardiness by Holliday et al. (2010a) that were polymorphic based on genotyping of 122 to 164 mature trees in each population, from Lobo (2011).

draw on, and much data on provenance variation is from a single nursery or field test environment, or from sites that are not warm enough to serve as proxies for future climates.

Shared patterns of adaptive variation in western North American species

To what extent are patterns of local adaptation along climatic gradients similar among species within a given geographic region? If clines in phenotypic traits are similar, can average patterns of sympatric variation guide AGF or identify critical climatic variables as a first approximation for untested species? We reanalysed data from the literature on provenance trials in temperate tree species from western North America to address these questions. This is an ideal region of focus because of the many provenance trials conducted on native tree species that are important for forestry, and because its high topographic complexity means that turnover in climate occurs rapidly and heterogeneously over short geographic spaces. Clines along climate gradients are thus especially likely to reflect local adaptation to climate, rather than non-adaptive phenomena resulting from population demographic history.

Provenance trial data sets

We focused on adaptive clines in three traits expected to impact fitness of natural populations that are commonly phenotyped: height growth potential, timing of spring shoot phenological events associated with growth initiation ('spring events'), and timing of fall phenological events associated with growth cessation ('fall events'). We identified clines along gradients in mean annual temperature (MAT), selected as a broad proxy for overall climate, and mean summer precipitation (MSP), intended to reflect growing season drought stress. Due to few studies on trees species from very dry climates, and less consistent adaptive clines identified along the gradient in MSP, we focus primarily on results for MAT and caution that our results may not be applicable to species and regions where climates are becoming much drier and drought-related mortality is a major concern (Allen et al. 2010).

We searched the literature for data sets from provenance trials in which height or timing of spring or fall shoot events was reported. Our search was restricted to temperate tree species native to western Canada and the United States, west of and including the Rocky Mountains. Species native to this region but found primarily in boreal forests, deserts, grasslands or Mediterranean climates were excluded. We initially searched using *Web of Science* (Thompson Reuters, New York, NY) for articles on provenance trials and common gardens individually for each tree species native to British Columbia (Klinka et al. 2000). We then expanded this search to include all conifers and common angiosperm trees (Little 1971) that met our broader geographic and ecological criteria, by scanning titles of search results for species plus the word 'provenance' in the University of Michigan Library (using *Summon*®, ProQuest, Ann Arbor, MI, USA). We retained data sets in which multiple populations were grown in a common environment, including greenhouse environments and field sites within and beyond the species' native range. All data sets for 'spring events' recorded the timing of bud flush, whereas we pooled timing of bud set, growth cessation and leaf abscission into a single category of 'fall events' because of an insufficient number of studies assessing bud set. All three fall events are steps towards the initiation of dormancy prior to development of cold hardiness, and the timing of these events reflects local adaptation to maximize the length of the growing season while avoiding fall frost injury (Howe et al. 2004; Rohde and Bhalerao 2007; Cooke et al. 2012). In natural populations of *Populus*, the timings of these events are highly correlated (Rohde et al. 2011, McKown et al. 2013). Although genetic mechanisms underlying these traits are complex (Cooke et al. 2012), pooling fall events is justified given the shared pressures from natural selection that underlie observed patterns in all three traits.

We applied four additional filters to control for quality and ensure comparability of data sets among species: (i) the common environment must have been free of major pest or pathogen outbreaks, severe frost or drought damage, and other biotic or abiotic stressors. These stressors could differentially impact certain genotypes and thus mask genetic differences in growth potential among populations. (ii) Provenance geographic coordinates must have spanned at least five degrees of latitude or 50% of the species distribution to ensure clines reflect broad-scale species-level patterns. Small, geographically isolated populations and populations from a different subspecies or variety compared to the rest of the other populations were also excluded. (iii) To avoid pseudoreplication, if height data were available for the same set of populations tested at multiple sites or measured at different ages, only the most recent data from the site with the greatest mean height were included. Because height was assessed at locations with relatively high site productivity, clines represent height growth potential under good growing conditions. If multiple observations of spring or fall events were available, only those from the year with the greatest variance in timing of these events were included. (iv) Studies must have met minimum sample size criteria. These criteria recognize the practical limitations to experiments in total sample size and tradeoffs between the number of individuals per population and the number of populations for estimating clines. While experiments with many individuals per population (bulk samples) or more families per population estimate means precisely, experiments with many populations provide better estimates of clines. Thus, we accepted studies that had (i) at least 50 populations with as few as three individuals each, (ii) at least nine populations of at least three open-pollinated families each with at least three individuals per family, or (iii) at least nine populations with 25 individuals each, regardless of family structure. Populations and open-pollinated families not meeting these criteria were excluded, if population size and family structure were known (Tables S1–S3). Timing of spring and fall events must have been measured in units of calendar days, not using a quantitative scale on a single day.

Provenance MAT was estimated for each population using *ClimateWNA* (Wang et al. 2012) with provenance latitude, longitude and elevation provided in original publications. Simple linear regressions of population mean values of phenotypic traits versus provenance MAT were performed for each species (Fig. 4A). To facilitate comparisons among species, regression slopes for height growth potential were rescaled to units of percent change per degree Celsius increase in provenance MAT ($\%{\cdot}°C^{-1}$), with 100% assigned to the expected height growth potential at the midpoint of provenance MAT. Regression slopes for timing of spring and fall events were retained in days per degree Celsius increase in provenance MAT ($d{\cdot}°C^{-1}$), but a value of zero was assigned to the expected date of spring and fall events at the midpoint of the provenance MAT values. Similar analyses were conducted for population MSP (Tables S1–S3). Although variation in phenotypic traits along climatic gradients may be nonlinear and better modelled by a quadratic function, visual inspection confirmed that most relationships were approximately linear (Figures S2–S9), and linear models were applied to all species to facilitate interspecific comparisons.

A total of 23 data sets (for 18 species) were available for height growth potential, 11 data sets (eight species) for spring events and six data sets (five species) for fall events (Fig. 4B, Tables S1–S3). Datasets containing population means from all studies are archived in Dryad (Aitken and Bemmels 2015). In addition to documenting adaptive clines, we determined how representative the provenance trial data sets are of climatic conditions found across each species' geographic range. To assess this, we compared the range of MAT and mean July precipitation (MJP) among provenances to the realized niche of each species along gradients in the same climate variables. Species realized niches were obtained from Thompson et al. (2000), who calculated niches based on the presence–absence data over a 25 by 25 km grid of North America. MJP estimates were used to evaluate breadth of precipitation among provenances as Thompson et al. (2000) did not estimate MSP. The 'full' climatic niche of the species corresponding to 100% of the presence observations is likely overestimated due to climatic outliers induced by scaling and methodological error, whereas the 'core' climatic niche represented by the middle 80% of the presence observations may be a more realistic estimate of niche (Thompson et al. 2000). Both the full and core climatic niches for each species were compared with the climatic scope of each provenance trial (Fig. 4B, Figure S1B). For two species (*Cornus nuttallii* and *Populus trichocarpa*) that were not included in the initial data set (Thompson et al. 2000), we estimated climatic niches ourselves: we converted species distribution maps (Little 1971, 1976) to the presence–absence data on a 25 by 25 km grid and extracted climate data (10-arcminute resolution; (White 1987; Hijmans et al. 2005)) from the geographic centre of each grid cell in which the species was present.

Strong, shared clines in growth potential along a temperature gradient

Regressions of population mean height growth potential on provenance MAT were statistically significant ($P < 0.05$) in 14 of 23 data sets (13 of 18 species; Fig. 4, Table S1). Population mean height growth potential increased by an average of 3.6% per degree Celsius increase in provenance MAT, which statistically differed from zero (*t*-test: $P < 0.0001$, 95% confidence interval 2.1 to $5.1\%{\cdot}°C^{-1}$, non-significant regressions included). Mean R^2 was 0.43 (range: 0.19 to 0.89, significant regressions only). The relationship between height growth potential and provenance MAT was positive in all statistically significant cases. It is remarkable that with such a simple analysis and such a broad proxy for overall climate, adaptive clines of similar magnitude and consistent direction were detected in so many species. There is undoubtedly much nuance to patterns of adaptation not captured by our results. For example, genotype-by-environment interaction, including the impacts of damage due to cold or drought, may create adaptive clines that are nonlinear, or vary in magnitude or even direction depending on the harshness of the test site (White 1987; Ying 1997; Porter et al. 2013). Our linear clines from data collected in relatively warm but productive sites, on average, could be considered indicators of growth potential of provenances, rather than predictors of growth on all sites. Differentiation may also be associated with other climatic and non-climatic factors. Despite these nuances, our consistent findings suggest that local adaptation to climate is common and that general clines in height growth potential along a temperature gradient in this region are shared among many species. While these analyses are simple and may not detect fine-scale patterns of variation associated with other environmental gradients, most seed zones and seed transfer guidelines for reforestation do not currently address nuanced patterns of adaptation either, but rather delineate broad map-based areas within which seed can be moved freely or within elevational limits. Developing highly complex models to incorporate all potential sources of variation for all species into management recommendations is not feasible without extensive data, operationally intractable to implement in reforestation or restoration, and unnecessary given high within-population variation.

The absence of a cline in height growth potential with MAT in five species does not necessarily mean that they are not locally adapted. Height growth potential was significantly correlated with provenance MSP in *Pinus monticola* ($P < 0.0001$, Figure S5) (Rehfeldt et al. 1984)), and the pattern was marginally non-significant in *Pseudotsuga menziesii* ($P = 0.070$, (Sweet 1965)) and *Quercus garryana* ($P = 0.055$, (Huebert 2009)). These results suggest that adaptation to drought may be more apparent in certain species than adaptation to temperature or that temperature-related adaptation may be expressed in traits other than height growth potential. For *Pinus albicaulis*, Bower and Aitken (2008) report higher Q_{ST} in traits related to cold adaptation than in growth traits, not surprising for an extremely slow-growing species found at the upper treeline in harsh subalpine climates. Only in *Abies procera* (Xie and Ying 1994), a species with a relatively narrow and discontinuous climatic distribution, did our reanalyses detect no evidence of adaptation, although traits that were not analysed may be locally adapted. At the other extreme, the steepest cline in growth potential was for *Picea sitchensis*, a species with a long, narrow distribution along the Pacific coast and strong local adaptation (Fig. 5).

Local adaptation appears to be extremely common in widespread tree species and more common than in plants in general, although we have not used stringent reciprocal transplant criteria to define local adaptation. Leimu and Fischer (2008) found evidence of reciprocal local adaptation *sensu stricto* in plants in only 45% of pairwise population comparisons and superior performance of local genotypes in 71% of test sites. They also found that species with large population sizes, true for most widespread tree species, are more likely to be locally adapted. While our criteria are less stringent for detecting local adaptation, they are more risk averse in terms of forest management and conservation, as it is safer to assume that populations differ when they do not than to assume that they are not locally adapted when they are.

Clines in shoot phenology are more consistent in fall than spring

Statistically significant regressions of timing of spring events versus provenance MAT were found in six of 11 data sets (four of eight species; Table S2). The signs of slopes varied and were mostly shallow, ranging from -5.1 to 4.6 $\mathrm{d \cdot °C^{-1}}$, with a mean R^2 of 0.46 (range: 0.26 to 0.82; significant regressions only). In three species, spring events occurred earliest in populations from colder provenances, while in one species, the opposite trend was observed. In contrast, regressions of timing of fall events versus provenance MAT were statistically significant and consistent in direction in all six data sets (five species), with fall events occurring earliest in populations from colder provenances (Table S3). Population mean date of fall events increased by an average of 6.3 $\mathrm{d \cdot °C^{-1}}$ (range: 0.89 to 11.4 $\mathrm{d \cdot °C^{-1}}$; t-test for significant difference from zero: $P = 0.0149$), with a mean R^2 of 0.63 (range: 0.25 to 0.90). Alberto et al. (2013) also concluded elevational and latitudinal clines in bud set were more consistent among species than clines in bud flush in a larger number of temperate and boreal tree species from multiple continents.

Weak or inconsistent clines in spring events, in contrast to strong, consistent clines in fall events, may reflect more complex patterns of local adaptation in spring. While fall events are usually triggered by critical photoperiod, or in some cases by completion of predetermined growth, spring bud flush is initiated after attaining both sufficient chilling and an adequate heat sum (Fig. 2). The average timing of bud flush for a population may depend on particular local climatic patterns that allow for adequate chilling and heat sum accumulation at the transition from winter to spring. Chilling and heat sum requirements, and the timing of bud flush in a given environment, can vary among sympatric species; for example, opposite directions of adaptive clines in bud flush have been reported along a shared elevational gradient in *Fagus sylvatica* compared to *Fraxinus excelsior* and *Quercus petraea* (Vitasse et al. 2010).

Complex and species-specific adaptive variation in bud flush timing would render the impacts of climate change and AGF much less straightforward for spring than for fall events or height growth potential. While climate change is increasing heat sum accumulation in the spring, its effects on chilling are mixed. In many locations, the occurrence of effective chilling conditions (between 0 and 5°C) is decreasing, but in some cold locations with common subfreezing temperatures, chilling is increasing with warming (Harrington and Gould 2015). Chilling and heat sum accumulation can occur simultaneously to some extent. Harrington and Gould (2015) predicted the effects of climate change on bud flush timing in 11 tree species in the US Pacific Northwest and concluded that most species in most locations would have far earlier bud flush with winter warming of 3 to 5°C, with only a small rear-edge portion of the range of a few species not receiving sufficient chilling and having delayed bud flush due to environmental effects.

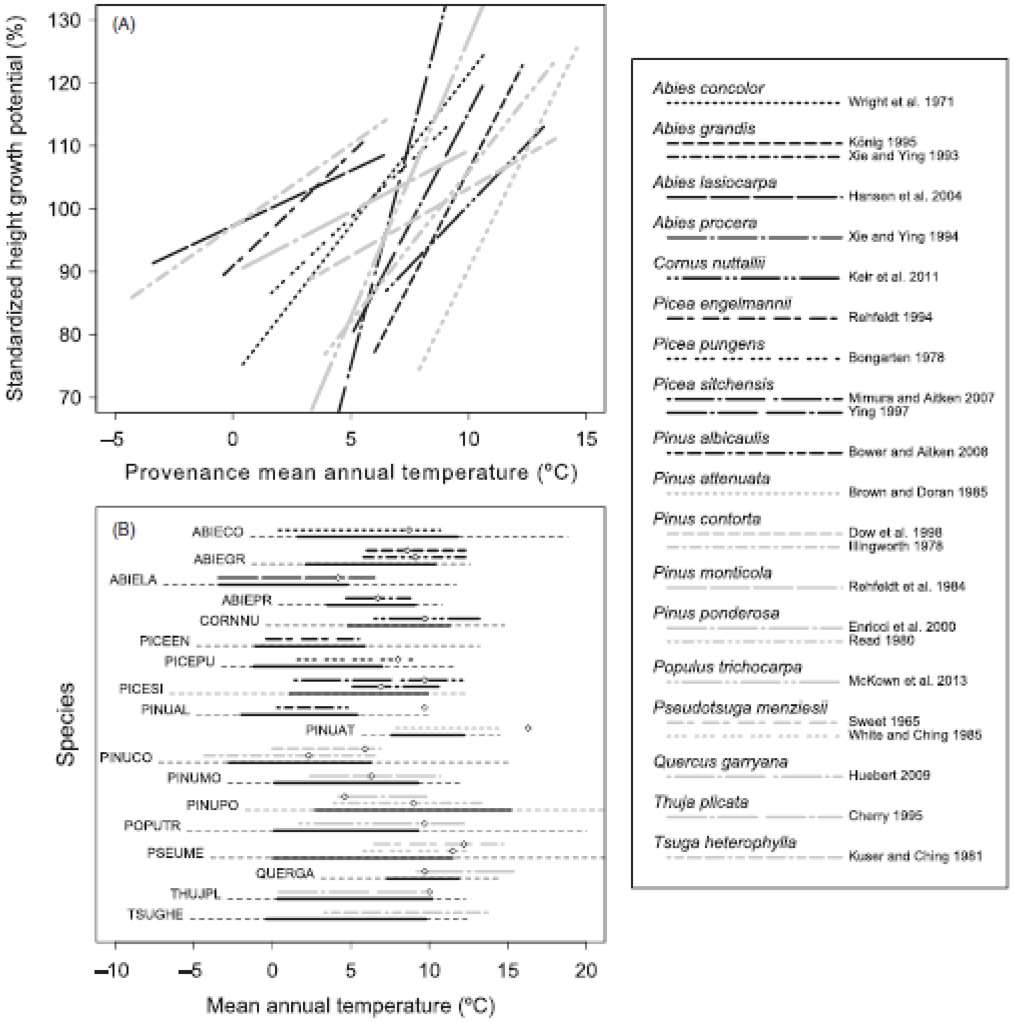

Figure 4 Adaptive clines in height growth potential along a temperature gradient are similar among many temperate tree species from western North America. (A) Regression slopes of standardized height growth potential versus provenance mean annual temperature (MAT), for populations grown in a common test environment. Each line represents an independent provenance trial, and line type corresponds to the species and reference indicated in the legend. Only statistically significant regression slopes are shown ($P < 0.05$). (B) The climatic scope of provenance trial data sets compared to the species realized niche. For each species, the bottom line represents the core climatic niche (solid black line) and full climatic niche (dashed extension) in MAT (see text; Thompson et al. 2000). The upper lines represent the range of provenance MAT values among populations within each provenance trial for that species. Open circles represent the MAT at the test site(s) for each provenance trial. Provenance trials missing an open circle were grown in a controlled environment. Note that the *y*-axis scale in (A) and *x*-axis scale in (B) do not cover the full range of data for some species; this scaling was applied to increase visibility for the majority of the data sets.

The genetic variation we observed in our analyses is far outweighed by this environmental variation. The potential for phenotypic plasticity in bud flush timing as a response to climate change is high, and this phenotypic plasticity is not always adaptive (Duputié et al. 2015). Even if a genetic mismatch were introduced between realized and optimal timing of bud flush under future climates through AGF, this mismatch would likely be minor.

Knowledge of adaptive clines is extensive

The climatic scope of the 23 data sets we reanalysed for height growth potential covers a large proportion of each species' realized niche in temperature (Fig. 4B) and precipitation (Figure S1B). Provenances sampled spanned on average 72% of the core climatic niche in MAT and 87% in MJP. A number of biases were evident in the data sets: (i) species composition is heavily biased towards commercially important conifers. (ii) The climatic scope of data sets is biased towards the warmer and wetter portions of species ranges (average difference between midpoint of provenances and midpoint of species core range: MAT = 1.4°C, $P = 0.0003$; MJP = 7.8 mm, $P = 0.0511$). This pattern likely reflects greater interest of foresters in faster-growing populations from milder environments, and greater sampling accessibility of these populations, and these are also areas where forest harvest and reforestation is most likely to occur. (iii) Test sites for common gardens were also warmer and wetter than average (average difference between test site and midpoint of species core range: MAT = 2.9°C, $P = 0.0001$; MJP = 20.8 mm, $P = 0.0349$). This may also reflect our deliberate avoidance of data sets for experiments with major damage due to biotic or abiotic stresses that could differentially inhibit growth potential among populations.

Despite these biases, the breadth of knowledge revealed from provenance trials in western North American tree species is large, and our analysis includes only a subset of these trials. Our results are consistent with studies including other species and regions (Howe et al. 2004; Savolainen et al. 2007; Alberto et al. 2013). Overall, (i) the number of species studied, (ii) the climatic breadth included in provenance trials, (iii) comparisons with analyses in other regions of the world, and (iv) the consistent finding of strong, shared adaptive clines in height growth potential and fall events support the conclusions that local adaptation is common in widespread temperate trees, and that patterns of adaptation along climatic gradients are often very similar among species. For sympatric species in which costly provenance trials have not been conducted and specific knowledge of local adaptation is lacking, the average patterns of adaptive variation in tree species from this region are likely to serve as a reasonable approximation of adaptive clines. These average patterns can be used for proceeding with AGF in untested temperate species, with high potential benefits and low risk of introducing genetic maladaptation to populations. These patterns can also be used to make genetic decisions for assisted species migration (Fig. 1), but because of the ecological effects of species introductions, we limit our discussion here to AGF within existing species ranges.

Recommendations for AGF for forest trees

It is time to change reforestation policies and practices from an emphasis on local seed sources to a framework for AGF in widespread temperate and boreal tree species. These changes are under consideration in some jurisdic-

Figure 5 Provenance variation in 8-year-old *Picea sitchensis* from across the species range grown in a common garden in Vancouver, BC, Canada. For illustrative purposes, trees were selected from each population that were closest to the provenance mean. The state or province of origin and the provenance mean annual temperature are indicated. This species shows the steepest cline of all species for height at age 2 in Figure 4(A). The population from Kodiak Island, AK (Fig. 3) has poorer growth than expected for an MAT of 5°C, likely due to inbreeding (Mimura and Aitken 2007b).

tions in North America and in Europe, but many others are waiting for more information before action, a delay syndrome common to most climate change adaptations. For all such species, we recommend that seed zones and seed transfer rules be adjusted so genotypes that are pre-adapted to near-future conditions are used for reforestation and restoration, either alone, or with composite provenancing in intimate mixtures with more local seed sources (Broadhurst et al. 2008). Here, we consider how to best mitigate risks and capture benefits of AGF.

Avoiding disruption of seasonal cycles of growth and dormancy

The risks of AGF need to be evaluated against *status quo* local seed use in projected future climates. We have shown above that most populations from warmer provenances compared with cooler provenances consistently have greater growth potential over a longer growing season, set bud and develop cold hardiness later, and may burst bud earlier or later (Fig. 2). Seedlings moved from milder to cooler locations through AGF should better match new temperature and moisture regimes than local populations, enabling them to better utilize the available growing season.

Climate warming could cause extreme disruption of growth cycles in local populations in some limited cases for environmental rather than genetic reasons. Relationships between chilling and heat sum requirements are complex. Some extreme southern and coastal populations of some species may no longer receive sufficient chilling to break bud and resume growth normally, while others may meet chilling sums earlier due to an increase in days with temperatures just above rather than below freezing and effective for chilling (Harrington and Gould 2015). Some species that achieve necessary heat sums for bud flush very early in spring may detect their critical night length well before the summer solstice, resulting in premature growth cessation, a phenomenon observed in *Populus balsamifera* transferred large distances south (Soolanayakanahally et al. 2013). However, if these extreme disruptions occur in local populations, they are unlikely to be exacerbated by AGF from warmer to cooler locations, and may result in areas moving outside of a species' bioclimatic niche space. Bioclimatic niche models should be used to determine whether an area is likely no longer within the climatic niche space of a species.

Research on individual species has shown that populations from drier environments can have greater drought hardiness (e.g. White 1987), although population differentiation is relatively weak for most water use and drought-related traits (Alberto et al. 2013). We recognize that our analysis does not directly address local adaptation to drought; however, it is interesting that phenotypic relationships between growth and MSP are non-significant or negative in species except *Pinus ponderosa* and *Picea pungens*, where growth is positively correlated with MSP, and *Pinus monticola*, where the California provenances have low growth potential (Figure S1A, Tables S1–S3). Moderate drought stress can reduce growth, while severe drought stress can result in tree mortality through hydraulic failure or carbon starvation (McDowell et al. 2008; Sala et al. 2012).

Drought is likely to be a major driver of range contraction at species rear range margins, and bioclimatic modelling should identify geographic areas becoming too dry for any provenances of a species. It will be important to prioritize such provenances as sources for AGF to suitable habitats expected to persist within the species climatic niche, and for *ex situ* conservation. In other parts of a species range remaining within the species bioclimatic niche but becoming warmer and drier, AGF of seedlings from warmer, drier environments should be better adapted to planting climates than local seedlings. We caution against moving seedlings from warmer, wetter locations to drier locations, although this risk will depend on the seasonal timing of these stresses as seedlings can tolerate considerable drought stress late in the growing season (Kozlowski and Pallardy 2002; McDowell et al. 2008). There is considerably more uncertainty around precipitation than around future temperature regimes in downscaled climate change projections. Assisted gene flow strategies should strive to locate source populations that match both temperature and moisture regimes, where possible, and managers should consider composite provenancing with more than one source population to increase diversity on drought-prone sites. Species- and population-specific research on variation in temperature and drought hardiness can be used to refine initial AGF strategies over time.

Climate projections and patterns of provenance variation for prioritizing source populations and sites for AGF

The projected rate of climate change varies geographically, for example with higher latitudes warming more rapidly than lower latitudes. Assisted gene flow strategies should be designed to re-match genotypes with projected climatic habitats in the near future. Depending on the information available, AGF strategies and policies can be designed based on: (i) climate models alone, (ii) climate models combined with patterns of local adaptation identifying climatic drivers of differentiation for sympatric species, or (iii) climate models combined with species-specific provenance trial data. Gray and Hamann (2013) used climatic data in their analysis of historic, current and future distributions of population-specific bioclimate envelopes of 15 tree species from western North America, assuming major ecosystem units were a reasonable proxy for populations. They concluded that populations already lag an average of

130 km in latitude or 60-m elevation behind their climatic niches, assuming populations occupied their optimal climates prior to anthropogenic warming. They forecast that this lag would increase to 340 km in latitude or 140 m in elevation by the 2020s. While estimated lags varied somewhat among populations within species, and among species within regions, they were generally of similar magnitude and always in the same direction. Given the rapidity with which these climate change-induced adaptational lags are growing over time, using generalized patterns of provenance responses or bioclimatic envelop shifts seems to carry less risks than continuing with local seed use. In some cases, projected near-future climates will have no analogues in the 20th century climate normal. In this event, both species and genetic diversity should be increased to buffer against uncertainty.

At any given location, the horizontal movement required to track a given climate spatially depends on both the local rate of climate change and the topographic heterogeneity, as climate changes more rapidly with increasing elevation than with increasing latitude or longitude. Loarie et al. (2009) developed the concept of velocity of climate change, an estimate of distance/time required to spatially track climate. Their method did not take into account that movements upslope end in cul-de-sacs once mountaintops are reached. Hamann et al. (2014) developed new algorithms to take such discontinuities into account. They produced maps of 'forward' and 'reverse' velocities and vectors of climate change that can be used to rank populations and sites for AGF.

Reverse velocities (future-to-present) can be used to evaluate planting sites that will benefit most from AGF, for example in terms of health, productivity and carbon sequestration. In general, valley bottom sites and large, relatively flat areas will likely benefit the most from AGF as they have the highest velocities and are farthest from pre-adapted populations.

Forward velocities (present-to-future) indicate the distance and direction that populations would need to move in order to track climate. Higher forward velocities indicate populations that are the farthest from suitable future habitat. These populations should be high priority for both *ex situ* conservation, and for AGF moving individuals to a location where they are more likely to persist as climates warm. Generally, mountaintops have the highest forward velocities as populations in these areas cannot migrate uphill farther and would have to travel large horizontal distances to find suitable future climates.

Local topographical variation can affect levels of genetic variation within populations due to gene flow across heterogeneous landscapes. Yeaman and Jarvis (2006) found lodgepole pine populations in mountainous areas of high topographic variability had greater quantitative genetic variation for phenotypic traits those in flatter landscapes. This suggests that in addition to higher velocities, populations in less topographically variable areas may have less genetic variation for evolutionary responses to climate change, and may benefit most from AGF.

Extent of adaptational lag

Historic seed transfer policies generally assumed that local populations in different parts of a species range were equally well adapted to their local climates. However, many widespread, continuously distributed tree species likely have abundant centre distributions, with higher population densities in the centre of the range than at the peripheries. If this is the case, gene flow is predicted to be asymmetrical and greater from central populations to the periphery than the reverse (Kirkpatrick and Barton 1997), as estimated for *Picea sitchensis* based on single nucleotide polymorphisms (Holliday et al. 2012). For a species distributed along a temperature gradient, for example latitudinal or elevational, this means populations originating from near the warmer species margin should be adapted to cooler conditions, on average, than they inhabited historically, and those towards the colder species margin should be adapted to warmer conditions. Lodgepole pine in British Columbia shows evidence of this pattern in northern provenances (Rehfeldt et al. 1999; Wang et al. 2006). The degree of maladaptation resulting from climate change will be greater for populations from the warmest portion of the species range, while those in the colder portion of the range may benefit from slightly warmer temperatures *in situ*, and are at less risk of maladaptation in the short term (Davis and Shaw 2001; Davis et al. 2005). For species with abundant centre distributions, populations towards the warmer species margins, but expected to still be within the species climatic niche, and central populations will benefit the most from AGF, with those towards the cooler margin still benefiting but to a lesser extent. The different slopes of some species in Fig. 4A may reflect varying effects of gene flow homogenizing populations, rather than different selection pressures.

Time frame to target for AGF

Climate change presents a moving target for matching genotypes to sites. For short-rotation length woody crops such as poplars and *Eucalyptus*, this is not a big problem, but for the majority of temperate species with rotation lengths ranging from 40 to 100 years, it is challenging to determine what life stage AGF should target. The first few years of a seedling's life are the most vulnerable to abiotic stress, for example cold injury and drought stress, but wood production and carbon sequestration rates are highest around mid-rotation. Trees that might be well adapted to conditions later in the rotation, but that do not grow well under conditions early in the rotation, are likely to die due to density-dependent competition and not become part of the overstory. We recommend that if a single seed source is used for reforestation, that it be matched for temperature regime, and if possible for moisture regime, with expected site conditions in about two decades. If composite provenancing of multiple sources is used, we recommend combining seedlings from a source population where climate matches current conditions with seedlings from a source where climate matches predicted conditions in approximately two decades.

Genetic diversity

For widespread temperate and boreal species, especially those that are wind-pollinated (e.g. all conifers), genetic diversity for selectively neutral genetic markers diminishes somewhat across species ranges from central to peripheral populations, on average (Hampe and Petit 2005), but this effect is generally very weak in widespread species with continuous ranges (S. Aitken and B. Fady, unpublished). Genetic polymorphisms associated with climate or climate-related traits (e.g. *Picea sitchensis*, Fig. 3) are generally widespread. Assisted gene flow is unlikely to introduce many adaptive alleles, but it will increase adaptive diversity, frequency of pre-adapted alleles and frequency of pre-adapted genotypes compared to local populations.

Increased genetic diversity should provide some buffering in the face of uncertain climates, as many more seedlings are planted than can co-exist in a mature stand. Natural hybrid populations provide an example of diversity facilitating adaptation across broad climatic conditions. They have higher levels of genetic diversity, on average, than parental species, and this diversity has facilitated adaptation to a wide range of climatic niches. For example, in western North America, *Picea glauca x engelmannii* populations are locally adapted to conditions spanning from boreal to subalpine climates (De La Torre et al. 2014), and *P. glauca x sitchensis* populations are locally adapted to climates ranging from maritime to continental climates (Hamilton and Aitken 2013). Limited introgression occurs among all three species in areas where these major climatic zones meet (Hamilton et al. 2015). In species forming natural hybrid complexes without evidence of outbreeding depression, AGF could be used to plant seedling mixtures with a wide range of hybrid ancestries in source populations, allowing competition and selection to favour those combinations that are well adapted to new climates.

Avoiding outbreeding depression

AGF is not recommended between long-diverged evolutionary lineages (e.g. varieties or subspecies) if those lineages and their hybrids have not been well studied, and if populations are expected to naturally regenerate in the future (Aitken and Whitlock 2013). Phylogenetic and phylogeographic studies provide the data necessary to evaluate divergence. Outbreeding depression could result from mixing long-diverged lineages, although it appears to be less common than previously thought (Whiteley et al. 2015) and is unlikely to occur between populations of wind-pollinated trees with a continuous distribution. Population simulations suggest natural selection will resolve mild outbreeding depression fairly quickly (Aitken and Whitlock 2013).

Role of epigenetics

At present, not much is known about the extent of epigenetic effects of maternal environments in forest trees. Research on *Picea abies* is the most comprehensive available. In this species, temperatures of maternal environment during seed maturation can have a profound effect on seedling physiological traits, with seed produced in warmer environments producing delayed fall phenology and decreased cold hardiness, with effect sizes varying genetically among families (Kvaalen and Johnsen 2008). If this effect exists more broadly across tree species, then the clines in Fig. 4A are likely inflated by epigenetic effects of provenance environments where seed was collected. Assisted gene flow can utilize both genetic and epigenetic variation for pre-adapting forests to climate change. Further research is needed in this area to understand epigenetic effects, but this should not delay implementation of the modest degree of AGF, we recommend here.

Selectively bred versus natural populations

Optimal climatic distances for AGF may differ between seedlots from selectively bred populations and those from natural populations. Selectively bred reforestation populations will typically have been tested over a range of environments within a breeding zone, and be better characterized than natural populations. Species with selective breeding programs will also usually have comprehensive provenance trials. While in most species, population average growth and cold hardiness are negatively correlated, the effects of selective breeding for increased growth on local adaptation to climate differ among species (Howe et al. 2004). For some species, selection for faster growth will result in delayed budset (e.g. *Larix occidentalis*, Rehfeldt 1995), potentially pre-adapting material in breeding programs to new climates. For other species, faster growth through selective breeding has been achieved through increased growth rate, not extended growing season duration.

Insect and disease resistance

We have not reviewed the literature on patterns of insect and disease resistance, but warmer winters, longer growing seasons and changing precipitation regimes are allowing pest and pathogen ranges to expand into areas that were previously too cold (Weed et al. 2013). It is unlikely that AGF from warmer to colder populations will increase susceptibility to currently temperature-limited insects and diseases compared to planting local, naïve populations that have not recently experienced pressure from these pests. High levels of genetic diversity from AGF may also provide some resilience in the face of changing pressures from both native and exotic pests and pathogens.

Local adaptation to non-climatic factors

For some species and environments, local adaptation to non-climatic factors may also need to be considered (Aitken and Whitlock 2013). Most temperate species cease height growth, set terminal buds, and initiate cold-hardiness development in response to a critical night length, and long latitudinal transfers northward may disrupt this relationship (Aitken and Whitlock 2013). We recommend AGF be limited to a few degrees of latitude, especially at high latitudes where photoperiod changes more quickly than at lower latitudes. Short latitudinal transfers or longer elevational or longitudinal transfers will not disrupt photoperiodic signals.

While to date there have not been many studies of local adaptation to edaphic factors, AGF of populations or varieties endemic to particular soil types or locally adapted to soil biota may lead to maladaptation, for example with mycorrhizal fungi (Kranabetter et al. 2012; Kranabetter 2014). In *Pseudotsuga menziesii*, a seedling greenhouse common garden was used to test the performance of several provenances with soils from each of those provenances (Pickles et al. 2015). 'Home' soils did not result in the highest growth for most populations, and growth was highest, on average, for populations planted in soils from drier locations than their provenances. Survival was higher in fungicide-treated soil than in non-treated soil, and showed no local adaptation. However, in non-fungicide-treated soil a signature of local adaptation for survival was observed, suggesting complex interactions may exist between fungal and tree populations.

Summary and recommendations

When Ledig and Kitzmiller (1992) first wrote about the potential for AGF, climate change was far from a certainty. That is no longer the case: the evidence for global climate change is now unequivocal, and it is time for both adaptation and mitigation strategies to be implemented broadly and rapidly. Here, we summarize our recommendations for AGF of forest trees, utilizing the broad knowledge that has accrued on local adaptation over the past several centuries.

1. For species with long-term field-based provenance trial data available, AGF strategies can integrate information on provenance productivity and other traits with climate change projections. Assisted gene flow can compensate for climate change and also increase productivity and carbon sequestration by correcting for pre-global warming adaptational lag, as well as expanding planting areas for exceptionally productive provenances.
2. For species with information on genetic clines from seedling experiments or comprehensive genome scans for adaptation, environmental drivers of local adaptation can be identified and populations adapted to similar climates can be identified and grouped. Assisted gene flow strategies can be designed to match these genetic groups with new climates.
3. For species without studies available on adaptive population divergence along climatic gradients, we suggest designing AGF according to average patterns for sympatric species, or using purely climatic data to match provenances with anticipated site conditions. This will be less risky than ignoring climate change and continuing with reforestation using local seed.
4. Forest managers should consider composite provenancing, mixing seedlings grown from local sources with AGF-selected non-local seedlings to increase diversity and resilience, and reduce risk of plantation or restoration failure. Many more trees are planted than can coexist to maturity, and competition will thin them over time, retaining the best adapted. The ratio of local to non-local seedling should depend on species genecological knowledge as well as forest management objectives.
5. To improve forest health and productivity, prioritize sites with high reverse velocities of climate change for AGF to increase forest productivity.
6. To conserve genetic diversity and genotypes adapted to climatic extremes, prioritize AGF of populations near species rear edges to areas expected to persist within the species bioclimate niche.
7. Until seed transfer guidelines or policies are rewritten to include AGF, all seed transfers from colder collection sites to milder planting sites within a seed zone should cease as a stopgap measure.
8. Match populations with middle-of-the-road climate projections for two or so decades in the future. Seedlings need to be able to grow under typical conditions and survive extreme climatic events during establish-

Box 1: Personal reflections on and lessons from a career in forest genetics – Sally Aitken[1]

I knew I wanted to be an evolutionary biologist from an early age. When I was 5 years old, my family spent a month camping at the Burgess Shale, while my father worked as part of an international team of geologists to quarry for branch origins in the tree of life in one of the world's most important fossil beds. At the age of 12, my father encouraged me to read Darwin's "*On the Origin of Species*". This was a transformative experience that drove my career interests in genetics and evolutionary biology. Guessing that genetics might matter in forestry, and wanting to work in an applied field, I started the Forest Resources Management program in the Faculty of Forestry at the University of British Columbia (UBC) in 1979.

Don't avoid male-dominated fields: The almost complete male domination of forestry in the 1970s did not dissuade me, thanks to my parents' influence. My mother had a degree in agriculture and had worked in various research labs prior to starting a family, and through my father I met many scientists, mostly men but a few women. At sixteen, when looking for a part-time job that would accommodate ski racing, I observed that only guys seemed to work as ski technicians. On hearing this, my father said he never wanted to hear me say I couldn't do something because I was female. I applied at three ski shops, and was offered three jobs.

The value of chance meetings: At UBC, there were no female professors in the Faculty of Forestry while I was an undergraduate. However, my cohort had had a higher proportion of female students than ever before, and the environment was supportive. A summer job in 1981 working on silvicultural research trials near Prince George, BC, landed me by chance next to Jon Dietrichson, a Norwegian forest geneticist, on a field trip bus. This encounter started my career in forest genetics; he hired me the next year as a Trainee in Tree Breeding at the Norwegian Forest Research Institute. I recommend that students and postdocs talk to people they don't know at conference coffee breaks, receptions and field trips, as these encounters might open doors unexpectedly.

The value of mentors: In 1984, I started graduate studies with W.J. (Bill) Libby at the University of California, Berkeley. Bill mentored many people, both women and men, in forest genetics. He was a prolific source of new ideas and something of a futurist in predicting technologies, and he taught me to think broadly. I had many other mentors in Berkeley, including Connie Millar, who completed her PhD with Bill Libby a few years ahead of me in conifer population and conservation genetics, and is now a well known expert on trees and climate change. Tom Ledig and Tom Conkle were generous with their advice and with their laboratory facilities at the USDA Forest Service Southwest Research Station. They hosted a weekly forest genetics coffee with W.B. (Bill) Critchfield, who inspired me to study the origins of *Pinus contorta* ssp. *bolanderi* in the Mendocino pygmy forest. An internship at the historic Institute of Forest Genetics with postdoctoral fellows Claire Kinlaw and David Neale in the early days of DNA sequencing helped me decide I did not want to become a molecular biologist, but instead wanted to stick with population, quantitative and ecological genetics. It is more than a little ironic that genomic methods now play a large role in my research.

The value of applied experience and collaboration: My first post-doctoral academic position was at Oregon State University, as first a Research Associate then as Research Assistant Professor with the Pacific Northwest Tree Improvement Research Cooperative, working with Director and Professor W. T. Adams (1990–1996). I gained experience in tree breeding and quantitative genetics, and developed a better understanding of seasonal growth and dormancy cycles through repeatedly phenotyping field common gardens. I also developed more fluency in operational forestry, which later helped me establish collaborations, successfully obtain applied funding, and identify genetic questions that addressed applied problems. Close collaborators included Katy Kavanagh, Barbara Bond, Barbara Lauchenbrach, and Les Fuchigami, all of whom taught me phenotyping techniques for drought and cold hardiness. I also learned how not to do some things: how not to be relegated to the role of a research assistant while an assistant professor; and how not to get bogged down by administration and service at the expense of publishing. My daughter was an infant when I started this position, and balancing work and motherhood was challenging. It gets much easier to publish and parent simultaneously with time. My daughter is now a PhD student herself, and I learn a great deal from her.

Good fortune and good people: In academia, we get little say in where a tenure-track offer might come from, so it felt like winning a lottery when I was offered the job of my dreams, an NSERC Industry Chair at my *alma mater* in 1996. Given my research record at the time, my department took a chance on me. In the 18 years since then I have been very fortunate to have hardworking, intelligent and kind graduate students, postdocs, research associates and research assistants; supportive colleagues; productive and thoughtful collaborators; and good research funding. We started the Centre for Forest Conservation Genetics in 2001, and I owe much to our talented Associate Director Tongli Wang and lab and project manager Pia Smets. Half the professors in my Department are now women, and our undergraduate students in Forest Resources Management, Forest Sciences, and Natural Resources Conservation are close to gender balanced. Judith Myers (featured in this special issue) has been a key mentor for me and many other women scientists at the University of British Columbia. The large-scale AdapTree genomics project has allowed me to collaborate in an emerging area of science with a group of outstanding evolutionary biologists, and they have taught me a great deal. My partner Jack Woods is very supportive of my career, which has been an enormous help. While subconscious gender bias in science and academia remains common, I increasingly see both male and female colleagues working cooperatively against it. One important lesson I've learned over my career is what really matters for wellbeing and productivity is maintaining a positive and supportive atmosphere in my research group, and choosing collaborators carefully. Finally, at this career stage, great pleasure comes from seeing young scientists I have worked with progress in their careers in the directions they desire.

[1] This paper has been written for a special issue featuring women in evolutionary biology; and these personal reflections are in response to a request by the editors.

ment. Projections farther into the future would also require choosing among or taking into account more variable and uncertain climate change projections.

9 AGF should be implemented with other silvicultural practices that will increase forest resilience, including mixing species and increasing planting density to allow for greater mortality during establishment.

10 The genetic origin of plantings should be tracked over time to allow for monitoring of health and effects of interactions with biotic and abiotic agents, and to facilitate adaptive management as climates change.

Acknowledgements

The authors thank the following individuals for providing original provenance trial data for the following species: A. Hamann for *Alnus rubra*; C.A. Huebert for *Quercus garryana*; G.E. Rehfeldt for *Picea engelmannii* and *Pinus monticola*; and T.L. Wang for *Pinus contorta*. Support for this research was provided by an NSERC Discovery Grant (SNA), Genome Canada (SNA), Genome BC (SNA), and an NSERC Undergraduate Student Research Award (JBB). SNA thanks the Peter Wall Institute for Advanced Studies at the University of British Columbia for providing a stimulating, interdisciplinary environment in which to discuss and write as a Wall Scholar. We thank Simon Nadeau for graphics, Jamie Myers for photography, and Jon Degner, Joane Elleouet, Ian MacLachlan, Loren Rieseberg, Pia Smets, C. Susannah Tysor, Tongli Wang, Michael Whitlock, Sam Yeaman, and all of the AdapTree project team for useful discussions on assisted gene flow. SNA thanks Maren Wellenreuther and Louis Bernatchez for the invitation to contribute a manuscript to an issue of Evolutionary Applications featuring women evolutionary biologists, and apologizes to readers for the number of self-citations and career anecdotes this venue has encouraged.

Data Archiving Statement

Data available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.rj15h

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Regressions of population mean height vs. provenance mean annual temperature (MAT) and vs. mean summer precipitation (MSP).

Table S2. Regressions of population mean timing of spring events vs. provenance mean annual temperature (MAT) and vs. mean summer precipitation (MSP).

Table S3. Regressions of population mean timing of fall events vs. provenance mean annual temperature (MAT) and vs. mean summer precipitation (MSP).

Figure S1. Adaptive clines in height growth potential along a precipitation gradient are relatively uncommon and inconsistent.

Figure S2. Height growth potential vs. provenance mean annual temperature from provenance trials in western North American tree species (Part I: continued in Figure S3).

Figure S3. Height growth potential vs. provenance mean annual temperature from provenance trials in western North American tree species (Part II: continued from Figure S2).

Figure S4. Height growth potential vs. provenance mean summer precipitation from provenance trials in western North American tree species (Part I: continued in Figure S5).

Figure S5. Height growth potential vs. provenance mean summer precipitation from provenance trials in western North American tree species (Part II: continued from Figure S4).

Figure S6. Date of spring events (see text) vs. provenance mean annual temperature from provenance trials in western North American tree species.

Figure S7. Date of spring events (see text) vs. provenance mean summer precipitation from provenance trials in western North American tree species.

Figure S8. Date of fall events (see text) vs. provenance mean annual temperature from provenance trials in western North American tree species. Each box represents an independent provenance trial, and each point represents a single population.

Figure S9. Date of fall events (see text) vs. provenance mean summer precipitation from provenance trials in western North American tree species.

Received: 11 August 2017 | Accepted: 20 October 2017
DOI: 10.1111/eva.12569

WILEY Evolutionary Applications Open Access

SPECIAL ISSUE REVIEW AND SYNTHESES

Guidelines for planning genomic assessment and monitoring of locally adaptive variation to inform species conservation

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Funding information
Next Generation Genetic Monitoring Investigative Workshop at the National Institute for Mathematical and Biological Synthesis, sponsored by the National Science Foundation through award #DBI-1300426; The University of Tennessee, Knoxville; P.E.O. Scholars Award; National Science Foundation; Duke University Interdisciplinary Studies

Abstract

Identifying and monitoring locally adaptive genetic variation can have direct utility for conserving species at risk, especially when management may include actions such as translocations for restoration, genetic rescue, or assisted gene flow. However, genomic studies of local adaptation require careful planning to be successful, and in some cases may not be a worthwhile use of resources. Here, we offer an adaptive management framework to help conservation biologists and managers decide when genomics is likely to be effective in detecting local adaptation, and how to plan assessment and monitoring of adaptive variation to address conservation objectives. Studies of adaptive variation using genomic tools will inform conservation actions in many cases, including applications such as assisted gene flow and identifying conservation units. In others, assessing genetic diversity, inbreeding, and demographics using selectively neutral genetic markers may be most useful. And in some cases, local adaptation may be assessed more efficiently using alternative approaches such as common garden experiments. Here, we identify key considerations of genomics studies of locally adaptive variation, provide a road map for successful collaborations with genomics experts including key issues for study design and data analysis, and offer guidelines for interpreting and using results from genomic assessments to inform monitoring programs and conservation actions.

KEYWORDS
adaptive management, conservation genetics, conservation planning, local adaptation, natural selection, next-generation sequencing, outlier detection

1 | INTRODUCTION

Natural selection is a powerful force that can shift the genetic makeup of a population through time, increasing average fitness of individuals. Some adaptations, such as resistance to a widespread disease, will increase fitness of individuals in most or all populations of a species, while other adaptations are advantageous only under certain local environmental conditions, termed local adaptation (Box 1). Information on the extent and nature of local adaptation can be used by managers to inform conservation actions to improve the evolutionary potential and adaptive capacity of populations under the diverse stressors imposed by changing environments (Box 2). For example, the success rate of restoration and reintroduction efforts can be improved by matching genotypes to current or future environmental conditions. In reforestation efforts,

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BOX 1 Definitions

Adaptive management: A structured decision-making framework for problems where decisions are recurrent and uncertainty is an impediment to action (Runge, 2011).

Bioinformatics: A scientific field at the intersection of mathematics, computer science, and statistics, which develops methods and software for analyzing and interpreting complex biological data. Bioinformatics is commonly used to analyze large next-generation sequencing datasets.

Common garden: An experimental approach in which organisms from two or more different environments are moved from their native environment into a common environment and reared through an entire life cycle under the same conditions. Traits are compared among individuals from different native environments to determine whether there is a genetic component to the differences among environments.

De novo assembly: Sequence reads are assembled without the aid of a reference genome. Instead, sequence reads are assembled into contigs (overlapping sequences that are nearly identical) and scaffolds (sets of contigs oriented approximately in relation to each other). Quality of de novo assemblies is assessed using metrics including the length of the contigs and the degree of sequence overlap. De novo assembly is common in studies of nonmodel organisms where reference genomes from the focal species or related species are not available.

Effective population size (N_e): The size of an ideal, randomly mating population that experiences genetic drift at the same rate as the census population (N_c). Typically, N_e is smaller than N_c due to processes that accelerate drift such as nonrandom mating, unequal reproductive success, and fluctuating population sizes. N_e/N_c is often 1/10 to 1/4, but sometimes much smaller. To simplify slightly, N_e is approximately the number of individuals in a population who contribute to offspring in the next generation.

Exome: The subset of the genome that is composed of exons, the parts of genes that are transcribed after RNA splicing occurs (i.e., sequence data not including introns or other noncoding regions of the genome).

Genetic drift: A change in allele frequencies over time due to stochastic processes (random transmission from generation to generation). Drift occurs in all populations but operates more quickly in small populations ($N_e \leq 1{,}000$, although there is debate on the exact threshold). Drift decreases genetic variation and drives alleles toward fixation (frequency of 0 or 1).

Genetic markers: Any type of genetic sequence information that can be used to identify differences between individuals, populations, and/or species. Examples include (but are not limited to) microsatellites, fragment length polymorphisms, single nucleotide polymorphisms, and gene sequences.

Genomic: A loosely defined term that can refer to the use of large numbers of anonymous genetic markers (thousands to millions), the use of targeted gene sequences, or analyses that account for genomic context such as linkage, recombination, or gene function (Allendorf et al., 2010; Garner et al., 2016). The distinction between "genetic" and "genomic" studies varies across the literature. Here, we differentiate genetic studies as those using smaller sets of markers that can be treated as independent, whereas genomic studies use many markers that are no longer presumed to be independent loci. Most genetic studies address questions related to neutral processes (e.g., gene flow, genetic drift), while genomic studies often address questions related to local adaptation, selection, and ecologically relevant traits. Due to the large number of markers produced by genomic studies, questions related to neutral processes are also frequently addressed, providing greater resolution than genetic studies.

Indicator variable: A variable that is being monitored, such as heterozygosity. When the indicator variable reaches a trigger point, a predefined conservation action will be taken which aims to bring the indicator variable back below the threshold.

Linkage: A statistical association between two genetic markers that arises due to the markers being physically located near each other on a chromosome, close enough that recombination between the two markers is unlikely. Genetic markers may exhibit statistical linkage if they are inherited together (i.e., do not independently assort), even if they are not physically proximal.

Local adaptation: Due to the action of natural selection, resident genotypes have higher relative fitness in their local environment than genotypes from other environments.

Microsatellites: Anonymous markers whose alleles are defined by polymorphism in the length of the DNA sequence. Microsatellite markers have many different alleles (in comparison with biallelic SNPs), meaning that genetic variation can be captured by fewer microsatellite markers than would be captured by the equivalent number of SNPs. Therefore, most microsatellite studies have fewer than 30 markers, compared to more than 1,000 markers for studies using SNPs. However, this low number of markers does not provide sufficient genomewide coverage for estimating genomewide parameters.

Reciprocal transplant: An experimental approach in which organisms from two different environments are raised in both environments. Traits are compared between environments to determine whether there is a genetic component to the differences between environments (adaptive differentiation).

(Continues)

BOX 1 (Continued)

Recombination: The exchange of genetic material either between multiple chromosomes or between different regions of the same chromosome. Recombination typically occurs during meiosis, when homologous chromosomes pair up to be passed on to the gametes (this process is also referred to as "crossover").

Sensitivity analysis: The process of testing a variety of parameter settings using the same starting data (e.g., raw reads) to compare the results from different parameter combinations. If the results from different parameter settings are qualitatively similar, then the results are likely a real signal. If the data are highly sensitive to parameter settings, it might be worth investigating to see whether there is a major source of bias in the dataset.

Single nucleotide polymorphism (SNP): One base pair in a DNA sequence that shows variation among individuals. SNPs are typically biallelic (have only two alleles) and occur frequently throughout genomes.

Transcriptome: The set of messenger RNA transcripts that are produced in a cell or tissue in response to factors such as the environment or developmental stage. To generate sequencing data for these messenger RNA transcripts, RNA from a particular tissue is converted to DNA and sequenced in short reads on high-throughput sequencing machines (e.g., Illumina machines). These short reads are then bioinformatically assembled to create sequences for genes; these consensus gene sequences are the "transcriptome."

Trigger point: A value for an indicator variable that is decided before monitoring begins. When the indicator variable reaches this point, a predefined conservation action will be implemented.

trees of local provenance outperform those from distant seed sources, with greater survival, health, and productivity due to local adaptation to climate (Aitken & Bemmels, 2016; Langlet, 1971). By contrast, if local adaptation exists but is not accounted for, restoration and reintroduction may be less successful because individuals fail to thrive under the local environmental conditions. This outcome wastes resources and may cause negative ecological impacts. For example, sowing poorly adapted seed from native plant species in the Great Basin has resulted in poor establishment despite a high price tag (Kulpa & Leger, 2013; Leger & Baughman, 2014; Rowe & Leger, 2012). Genetically based heat tolerance may be similarly crucial for restoring or managing fisheries and coral systems (Jensen et al., 2008; van Oppen, Oliver, Putnam, & Gates, 2015). In situations like these, identifying geographic patterns of local adaptation informs and improves conservation actions.

While the traditional method for testing local adaptation is to assess the relative survival and fitness of populations in reciprocal transplant or common garden experiments, this is costly, time-consuming, and often not feasible for species at risk. Another complementary approach that can be used in any species is to screen large numbers of genetic markers to identify variation associated with environmental factors or adaptive traits. These analyses, made possible due to advances in genetic sequencing technologies (i.e., next-generation sequencing, NGS), provide unprecedented opportunities to integrate genomic data into conservation management of nonmodel species (Harrisson, Pavlova, Telonis-Scott, & Sunnucks, 2014; Hoffmann et al., 2015). However, genomic studies of local adaptation are not appropriate, informative, or necessary in all cases (Allendorf, Hohenlohe, & Luikart, 2010). Additionally, despite falling costs, these studies still require significant financial and computational resources, as well bioinformatics expertise.

Several reviews already exist on the *potential* of using genomic data to detect adaptive variation for conservation purposes (Allendorf et al., 2010; Harrisson et al., 2014; Hoffmann & Sgro, 2011; Hoffmann et al., 2015; Sgro, Lowe, & Hoffmann, 2011; Stapley et al., 2010; Stillman & Armstrong, 2015). Here, we aim to provide a *guide* to help conservation biologists and managers decide whether using genomics to detect local adaptation is an appropriate investment, as well as a road map for successful collaboration with genomics experts. We emphasize the iterative and challenging nature of studies of adaptive variation and the specific need for monitoring programs that are linked to conservation actions, which are often characterized by high uncertainty. We also describe situations when identifying local adaptation using genomic approaches is not likely to be useful. We use a modified adaptive management framework (Runge, 2011; Williams & Brown, 2016) to highlight the important steps in a genomic study of adaptive variation that includes both assessment and monitoring (Figure 1): Plan, Design and Implement, Evaluate and Act, and Adjust. A key distinction we make within this framework is between genomics-based *assessment*, which is a point-in-time evaluation to identify existing adaptive variation in the populations or species of interest, and population genetic or genomics-based *monitoring*, which has a temporal component to monitor change (Schwartz, Luikart, & Waples, 2007). In most cases, as reflected in Figure 1, monitoring protocols will be developed from the initial genomic assessment. The best results will come from team members (ecologists, geneticists, bioinformaticians, conservation managers) working together through the entire adaptive management cycle and sharing their expertise while communicating uncertainties, practicalities, and assumptions to other team members.

2 | PLAN: INCLUDING ADAPTIVE VARIATION

2.1 | Determine whether knowledge of local adaptation informs conservation objectives

Many projects with conservation goals can be informed by knowledge of local adaptation (Box 2). In some cases, such as assisted gene flow (Box 2), incorporating adaptive variation into the assessment plan is a primary objective (Aitken & Whitlock, 2013). Alternatively, conservation

Box 2 Conservation actions benefiting from knowledge of local adaptation

Identifying geographic patterns of local adaptation, the environmental drivers of divergent selection among populations, and genes and their variants involved in local adaptation can inform conservation strategies for species at risk (Allendorf et al., 2010; Shafer et al., 2015), especially in the context of changing environmental conditions (global changes in climate or local changes in land use, fire, hydrology, and other processes altering a species' local habitat). Genetic variants that help individuals within populations survive or reproduce more under new environmental conditions would be considered adaptive. If adaptive genetic variants are identified, individuals with genotypes more likely to have higher fitness in local environments could be used in breeding, reinforcement, or reintroduction programs to help ensure success of those programs (He, Johansson, & Heath, 2016; Kelly & Phillips, 2016; Sgro et al., 2011). Managers could also monitor the frequency of these genetic variants over time to gauge the genetic health of a population, or to assess changes in allele frequencies following management interventions (Schwartz et al., 2007; Shafer et al., 2015).

Although adaptive genetic variation is an important consideration for conservation actions, it is clear that managing for specific adaptive variants without regard to genetic variation across the rest of the genome should generally be avoided (Pearse, 2016), unless such variants are well verified by other evidence (e.g., aridity tolerance in eucalyptus; Steane et al., 2014) and the situation is urgent (e.g., disease progression). Even in cases where the evidence for genetic adaptation is strong, management interventions should strive to conserve adaptive variation without eroding genomewide variation (Giglio, Ivy, Jones, & Latch, 2016; Haig, Ballou, & Derrickson, 1990; Spielman, Brook, & Frankham, 2004). Conversely, management actions designed to preserve genomewide variation may either involve risks of disrupting local adaptation to nonclimatic factors (e.g., biotic interactions, soils) if local adaptation is not well understood, or could result in outbreeding depression if individuals from long-diverged populations are mixed and interbreed (see Frankham et al., 2011 for guidance on when this might occur). However, many conservationists argue that the benefits of introducing needed genetic variation for challenging environmental conditions may outweigh these risks (Aitken & Whitlock, 2013; Whiteley, Fitzpatrick, Funk, & Tallmon, 2015).

Below we provide some specific conservation actions that would benefit from the inclusion of assessment and monitoring of adaptive variation.

Assisted gene flow: Assisted gene flow is the movement of individuals within the species range from an adaptively divergent source population that has genetic variation predicted to be adaptive under future environmental conditions (Aitken & Whitlock, 2013; Prober et al., 2015). NGS can be used to characterize local adaptation based on environmental conditions. Then, "preadapted" genetic variants from a source population can be moved into a recipient population to improve evolutionary potential. While appropriate source and recipient populations could be selected based on climatic and other ecological data (a "best guess" approach), such efforts would be better informed by knowledge of adaptive variation and climatic drivers of local adaptation. Assisted gene flow is expected to be especially beneficial in dispersal-limited, long-lived species such as trees (Aitken & Bemmels, 2016; Gugger, Liang, Sork, Hodgskiss, & Wright, 2017; Steane et al., 2014).

Defining conservation units: Starting in the 1990s, a few (5–25) selectively neutral markers (e.g., microsatellites and organellar DNA) were commonly used to delineate conservation units. NGS provides increased resolution, while also allowing for characterization of adaptive differentiation among populations. Funk, McKay, Hohenlohe, and Allendorf (2012) explain how to use both neutral and adaptive data in a complementary way to delineate conservation units that maximize adaptive capacity, while Ahrens et al. (2017), Guo, Li, and Merilä (2016), Lah et al. (2016), and Peters et al. (2016) provide empirical examples.

Environmental epidemiology and disease dynamics: NGS can be used to investigate the genetic basis of disease, parasite, and toxin resistance. This is a relatively underutilized application of NGS in wild populations, although a few excellent examples exist, including identifying the genetic basis of adaptation to harmful algal blooms in coastal and estuarine common bottlenose dolphins (Cammen, Schultz, Rosel, Wells, & Read, 2015), and identifying a rapid evolutionary response to transmissible cancer in multiple populations of Tasmanian devils (Epstein et al., 2016).

Genetic rescue: The aim of genetic rescue is to improve the fitness of small populations by increasing (neutral) genetic diversity by moving individuals between populations (Whiteley et al., 2015). The main concern with genetic rescue is outbreeding depression, a reduction in fitness due to the mixing of divergently adapted genotypes and/or the disruption of co-adapted gene complexes. Adaptive markers identified with NGS can characterize adaptive differences among source and target populations, while neutral markers can be used to estimate the extent of gene flow between these populations. This information can then be used to minimize the risk of outbreeding depression. See Weeks et al. (2011) for a definitive discussion.

Identifying hybridization: Although not strictly a conservation action, identifying hybrids has direct relevance for conservation managers, because hybridization can be both a conservation problem, threatening species identity and genetic integrity (Bohling, 2016; Wayne & Shaffer, 2016), and a conservation opportunity, enhancing evolutionary potential in changing environments through adaptive introgression (Hamilton & Miller, 2016). In both cases, NGS provides both improved resolution to identify hybridization and the data needed to develop monitoring panels (Hohenlohe et al., 2011).

(Continues)

BOX 2 **(Continued)**

Minimizing adaptation to captivity: Although no examples are published to date, adaptive NGS could be used in captive breeding programs to monitor for rapid changes in allele frequencies that could be indicative of adaptation to captive conditions (Allendorf et al., 2010), which can have severe fitness consequences for reintroduced populations (Black, Seears, Hollenbeck, & Samollow, 2017).

Site prioritization to maximize evolutionary potential: Site prioritization conventionally involves maximizing the amount of biodiversity protected (e.g., number of species) while minimizing financial costs. Under climate change, protecting populations with complementary sets of intraspecific adaptive genetic diversity has become increasingly important, as this adaptive variation is indicative of the evolutionary potential of populations under changing conditions (Bonin, Nicole, Pompanon, Miaud, & Taberlet, 2007). NGS can provide both the neutral and adaptive data needed for these analyses.

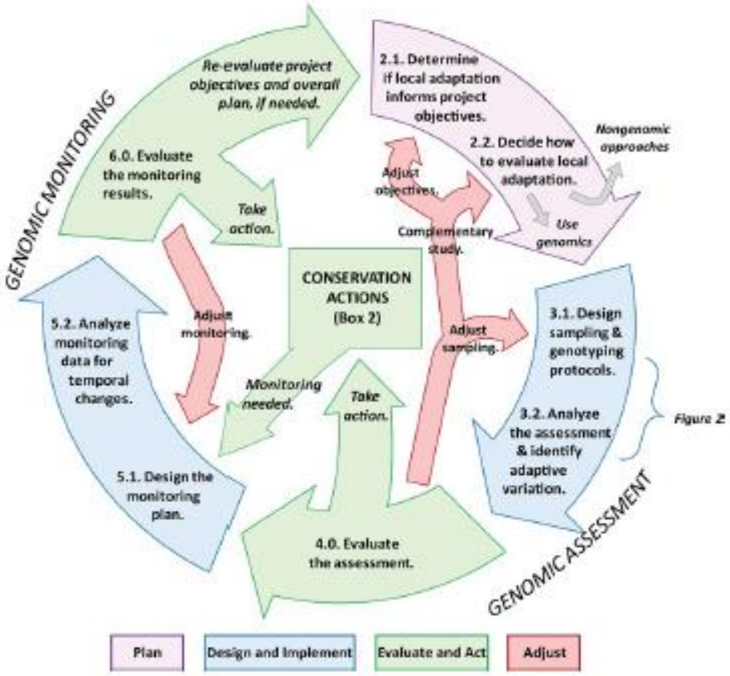

FIGURE 1 Adaptive management cycle for NGS-based assessment and monitoring of adaptive genetic variation. Cycle stages numbered to match sections in the text. Stage 2 outlines the initial planning phase, stages 3 and 4 are the genomic assessment, and stages 5 and 6 are the genomic monitoring phases. The red, un-numbered arrows highlight the need for adjusting the plan throughout the adaptive management cycle

goals may be adequately addressed using neutral genetic variation (e.g., to infer demographic parameters), and data on adaptive variation may be unnecessary or secondary to the project. For example, assessment and management of inbreeding through genetic rescue only requires knowledge of neutral variation, although an understanding of local adaptation may reduce the risks of outbreeding depression by minimizing adaptive divergence between source and target populations (Box 2).

Several features of species and their populations should be considered when determining whether to use genomic approaches to study adaptive variation. Species where local adaptation is most likely to occur and be detected using genomics are characterized by strong environmental variation among populations (producing divergent selection), and large **effective population size** (minimizing the effects of **genetic drift**). When divergent selection is strong, local adaptation is likely to develop, even in the face of high gene flow (Yeaman & Whitlock, 2013). Signatures of local adaptation are more likely to be detected in species with minimal neutral population structure, such as mobile species with high gene flow (common in marine systems), because strong population structure or complex evolutionary history can create many false positives (De Mita et al., 2013; Lotterhos & Whitlock, 2014; de Villemereuil, Frichot, Bazin, François, & Gaggiotti, 2014). By contrast, local adaptation is less likely in systems with homogenous environmental conditions or where environmental conditions fluctuate over time. Local adaptation is also less likely in populations with small or highly variable effective sizes (where genetic drift has stronger effects). Very low levels of gene flow can lead to strong neutral population structure that can make it difficult to distinguish patterns due to selection from those resulting from demography. If managers are working with species that have characteristics making local adaptation less likely to develop or to be detectable, and where there is no prior evidence of local adaptation, managers might consider allocating scarce resources to other conservation activities, rather than investing in genomic methods that may produce ambiguous results.

2.2 | Decide how to evaluate local adaptation

If the project will benefit from understanding local adaptation, several options exist. For species that are amenable to experimental approaches (e.g., plants), patterns of local adaptation can be reliably addressed by traditional methods such as common gardens and reciprocal transplants (Blanquart, Kaltz, Nuismer, & Gandon, 2013; Endler, 1986; Hereford, 2009; Kawecki & Ebert, 2004). Longer-term field studies of wild populations can also be used to assess adaptive variation in some contexts (Charmantier, Doutrelant, Dubuc-Messier, Fargevielle, & Szulkin, 2016; Charmantier et al., 2008; Ozgul et al., 2009). For example, in Mediterranean blue tits, egg laying date is heritable and differs between populations in deciduous and evergreen forests, and those differences are maintained in common garden conditions (Charmantier et al., 2016). These types of studies may be more affordable and can be just as effective as genomic approaches in providing necessary information on local adaptation. While transplantation or long-term studies are not possible for all species of conservation concern, it will be an option for some, including many plants (McKay et al., 2001; Raabová, Münzbergová, & Fischer, 2007).

In many cases, however, phenotypic methods will not be feasible for the focal species, and genomics may be the preferred alternative. Many management issues related to local adaptation do not require a complete assessment of adaptive variation, nor the functional validation of candidate adaptive variants. Instead, managers may simply need to characterize geographic or environmental patterns of adaptive variation across populations, information which can be generated for species without prior genomic information (Catchen et al., 2017). However, there are advantages to working with species that already have some genomic resources developed (sometimes called a "genome-enabled" species; Kohn, Murphy, Ostrander, & Wayne, 2006), such as an assembled reference sequence or transcriptome. These resources maximize useable data and can help validate and interpret potentially adaptive variation (e.g., by comparing to genes with known function). Additionally, any genomic study is more difficult (e.g., laboratory protocols will require more troubleshooting and modification) and potentially costlier in species with large genomes (e.g., conifers, salamanders). Overall, before deciding to embark on a genomic study of adaptive variation, we recommend clearly defining the biological or management questions, identifying how genomic data will help address these questions, evaluating alternative nongenomic approaches, researching any existing genetic resources for the focal or a closely related species (or identifying whether those resources need to be developed), considering biological and genomic characteristics of study species, and evaluating budgetary constraints for both assessment and management.

3 | DESIGN AND IMPLEMENT: ASSESSMENT

3.1 | Design the sampling and genotyping protocols

In every genomics study, researchers make many small decisions about sampling, genotyping, bioinformatics, and analysis, all of which can have a substantial impact on downstream results. Managers should not be expected to know every detail, but some decisions, which we highlight in this section and in Figure 2, should be discussed carefully among the team members as they can impact the interpretation of the study.

3.1.1 | Sampling

Sample size and the number and location of populations sampled are primary considerations that can dramatically facilitate or impede detection of local adaptation. All methods for detecting local adaptation will benefit from sampling that is stratified across environmental gradients likely driving selection and replicated across those gradients (Lotterhos & Whitlock, 2015; Schoville et al., 2012). How individual samples are specifically arrayed (e.g., individual- or population-based sampling, number of individuals per population, transects, or paired designs) is less generalizable and depends on the analytical approaches to be used and the biology and distribution of the species. For example, many genotype–environment association (GEA) methods for detecting local adaptation can be used on either individual or pooled population samples, while differentiation-based approaches require population-based sampling (see below). Researchers will often try to accomplish multiple goals when collecting genomic data (e.g., estimate effective population size, inbreeding, gene flow, and adaptive differentiation), and characterizing adaptive variation may be only one of several objectives. One sampling plan may not fit all objectives; it is therefore important to plan ahead and target sampling to meet primary objectives, while consulting with collaborators on how data may be used to meet secondary goals. For this reason, sampling will involve trade-offs, including accommodating multiple analytical goals, achieving sufficient geographic coverage to sample known or suspected genetically differentiated populations, sufficiently sampling the environmental conditions thought to be driving selection, sufficiently replicating sampling along environmental gradients, and sampling sufficient numbers of locations and individuals per location. For example, De Mita et al. (2013) showed via simulation that relatively good performance could be achieved with at least eight sampled populations, using a strategy that samples the extreme ends of the environmental gradient, but the best sampling in real situations is not fully known.

Most genomics protocols (Etter, Bassham, Hohenlohe, Johnson, & Cresko, 2011; Peterson, Weber, Kay, Fisher, & Hoekstra, 2012; see below) require 50–300 ng of high-quality DNA, taken from small (often nonlethal) tissue samples. Recent studies have successfully used NGS on as little as 1 ng of DNA extracted from noninvasively collected samples (i.e., hair snags) and museum samples, indicating that even low-quality samples can be used, but do require additional precautions and genomic resources because DNA degrades over time (Bi et al., 2013; Russello, Waterhouse, Etter, & Johnson, 2015). These advances have the potential to extend local adaptation studies to species that are difficult to sample, and allow for the retrospective study of genetic variation.

For analyses that incorporate environmental variation, such as GEA, environmental sampling will also be required. Key environmental

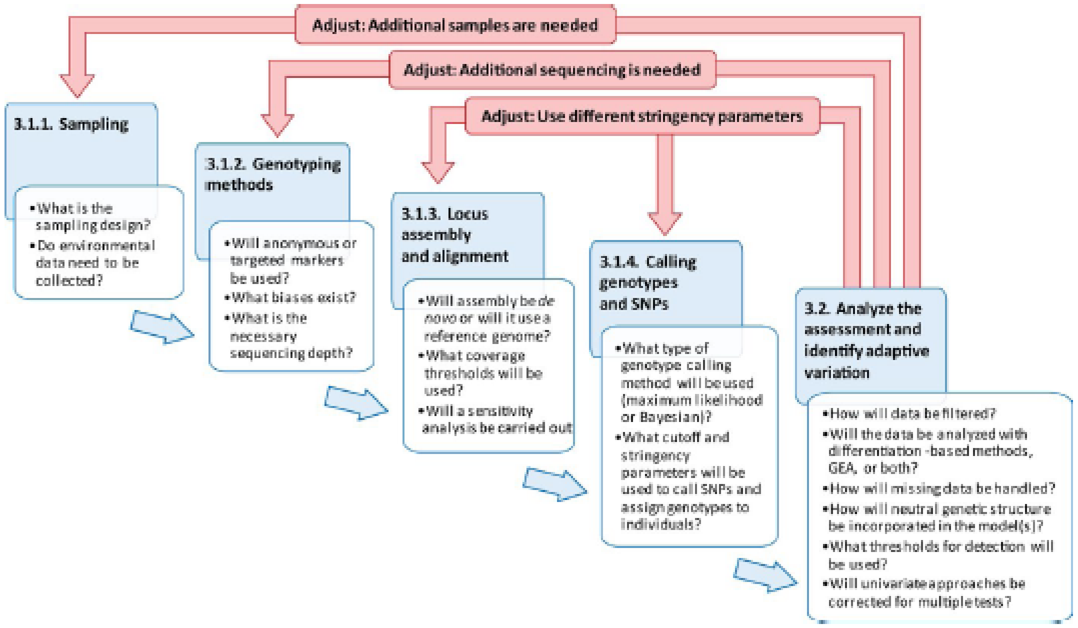

FIGURE 2 Key questions to ask when conducting a genomic assessment of adaptive variation. The steps here correspond to stage 3 in Figure 1. As in Figure 1, the red, un-numbered arrows identify potential points where adjusting the planned assessment is required

factors will depend on the focal species, and experts with in-depth knowledge of species biology can suggest potentially important habitat (e.g., soil type, plant community, water quality, pollution) or climatic factors (e.g., seasonal and annual temperature and precipitation averages and extremes). Environmental characterization may be as simple as collecting weather station data or relevant GIS layers from online databases (see Daly 2006 for guidance on assessing the suitability of spatial climate datasets). In these cases, the temporal scale of environmental data should be considered in relation to the generation time of the species, such that environmental covariates include multiple generations of selective pressures. Researchers should also consider selection pressures that occur at specific life history stages, such as seedling establishment in long-lived trees, which may experience different selective pressures than those observed in fully grown trees. When covariates such as environmental contaminants need to be measured directly in the field, additional planning is required (e.g., for instrument acquisition, deployment, maintenance, and data analysis). When available, it is best to use proximal (e.g., temperature, precipitation) as opposed to distal (e.g., elevation, latitude) predictors, as proximal variables may decouple from their distal proxies, for example, under climate change (Lookingbill & Urban 2005). Finally, consideration of environmental variability should be included with mean predictors, especially as temporal and spatial variability in climate may be magnified by climate change (Buckley & Huey, 2016; Reusch, Ehlers, Hammerli, & Worm, 2005; Schoepf, Stat, Falter, & McCulloch, 2015). Detailed genetic and environmental sampling guidelines are reviewed elsewhere (Balkenhol & Fortin, 2016; De Mita et al., 2013; Hoban et al., 2016; Lotterhos & Whitlock, 2015; Manel et al., 2010; Prunier et al., 2013; Rellstab, Gugerli, Eckert, Hancock, & Holderegger, 2015; Schoville et al., 2012).

3.1.2 | Genotyping methods

Genomic data are most often produced using NGS technologies that can sequence millions of DNA fragments across the genome (Davey et al., 2011; Goodwin, McPherson, & McCombie, 2016). In most cases, only a subset of the genome is sequenced. Two primary methods are used to reduce the amount of the genome sequenced: anonymous sequencing methods that sequence DNA adjacent to restriction enzyme cut sites, and targeted sequencing methods that focus on known genes or sequences. The most commonly used anonymous approaches in ecological and evolutionary studies are the family of restriction-site-associated DNA sequencing (RADseq) protocols, which include a diversity of library preparation methods (Andrews, Good, Miller, Luikart, & Hohenlohe, 2016). By contrast, targeted sequencing focuses on capturing specific genomic regions, ranging from specific neutral markers, to candidate genes to entire exomes (Grover, Salmon, & Wendel, 2012). Of the targeted sequencing methods, sequence capture is the most scalable to whole-genome applications (Grover et al., 2012; Jones & Good, 2016) and is particularly useful for species with large genomes (Suren et al., 2016).

Anonymous and targeted sequencing methods have trade-offs in cost, accuracy, and bias. Anonymous sequencing methods require no prior genomic information and less starting DNA and are usually considerably less expensive than targeted sequencing. However, depending on the protocol used, they are subject to problems with error, bias, and missing data. These issues include genotyping biases (e.g., false homozygosity) due to sources of error such as PCR bias (Davey et al., 2011), PCR duplicates (Davey et al., 2011), polymorphic restriction sites (i.e., allele dropout; Arnold, Corbett-Detig, Hartl, & Bomblies, 2013; Cariou, Duret, & Charlat, 2016; Gautier et al., 2013), and shearing bias (Davey et al., 2013). Many of these issues are specific to particular RADseq protocols and can be addressed with appropriate planning and study design (for a review of problems, solutions, and RADseq study design, see Andrews et al., 2016; Catchen et al., 2017; Lowry et al., 2017a,b; McKinney, Larson, Seeb, & Seeb, 2017). Because RADseq genotypes a subsample of regions across the genome, it will include both selectively neutral and adaptive markers.

Targeted sequencing requires prior sequence resources (e.g., a transcriptome assembled from RNA sequencing, reference genome, or anonymous sequences) for the design of capture probes (Grover et al., 2012; Jones & Good, 2016). The success rate of sequence capture probes increases with the use of a reference genome for identifying intron–exon boundaries. If targets are designed based on a reference genome from another species, the suite of loci may be biased when applied to the focal species (a form of ascertainment bias), although aligning to a congener should reduce bias.

Regardless of the genome complexity reduction method used prior to sequencing, in most cases multiple individuals will be individually barcoded, then pooled in a lane of sequencing. Because of error and bias that can arise from library preparation and sequencing, randomizing samples throughout the process is instrumental in reducing bias (Meirmans 2015). Individuals from the same populations or from nearby locations should be distributed among sample plates and sequencing libraries. Otherwise, estimates of population genetic statistics may be biased.

Decisions on whether to use anonymous or targeted sequencing should be based on the overall study goals and the availability of prior genomic resources. As total gene content does not vary as much as genome size, anonymous sequencing will be relatively poorer for detecting adaptive variation in species with larger genomes, as fewer sequences will contain coding regions, and more missing data will result from sequencing efforts scattered over a larger number of sequences (Lowry et al., 2017a,b). Prior to choosing a sequencing method, researchers and managers should discuss and be aware of biases and sources of error that will impact the downstream analyses.

3.1.3 | Assembly and alignment of sequence reads

Next-generation sequencing generates many short sequence reads that need to be assembled into groups of similar, homologous sequences and then aligned to a genomic location within a reference genome (if one is available). Polymorphic loci are then identified and the genotypes of individuals inferred from their reads for these loci (described in Section 3.1.4). In targeted sequence capture, probes are often designed for exons of known genes. In anonymous sequencing methods, sequenced regions are scattered across the genome in introns and exons within genes, but also in intergenic regions, and so are more vaguely referred to as "loci." Here, we will use the term "loci" to refer to sequenced regions used in the analyses for simplicity.

For anonymous sequencing approaches, an important decision is whether to use a reference genome to guide the assembly of loci or to conduct a de novo assembly with the sequence data. This choice will determine the appropriate type of assembly program to use (e.g., GATK: McKenna et al., 2010; dePristo et al., 2011; Van der Auwera et al., 2013 with a reference genome; Stacks: Catchen, Amores, Hohenlohe, Cresko, & Postlethwait, 2011; Catchen, Hohenlohe, Bassham, Amores, & Cresko, 2013; Paris, Stevens, & Catchen, 2017; or dDocent: Puritz, Hollenbeck, & Gold, 2014 for a de novo assembly). Using a high-quality and well-annotated reference genome facilitates the identification of candidate genes and gene regions and allows for a truly genomic approach (e.g., considering physical linkage between regions with adaptive variation; Manel et al., 2016). However, using a reference genome from another species can also result in confirmation bias, because the focal species may have divergent gene sequences or different structural features of the genome that may result in informative loci being removed from the analysis (Tamazian et al., 2016). Developing a high-quality reference genome for the focal species would ameliorate some of these issues, but is not always necessary, depending on objectives. Managers should be aware of whether a reference genome is available, and whether it is for the focal species or a congener.

A major decision that will determine which loci are included in the dataset is choosing the parameters determining how closely the sequences must match (either match the reference sequence or match other sequences in de novo approaches; Catchen et al., 2011; McKenna et al., 2010; dePristo et al., 2011; Van der Auwera et al., 2013) and how often the sequences occur in individuals (i.e., coverage). If the sensitivity of these parameters is too low, sequences will be combined that are not from the same genomic region (i.e., paralogs; McKinney, Waples, Seeb, & Seeb, 2017). Alternatively, if settings are too stringent, few loci will be included. To help identify the best parameters and understand the limitations of the dataset, sensitivity analysis should be performed (Andrews & Luikart, 2014; Escudero, Eaton, Hahn, & Hipp, 2014; Mastretta-Yanes et al., 2015; Paris et al., 2017). Biases identified by sensitivity analysis, such as a large number of PCR duplicates or excessive missing data, may be addressed through more stringent filtering, or it may be necessary to collect more data (resequencing, sampling more individuals, or considering another sequencing approach). For anonymous methods, including technical replicates (i.e., using the same DNA but barcoding and processing the replicate independently) in the genotyping library is recommended to improve quality control (e.g., estimating error rates) and parameter optimization (Mastretta-Yanes et al., 2015).

3.1.4 | Calling genotypes and SNPs

Once loci are selected for analysis, sequence reads spanning each locus from each individual are used to call genotypes (i.e., infer the genotype at a locus for each individual; Nielsen, Paul, Albrechtsen,

& Song, 2011). Genotype-calling software programs use either maximum-likelihood (e.g., Stacks; Catchen et al., 2011) or Bayesian models (e.g., GATK; McKenna et al., 2010; dePristo et al., 2011; Van der Auwera et al., 2013) to assign individuals with genotypes. These models often incorporate some element of sequencing error, but the primary determinant of whether individuals are accurately genotyped as heterozygous or homozygous is the number of reads assigned to each individual. While most polymorphisms will be SNPs, one major consideration when grouping reads into exon regions (applicable when a reference is available) is identifying and correctly aligning insertion and deletion mutations (INDELs). The importance of correcting for INDELs in accurate SNP calling depends on the mapping and calling programs used (O'Rawe et al., 2013).

Similar to filtering polymorphic loci for analysis in the dataset, the thresholds set for SNP calling for individuals influence the quality of the data (Nielsen et al., 2011). For example, if the dataset contains too few sequences for an individual across a given SNP, an individual that is a heterozygote may be wrongly genotyped as a homozygote if only one of the two alleles is sequenced. Software programs typically allow the user to specify coverage cutoffs and other parameters determining SNP calling stringency. Changing the parameters of these models, especially the number of reads required to call heterozygotes, can affect genotypic frequencies in the populations and alter population genetics statistics estimated in the analyses. Depending on the depth of coverage, this threshold can also reduce the size of the dataset (Huang & Knowles, 2014). In exome capture studies, quality control that is too stringent can lead to a loss of power if causal variants are removed (Auer, Wang, & Leal, 2013). An additional consideration is whether the phased haplotype within a locus can be analyzed instead of single SNPs (Benestan et al., 2016; Manching et al., 2017). Many loci have multiple SNPs within an exon or locus, and those SNPs can be combined to infer a haplotype (Helyar et al., 2011). Additionally, if a reference genome is available, the position of the SNPs in a broader genomic region can be used to infer haplotypes (Andolfatto et al., 2011; Andrews et al., 2016). However, many of the common and user-friendly downstream analytical programs only consider independent SNPs.

To summarize, we encourage conservation managers to become familiar with the primary steps that can influence data quality and interpretation of results. When planning a project, based on the objectives of the project, the team must decide (i) which NGS method will be used; (ii) whether a reference genome is available; (iii) how the genotype-calling coverage and mismatch thresholds will be set, and whether the sensitivity of the data to those parameters will be evaluated; and (iv) what coverage cutoffs will be used to select loci and assign genotypes to individuals (Figure 2).

3.2 | Analyze the genomic assessment and identify adaptive variation

The first step in analyzing genotypic data collected during the assessment is quality control filtering. Data filtering is a multistep process, with specific criteria dependent on the analyses to be performed (see Benestan et al., 2016 for a recent overview). Quality control filters are used to ensure that uninformative markers and statistical artifacts are removed prior to analyses. These filters consider sequencing error, locus coverage, genotyping level (across loci, individuals, and populations), number of alleles per marker, and linkage (e.g., number of SNPs per genomic contig or exon). Filters may also be applied based on minor allele frequency and deviations from Hardy–Weinberg proportions. These filters can reduce the size of the dataset, but increase the quality of the analysis (Huang & Knowles, 2014). Patterns of missing data across samples should also be evaluated both before and after filters are applied to reduce the risk of detecting spurious (nonbiological) signals in downstream analyses. This includes visualizing relationships between missingness and factors such as sequencing lane, sample site, population, and heterozygosity (Gosselin & Bernatchez, 2016). These visualizations can help determine if populations or individuals should be excluded, for example, if they have both high missing data and elevated homozygosity, suggesting allele dropout (i.e., one allele is not being sequenced). In some cases, populations may need to be resampled or samples resequenced to compensate for missing data (Figure 2).

Many methods for identifying local adaptation require a dataset without missing values, so missing data must either be pruned (e.g., removing loci or individuals) or imputed. The impact of these different strategies on downstream analyses is an area of active investigation (e.g., Chattopadhyay, Garg, & Ramakrishnan, 2014). Research in related fields indicates that strict filtering of missing data can reduce statistical power (Nakagawa & Freckleton, 2008), undermine inferential accuracy (Dai, Ruczinski, LeBlanc, & Kooperberg, 2006), and introduce bias (Huang & Knowles, 2014). With a lack of firm guidelines for anonymous sequencing data, which tends to have relatively high levels of missing data, the best current approach is to perform a sensitivity analysis using different filtering and imputation strategies. Gosselin and Bernatchez (2016) provide a large (and growing) set of imputation methods for anonymous sequencing data.

Methods for identifying candidate adaptive loci from genomic data can be divided into two main approaches, those based on population genetic differentiation (e.g., F_{ST} outlier methods) and genotype–environment associations (GEAs). These approaches, recently reviewed in Hoban et al. (2016) and Rellstab et al. (2015), differ in their data requirements and assumptions, and also in the information they generate for conservation planning. A third method associates genotypes with phenotypic traits involved in local adaptation to identify adaptive SNPs (i.e., genomewide association studies; reviewed in Savolainen, Lascoux, & Merilä, 2013), but we do not cover this method as sufficient phenotypic data are often unavailable for species of conservation concern. Differentiation-based methods identify loci with extreme allele frequency differences among populations relative to overall population structure, a pattern consistent with divergent selection. These studies can be performed without prior knowledge of the environmental factors driving local adaptation and for species that exist in discrete populations, but often lack a specific hypothesis and will not identify environmental drivers of selection. Results are dependent on assumptions about the underlying distribution of selectively neutral differentiation (e.g., F_{ST}) across loci. Some commonly used methods include tests based on the island model of migration as proposed by Beaumont and Nichols (1996) and implemented in LOSITAN (Antao, Lopes, Lopes, Beja-Pereira, & Luikart, 2008), Mcheza/DFDIST (Antao & Beaumont, 2011), Arlequin (Excoffier & Lischer, 2010), and BayeScan (Foll & Gaggiotti, 2008). However, these methods are sensitive to deviations from the assumptions of the infinite island model (Flanagan & Jones, 2017; Hohenlohe, Phillips, & Cresko, 2010; Lotterhos & Whitlock, 2015) and are increasingly discouraged for empirical studies. Alternative approaches test other population genetic models (e.g., deviation from random genetic drift; Vitalis, Glemin, & Olivieri, 2004), relax the assumptions of a specific model (Lotterhos & Whitlock, 2015), or use methods that do not rely on population genetic models, such as principal components analysis (e.g., pcadapt; Luu, Bazin, & Blum, 2017).

By contrast, GEA methods identify potentially adaptive loci based on associations between allele frequencies and environmental variables hypothesized to drive selection, a pattern that is consistent with a selective advantage of certain alleles in certain environments (Joost et al., 2007). Unlike differentiation-based approaches, these methods do not use an underlying population genetic model, and most can use either individual genotype or population allele frequency data. These methods generally have higher power than differentiation-based methods, and can detect divergent selection even when it does not produce strong differentiation among populations (De Mita et al., 2013; Rellstab et al., 2015; de Villemereuil et al., 2014). Most GEA methods use some form of statistical control for population structure and demography, which, when unaccounted for, can produce high false-positive signals (Hoban et al., 2016; Rellstab et al., 2015), although adjustments for population structure, especially when it is concordant with environmental gradients, can produce false negatives (e.g., Yeaman et al., 2016). Additionally, because most commonly used GEA methods (e.g., Bayenv2: Coop, Witonsky, DiRenzo, & Pritchard, 2010; Gunther & Coop, 2013; latent factor mixed models (LFMM): Frichot, Schoville, Bouchard, & François, 2013) use a univariate statistical framework in which one locus and one environmental predictor are tested at a time, these methods require corrections for multiple tests to prevent elevated false-positive rates (François, Martins, Caye, & Schoville, 2016). Multivariate GEAs (e.g., redundancy analysis), which analyze many loci and environmental predictors simultaneously, identify how groups of loci covary in response to environmental predictors and may reduce or eliminate the need for multiple testing while potentially identifying polygenic selection (Rellstab et al., 2015). In simulations, multivariate GEAs are more effective than univariate methods at detecting important adaptive processes that result in weak multilocus signatures (e.g., selection on standing genetic variation) and are robust to multiple sampling designs and sample sizes (Forester, Lasky, Wagner, & Urban, 2017). Brauer, Hammer, and Beheregaray (2016) provide a clear example of local adaptation in a threatened fish species that is mediated by both divergent selection (detected through differentiation-based methods) and polygenic selection from standing genetic variation (detected with a multivariate GEA).

For all of these methods of detecting locally adaptive variation, we recommend considering four key points: (i) Do the data meet the model assumptions? (ii) How is neutral genetic structure incorporated into the model? (iii) Are univariate approaches corrected for multiple testing? And (iv) what are the thresholds for detection? Thresholds for differentiating loci potentially under selection are generally arbitrary (e.g., FDR = 0.1) and should be tested and modified based on the study goals (François et al. 2016, de Villemereuil et al., 2014; Figure 2).

Conservation managers also must evaluate the risks of acting based on type 1 errors (concluding populations are not locally adapted when they actually are) from the risk of type 2 errors (concluding they are locally adapted when they are not), as different sequencing and analytical approaches carry different type 1 and type 2 risks. For example, if the proposed conservation action is genetic rescue, then acting on type 1 error increases the risk of outbreeding depression, whereas acting on type 2 error would minimize the number of available source populations. The conservation team can evaluate the risks of each type of error through sensitivity analysis. While to our knowledge, sensitivity analyses have not yet been used in applications of adaptive genomics in management, the benefit of these analyses is clearly evident in other aspects of conservation planning, including climate change vulnerability assessments (Wade et al., 2017), systematic conservation network planning (Levin, Mazor, Brokovich, Jablon, & Kark, 2015), and population viability analysis (Naujokaitis-Lewis, Curtis, Arcese, & Rosenfeld, 2009). Testing the sensitivity of downstream management choices to upstream parameters will be an area for development in applied adaptive genomics.

4 | EVALUATE AND ACT: ASSESSMENT

4.1 | Evaluate the assessment

Next, the assessment should be interpreted in light of the conservation objectives and analytical limitations to determine whether the information is sufficient to inform conservation actions or whether further study is needed (Figure 1). Conclusions from the assessment may be equivocal, so a manager may decide to collect more data (i.e., sample more individuals, compare more populations, and sequence targeted genes; Figure 1). Alternatively, the assessment may clearly identify patterns of local adaptation and adaptive variants, providing the groundwork for initiating monitoring or conservation actions (e.g., identifying source populations for restoration, genetic rescue, or assisted gene flow). This will depend on the overall conservation plan and predefined thresholds for action.

In anonymous NGS studies, the number of candidate adaptive markers will be determined by the detection threshold, so this number is not reflective of the underlying processes but rather the chosen cutoff. While these methods are useful in detecting patterns of local adaptation, we caution against putting too much emphasis on any particular locus or set of loci identified (Pearse, 2016). Instead, broadscale patterns of geographic variation and relationships between genotypes and environmental drivers will be more informative, as will seeing if effects are localized on particular genomic regions (e.g., sex chromosomes). Another potential challenge for these studies is parallel evolution of adaptive traits via different genes and genetic architectures (Bernatchez, 2016; Ralph & Coop, 2015). This can confound sampling designs that are intended to improve the strength of inference by detecting local adaptation along replicated environmental gradients. In this case, the lack of a replicated signal of SNP–environment correlations does not necessarily mean that the detected signals are spurious, but may instead point to "imperfect" parallelism (Bernatchez, 2016). Finally, the differences in phenotypes underlying local adaptation are often the product of small changes in allele frequency across many genes, as well as the correlations among and interactions between these loci (Boyle, Yang, & Pritchard, 2017; Le Corre & Kremer, 2012). While different approaches may identify some of the same "core" genes involved (sensu Boyle et al., 2017), different subsets of the many "peripheral" genes will be detected with different sampling approaches and analytical methods. However, the patterns of variation identified will nonetheless provide important information for conservation actions.

Incorporating environmental data in GEA methods is a useful way to identify links between genetic mechanisms and environmental factors driving adaptation. However, it is important to remember that these studies cannot pinpoint causative relationships, as they are inherently correlative (Gunther & Coop, 2013). If it is necessary to identify a causative relationship before any management decisions can be made, then conducting experiments such as common gardens, genetic crosses, or genetic manipulations (e.g., gene editing or gene knockouts) will be required. Confirming causal relationships is very challenging, and to our knowledge has not been done for locally adaptive variants; nor is it necessary to inform conservation strategies for species in rapidly changing environments.

5 | DESIGN AND IMPLEMENT: MONITORING

5.1 | Design monitoring plan

Evaluating changes in genetic variation over time (e.g., detecting loss of genetic variability or changes in the frequencies of adaptive variants) requires a monitoring program. In an adaptive management context, monitoring is a means for both learning more about the system and evaluating the effectiveness of management actions once they are initiated (Lyons, Runge, Laskowski, & Kendall, 2008). While monitoring can include genetic or demographic assessments, in all cases effective monitoring programs identify threshold criteria for detecting biologically significant changes and spell out management interventions to be triggered by changes prior to initiating monitoring (Schwartz et al., 2007). Identifying **trigger points** can be challenging as threshold values are case-dependent and likely differ among species (Atkinson et al., 2004). An effective approach is to set trigger points throughout the range of the **indicator variable** to ensure that management action is initiated before a crisis point is reached. Management interventions should be closely tied to the indicator variables, such that a triggered management action will directly affect the indicator and increase its value above the trigger point. For example, a continuous decline in allelic richness at putatively adaptive loci, or an observation of low survival or fecundity over multiple sampling periods may trigger a management intervention such as genetic rescue (Box 2) to increase allelic richness or fitness. By contrast, upgrading the species' listing status would not directly impact the genetic indicator. Unfortunately, best practices for designing sampling protocols and interpreting genetic and other indicators for monitoring are sparse (more below). However, like other steps in the adaptive management framework, it is expected that monitoring plans will be adjusted to reflect new information (Section 6.1). This learning approach in the face of uncertainty best ensures that monitoring will trigger effective and timely management intervention, rather than simply documenting decline and "monitoring to extinction" (Lindenmayer, Piggott, & Wintle, 2013).

Monitoring panels of neutral and candidate adaptive markers can be developed from the initial genomic assessment using sequence capture or SNP arrays (Ali et al., 2015; Hoffberg et al., 2016; Jones & Good, 2016). These methods allow for consistent, efficient, and inexpensive genotyping of many individuals over time to inform diverse management objectives (Amish et al., 2012; Aykanat, Lindqvist, Pritchard, & Primmer, 2016; Hohenlohe, Amish, Catchen, Allendorf, & Luikart, 2011; Houston et al., 2014; Wright et al., 2015). This targeted approach to monitoring is preferred over repeated anonymous sequencing runs, as stochasticity inherent in that process will yield overlapping but distinct sets of loci. Targeted genotyping, by contrast, will optimize efforts by ensuring coverage of the same neutral and adaptive loci across multiple time points. Hess et al. (2015) provide a particularly good example of how a genomic assessment was effectively transitioned into a monitoring program for declining Pacific lamprey. Based on a genomic assessment (Hess, Campbell, Close, Docker, & Narum, 2013), they developed a SNP panel consisting of 96 neutral and candidate adaptive markers that were diagnostic for parentage analysis, cryptic species identification, and characterization of neutral and adaptive genetic variation. These SNPs were chosen to monitor the effectiveness of a diverse set of management actions including translocations, artificial propagation, and habitat restoration, as well as to track population size and facilitate species identification at early life stages. Adaptive markers linked to lamprey phenotypes (body size and migration timing) were included in the SNP panel to monitor the genetic basis of fitness-related traits across different habitat types. Using one modest set of SNPs, the managers were therefore able to track fitness, population size, and individual movements to identify the success of conservation actions, which would have required much more intensive sampling and experimental work without the aid of genomics. However, because the number of adaptive markers (9) was very small in the monitoring panel, the authors warned against using these markers as an indication of overall adaptation, an important cautionary note when managing populations based on subsets of adaptive genetic variation.

Once the monitoring panel has been developed, the sampling design (number and distribution of samples) and temporal frequency of sampling must be designed to detect significant changes in allele frequencies or loss of adaptive variants in key populations (Allendorf, England, Luikart, Ritchie, & Ryman, 2008; Hoban et al., 2014; Schwartz et al., 2007). Because variation at neutral and adaptive loci is usually not correlated (Grueber, Hogg, Ivy, & Belov, 2015; Hartmann, Schaefer, & Segelbacher, 2014; Holderegger, Kamm, & Gugerli, 2006; Kremer et al., 2002), the appropriate number of loci and individuals monitored will depend on conservation objectives, biology of the organism, recent demographic history, and power of the genetic markers to detect change. While broad guidelines for demonstrating adaptive genetic changes have been outlined (Hansen, Sato, & Ruedy, 2012), little specific advice exists on temporal monitoring of adaptive variation (but see Landguth & Balkenhol, 2012). As a general rule, if the goal is to monitor change in allele frequency at a single locus, 30 individuals per population is often considered a sufficient sample size to detect an allele at a frequency of 5%; however, we suggest using simulations to determine a best sample size (Hale, Burg, & Steeves, 2012).

While simulations have been used for decades to aid in the development of genetic monitoring and the interpretation and evaluation of monitoring results (Palm, Laikre, Jorde, & Ryman, 2003; Waples, 2002; Waples & Teel, 1990), they have generally been underutilized for these purposes. Fortunately, user-friendly simulation programs can be used to optimize sampling design and frequency to detect varying degrees of change. These can be customized to the biology of the focal species, seeded with current allele frequencies (Balkenhol & Landguth, 2011; Hoban, 2014), and parameterized for different outcomes in terms of selective changes or bottlenecks (Hoban, Gaggiotti, & Bertorelle, 2013a,b; Peery et al., 2012). Simulations can also be updated based on monitoring results to adjust trigger points and interventions and improve the effectiveness of management actions. Finally, simulations can be used to aid in the interpretation of genetic monitoring results. For example, Waples and Teel (1990) used simulations to test a set of potential drivers of substantial allele frequency changes in hatchery, but not wild, Pacific salmon populations. They were able to eliminate selection and admixture as potential causes and identify a low number of breeders per year as the driving factor.

5.2 | Analyze monitoring data to detect temporal changes

In the case of both demographic monitoring and genomic monitoring, detecting temporal change depends on the frequency of sampling and the generation length of the organism. Monitoring data need to be analyzed regularly, on a timescale that is relevant to the indicator variable and the biology of the organism. For example, sampling allele frequencies multiple times within a single generation may confound changes in genetic structure across life history with changes across generations, whereas analyzing one age cohort in successive generations would be more informative. Monitoring data should be analyzed soon after collection to ensure the prompt detection of changes that might require conservation action. "Phase shifts," sudden changes that occur with little warning (such as rapid declines in population status), are common aspects of biological changes, but some methods can help predict whether a phase shift is imminent (Dakos et al., 2012; Scheffer et al., 2009). Comparing change in adaptive markers to change in a reference set of selectively neutral markers can differentiate shifts due to genetic drift (which would affect all loci approximately equally) from those only occurring in candidate adaptive markers.

It may be necessary or useful in some cases to use museum or other historical ex situ samples (e.g., from a seed bank) to determine historical genetic variation conditions and compare those to contemporary and future changes (Bi et al., 2013; Hartmann et al., 2014; Larsson, Jansman, Segelbacher, Hoglund, & Koelewijn, 2008; Mikheyev, Tin, Arora, & Seeley, 2015; Schwartz et al., 2007). A disadvantage is that historical samples may not have all been collected at the same time or locations and may not have adequate sample sizes (which can reduce power) or DNA quality (which can cause errors). Regardless, keeping sample sizes consistent between sampled time points or adjusting estimates for sample size (e.g., through rarefaction) is important to maximize power to detect change (Dornelas et al., 2013). Sampling in excess of the target number of samples for monitoring is recommended (when feasible), as some samples may fail to be genotyped, and additional samples may be useful for some future objective (Schwartz et al., 2007).

6 | EVALUATE AND ACT: MONITORING

6.1 | Evaluate the monitoring results

Results from genetic monitoring should be evaluated in the context of the prespecified criteria for significant change: Have trigger points been met, and if so, when and how will management interventions be initiated? Do criteria indicate that a management intervention has been successful? If so, does the monitoring program need to be adjusted or discontinued? Do project objectives need to be revisited and updated? If the results are equivocal, what can be learned from the data to effectively adjust the monitoring plan (Figure 1)? For example, consider a management intervention of assisted gene flow has been implemented with the goal of introduced genotypes surviving and reproducing at least 5% more than local genotypes. If monitoring identifies that this threshold has been met, then the intervention is likely successful and should be continued or successfully concluded, whereas the reverse pattern would indicate that the assisted gene flow program needs adjustment or termination. While examples of genetic monitoring of this sort are currently scant, monitoring of phenotypes and reproductive rates has been used successfully in wolves and panthers (Hedrick & Fredrickson, 2010), and monitoring whether translocated individuals have reproduced is increasingly common (Koelewijn et al., 2010; Mulder et al., 2017). So far, temporal genetic monitoring of conservation interventions has been most widely used to understand the extent and efficacy of genetic rescue, including in bighorn sheep (Miller, Poissant, Hogg, & Coltman, 2012) and Florida panthers (Johnson et al., 2010).

When monitoring adaptive variation, unexpected outcomes may arise. One possibility is that a follow-up study reveals some candidate loci are false positives or identifies additional adaptive markers. If this is the case, a revised set of adaptive markers will need to be included in genotyping and monitoring. Another possibility is that truly adaptive genetic variants are not changing in frequency, leading to the conclusion that the environment is not changing. However, genome complexity can constrain allele frequency changes in adaptive variants, even in changing environments, through antagonistic pleiotropy (one gene has multiple phenotypic effects, and positive effects of an allele on one trait are associated with negative effects on another), epistasis (a gene has a different phenotypic consequence when in a new genetic background due to interaction with another gene), or other evolutionary constraints (Hoffmann & Willi, 2008).

In all cases, data from genomic monitoring should be considered in the context of all available data for the species or population. For example, if demographic monitoring identifies population declines not reflected in the genetic data, the monitoring protocol and management strategies should be adjusted accordingly. Genetic indicators assess one aspect of a population (e.g., loss of genetic diversity) that is influenced by multiple ecological (population size, dispersal, breeding) and evolutionary processes (drift, migration, selection) that often interact. Therefore, interpreting causes of change (or lack thereof) in indicators over time may be challenging.

7 | CONCLUSION

In this study, we present a modified adaptive management framework to help managers better understand the process of collecting NGS data and the potential applications for assessment and monitoring of adaptive variation (Figure 1). This framework emphasizes the iterative nature of adaptive management and highlights the importance of key decisions, particularly in the experimental design phase prior to the bulk of data collection (Figure 2). Considering the entire assessment and monitoring cycle prior to developing a project plan will enable researchers and managers to identify the scope of the project, clearly state assumptions and limitations of the chosen approach, and ensure that resources for the monitoring and action are available.

Assessing and monitoring adaptive and neutral genetic variation can be a powerful tool for conservation biologists and wildlife managers, but it has limitations. NGS is not a "silver bullet," but it may be a useful tool, particularly when the entire adaptive management framework is considered prior to embarking upon a study, and with the understanding that implementation of management will be an iterative process that is likely to require adjustments and improvements over time.

ACKNOWLEDGEMENTS

This work was assisted through participation in Next Generation Genetic Monitoring Investigative Workshop at the National Institute for Mathematical and Biological Synthesis, sponsored by the National Science Foundation through NSF Award #DBI-1300426, with additional support from The University of Tennessee, Knoxville. This work was conducted while SPF was a Postdoctoral Fellow at the National Institute for Mathematical and Biological Synthesis. BRF was supported by a Duke University Interdisciplinary Studies Grant, a PEO Scholar Fellowship, and NSF Award #DDIG-1501693.

DATA ARCHIVING

There are no data associated with this review.

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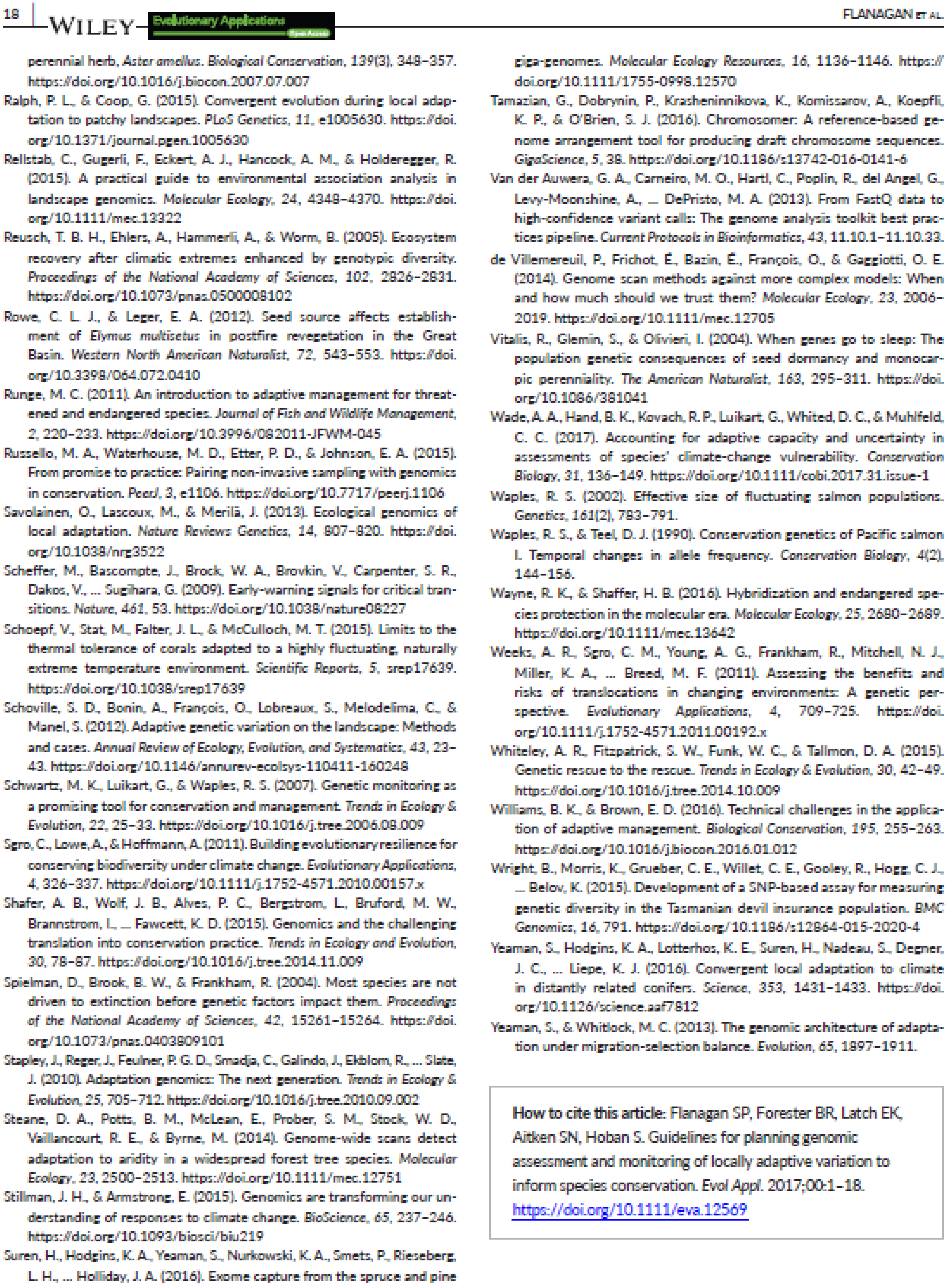

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How to cite this article: Flanagan SP, Forester BR, Latch EK, Aitken SN, Hoban S. Guidelines for planning genomic assessment and monitoring of locally adaptive variation to inform species conservation. *Evol Appl*. 2017;00:1–18. https://doi.org/10.1111/eva.12569

Harnessing Forest Genetic Resources for Climate Resilience, and Forest Health

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A. Forest Genetic Resources for Climate Resilience

Introduction

Forest genetic resources (FGR) are the heritable materials maintained within and among tree and other woody plant species that are of actual or potential economic, environmental, scientific or societal value and benefit to humans in present or future. FGR are essential for the adaptation and evolutionary processes of forests and trees as well as for improving their productivity.

Trees and other woody species differ from other living organisms;they are generally long-lived,and over the years, develop natural mechanisms to maintain high levels of genetic variation within species. This is achieved through high rates of out-crossing and long-distance dispersal of pollen and seed. These mechanisms, combined with the variable native environments, have enabled the evolution of forest tree species into some of the most genetically diverse organisms.

Research, development, conservation and use of tree species, in particular tropical species, has been insufficient with inadequate taxonomic knowledge (Newton and Oldfield, 2008). Based on a literature review, it is conservatively estimated that more than 34000 tree species in more than 1000 genera are of socio-economic, environmental and scientific importance and used on a regular basis by people throughout the world. It includes trees, large woody shrubs attaining more than 2 to 3 m in height, fruit- and nut-trees and their wild relatives. The total comprises both angiosperms (33,500 species in 976 genera and 131 families, including bamboos and palms) and gymnosperms (530 species in 67 genera and nine families).

1. FGRs and their role in Nation building

Rural livelihood support: FGR have the potential to liberate people from hunger and alleviate poverty. FGR provideswood, medicine, food, fibres, timber etc. In addition, Forest genetic resources are the source material for the development of improved varieties. It also attends to the most basic needs for sustainable development of the forest dependent communities. Forests can provide a crucial contribution to Millennium Development Goals especially in achieving environmental sustainability, poverty alleviation and women empowerment. With new policies in place, planted forests and trees outside forests will also provide an increasing share of forest products.

Forests have traditionally been valued as a source of timber, pulp and fuel. All other products, have been classified as Non-timber forest products (NTFPs). NTFPs are obtained from about 3,000 species in the country and form an important source of livelihood for communities, particularly tribals and rural poor living adjacent to forests. Rural populations depend on NTFPsfor food and environmental services. It is estimated that 340 million poor rural people in India depend on NTFPs for their livelihood. In some areas, forests are the primary source of energy, oils, medicines and even staple foods. Edible wild fruits, bamboo seeds and wild legumes have played a very vital role in supplementing the diet of the rural communities. Tribal communities and ethnic tribes use wild edible plant species, including roots and tubers, leafy green vegetables, bulbs and flowers, fruits, seeds and nuts. These foodsgain significance due to their seasonality, in the wake of periodic famines or shortages of crop-based foods. Rural populations also use, protect and create forests as sources of agricultural inputs; they depend on tree products to feed livestock and to maintain water flows.

In India, NTFPs contribute an income equivalent of US$ 2.7 billion per year and absorb 55% of the total employment in the forestry sector. NTFP sector with annual growth rate between 5-15% contributes to 75% of forest sector export income. They provide 50% of the household income for approximately one-third of India’s rural population. The undisclosed indigenous knowledge on medicinal trees held by the tribal communities is one of the valuable resources integrated with biodiversity (FAO, 2012).

*A potential source of revenue:*Forests supply products for export in the form of wood, fibre, processed goods, medicinal and ornamental products.Timber has been a major source of investment for many tropical countries. In some countries, wood is processed into finished goods to enhance employment and increase income. Foreg.Thailand derives substantial foreign exchange from trade in furniture, orchids, specialty foods, medicines and wildlife. Forests also attract recreational users.

FGR generate in-kind forest incomes, which in many instances, goes unaccounted.It is essential to consider this contribution to the national economy, as hundreds of millions of people depend on the forest as their only source of cash income.

Forests store carbon; maintain diverse, unique and rare forms of life; store biotic potential; and encompass natural phenomena that have yet to be understood. These global attributes are gaining value rapidly as institutions evolve to protect them and develop means to translate them into tradable forms in the international market. Some examples of FGR in international trade in global environmental services include debt-for-nature swaps, long-term purchases of forest carbon storage for industrial atmospheric emissions, environmental conditions in trade agreements and international contracts for biological prospecting rights.

Social, cultural, medicinal and scientific value: FGR have major social, cultural and spiritual values, mainly at tree species level, with many individual tree species distinguished and named in local languages. In India 100000 - 150000 sacred groves have been preserved. These groves are natural temples, ancestral places and spiritual retreats that contribute to the strength of the community. Certain tree species have tremendous social and cultural importance, e.g. *Ficusreligiosa* in religious ceremonies, *Santalum album* in burial ceremonies and

Azadirachtaindica in traditional medicines. FGRs are of major scientific value also. Intraspecific diversity can be used, for example, to help understand the genetic, biochemical and physiological basis for resistance to pests and diseases or environmental stresses such as extreme climatic events (drought, flooding) and edaphic extremes (salinity, acidity, etc.). It can also be used to identify biosynthetic pathways for production of important products and metabolites.

2. Status of FGRs in India

The forests of India are classified into 16 major forest types and these forests house a wide array of species diversity. In terms of plant diversity India ranks 10thin the world and 4thin Asia. It is reported that 46042 species of plants occur in India, representing 11% of world flora, of which flowering plants account for 17527 species. Of this 2863 are trees that include some of the highly valued timbers of the world.For about 145 species domestication and breeding efforts are in progress.

The initiation of tree improvement programmes has been the motivation for studying the intraspecific variation in many of the species. In these species, there is production and supply of Forest Reproductive Material (FRM) in the form of seeds, seedlings and clones. Various SFDs, research organizations and universities have established the FGR in the form of Seed Production Areas, Clonal Seed Orchards, Seedling Seed Orchards, Vegetative Multiplication Gardens, modern nurseries, provenance stands etc for production of quality planting stock. Recently, attention towards improvement of fast growing native species and economically important indigenous species to support the TOF programme has become the priority.

A mechanism and monitoring body (Variety Release Committee) for release of clones/ varieties of forestry species has been evolved by the ICFRE. In species like Eucalypts, Casuarinas and Poplar, genetically improved elite clones have been released in the market. Simultaneously, DUS (Distinctness, Uniformity and Stability) descriptors have also been developed for species like Eucalyptus, Casuarina, Neem, Artocarpusheterophyllus, Poplars, Melia, Salix, Pungametcas per the guidelines of Protection of Plant Varieties and Farmers' Rights Act, 2001 (PPV & FRA) to mark specific identity to clones and ensure authority over the clones developed. Guidelines are being developed for teak, sandal, red sanders and other species of commercial importance.

The Government of India has plans to establish a National Bureau of Forest Genetic Resources (NBFGR) and as a precursor to that, a Forest Genetic Resources Management Network (FGRMN) has been established in 2011 under ICFRE with its nodal centres at IFGTB, Coimbatore and Forest Research Institute (FRI), Dehradun. The FGRMN has been established with the objectives to plan, prioritize, organize, conduct and coordinate exploration, collection and documentation of indigenous and exotic forest genetic resources to strengthen *in situ*and *ex situ*conservation. It shall also undertake introduction, exchange and quarantine of genetic resources of forest origin. It shall characterize, evaluate and conserve forest genetic resources and ensure their sustainable management in collaboration with the user agencies. In this process a large number of studies would be undertaken to understand the intraspecific diversity of the economically important species and those of conservation importance. The FGRMN will also be required to develop and maintain a national information network on FGR, develop molecular tools, techniques and approaches to characterize and validate the germplasm and conduct research, teaching and generation of public awareness on FGRs.

In situ conservation: India has 102 National Parks, 514 Wildlife Sanctuaries, 47 Conservation Reserves and 4 Community Reserves. Besides these there are 25 wetlands declared as Ramsar sites and 15 areas in different biogeographic zones declared as Biosphere Reserves. The extent of protected area (PA) network is around 157 826.773 sq. km over 4.8 % of the land area. The National Wildlife Action Plan envisages increase of this to 10% of the land area. The conservation of biodiversity within the PA network takes care of the FGRs also. Other means of *in-situ*conservation like Sacred Groves (SG), Gene Pool Conservation Areas (GPCA), Medicinal Plant Conservation Areas (MPCA), Seed Production Area (SPA) and Permanent Preservation Plots (PPP) are maint. To conserve wild germplasm, revitalize the indigenous health care and livelihood security a 'National Programme on Promoting Conservation of Medicinal Plants and Traditional Knowledge for enhancing Health and Livelihood Security' is under implementation.

Ex situ conservation: More than 150 species are conserved in*ex situ*with a focus on tree improvement, productivity and species conservation. India has more than 100 botanical gardens under the Indian Botanical Garden Network (IBGN). There are ongoing long-term breeding programmes for a large number of species, including provenance trials, progeny trials, clonal trials, and seed orchards. Though these trials and seed orchards are established primarily for genetically improved seed, they are also put under selective conservation, as one of the objectives in *ex-situ*conservation. Germplasm banks and clone banks have also been established for economically important tree species. The germplasm in these banks are characterized for morphological characters for the purpose of identification and registration of clones and biochemical and physiological characters for the purpose of selection and breeding.

Defence Institute of High Altitude Research (DIHAR) under Defence Research and Development (DRDO) has created a National Perma Frost Based Germplasm Storage Facility at an altitude of 5360 m above mean sea level which will serve as a germplasm storage facility for current and future food security in the era of global warming and climate change, and the same can also be used for *ex situ*conservation of FGR for the country.

Organizations involved: The main organizations actively engaged in forest genetic resource conservation are the state Forest Departments, directlyconcerned with*ex situ*and *in-situ*conservation of forest genetic resources. Around 25 per cent of forest areaextending over 22 m ha is under Joint forest management (JFM) with the people of villages adjoiningforests. The forestry research organizations, NGOs and wood based industries are mainly concernedwith the *ex situ*conservation of forestry species of their interest. The ICFRE Institutes maintainsa large number of seed production areas, seedling seed orchards, clonalseed orchards, clone banks and vegetative multiplication gardens, as a part of FGR conservation anduse. The Indian Council of Agriculture Research (ICAR) and its institutes concerned with agroforestry,the National Bureau of Plant Genetic Resources (NBPGR), New Delhi and the Agricultural Universitieswhich conduct courses on forestry also maintain collections of forestry species as National Active Germplasm (NAG) sites and as orchards in their *ex situ*conservation and tree improvement programmes. The Botanical gardens under the Indian BotanicalGarden Network (IBGN) maintain forestry species in their collections all over India. There are alsoNon-governmental organizations, private research organizations and nurseries and wood-basedindustries maintain collections of germplasm of forestry species.

3. FGRs prioritised by National and International bodies

The degree of endemism in plant species is high in India. About 11058 species are endemic to Indian region, of which 6 200 are flowering plants. As per IUCN Red List India has 246 globally threatened plant species, which is about 3% of the world's threatened plants. About 1 500 species of flowering plants and few hundreds of Pteridophytes, Bryophytes, Lichens and Fungi have been identified as threatened. After critical evaluation of their status and threat perceptions, data sheets on 1182 species have been prepared out of which account of 708 species have already been published as Red Data Book of Indian Plants.

Based on the economic utility and conservation value, a large number of forest tree species have been prioritized for conservation and use, by the APFORGEN (Asia-Pacific Forest Genetic Resources Network), the state Forest Departments and in the 'Consultative Workshop on Strategies for Formulation of Forest Genetic Resources Management Network' held at the Institute of Forest Genetics and Tree Breeding (IFGTB), Coimbatore in 2011.

Apart from this Indian Council of Forestry Research and Education (ICFRE) has identified important tree species for research under All India Co-ordinated Programme (AICP). While some of these species are extracted from the natural forests many are raised in the planted forests and agroforestry systems.

4. Climate Vulnerability and FGRs

The major cause of concern for FGR in the global context is the increasing levels of atmospheric CO_2 resulting from human activities such as burning of fossil fuels and forest destruction. Deforestation and forestdegradation, due to human activities,account for nearly 20 percent of greenhouse gasemissions.Elevated levels of CO_2 are predicted to contributeto more extreme climatic events (IPCC, 2013). Climate alterations andincreased occurrence of extreme climatic eventsare considered a threat to FGR.Prolonged drought, high mortality due to extreme climatic events, incombination with regeneration failure, can resultin local population extinction and the loss of FGR,particularly at the receding edge of a species'distribution.

Climate change could alter the frequency andintensity of forest disturbances such as insectoutbreaks, invasive species, wildfires, and storms.A greater incidence of intense cyclones, extremedrought, fires, flooding and landslides has beenobserved in tropical forest ecosystems whichhave experienced increased temperatures andmore frequent and extreme El Nino–SouthernOscillation (ENSO) events. Some climate changemodels predict substantial dieback in parts of theAmazon and other moist tropical forests (Bernier and Schoene, 2009).

Predictions regarding the impact of climatechange on FGR in natural forests, in plantedforests and on farms vary. Hamrick (2004) in his report supports that treeshave sufficient phenotypic plasticity and geneticdiversity at the population level to withstandthe negative effects of climate change. On the contrary, another grouppredicts severe impacts on FGR depending on the types of species and environments they exist. (Vendraminand Fady, 2009; Rehfeldt *et al.*, 2001). Manycountries urgently need to generate baseline information on the impacts of climate change on FGR andto promote and use FGR to help with climatechange adaptation and mitigation.

In India, there has been a simultaneous depletion of state forests and rapid growth of farm forests outwards from urban centres. Natural forest depletion has been driven by the growth of population relative to non-farm employment opportunities and the resulting quest for additional land. The most extreme depletion has occurred just outside protected forests, displaying a backwash effect against the protective boundaries. Forest growth and investment in tree crops occurring outwards from cities are driven by market incentives, including rising prices for wood products relative to agricultural crops, input prices and wage differentials. Forest growth also occurs within irrigated areas, where tree crops fit in with other production activities through complementary uses of the same inputs, household management systems and market networks. This shift in the aggregate forest cover towards settled areas is accompanied by significant changes in the species composition and social organization of forests. An added factor of climate change is likely to worsen the scenario.

An example of the vulnerability of Indian forests to climate change is given below.

- Himalayan mountain system is highly fragile and sensitive to climate change, the rate of warming is greater than the global average warming (IPCC, 2013; Pradhan and Shrestha, 2007; Xu *et al.*, 2009)
- Studies indicate shifts in the Himalayan forests; western and central Himalaya more vulnerable to projected impacts of climate change (Chaturvedi *et al.*, 2011; Gopalakrishnan *et al.*, 2011; Joshi *et al.*, 2012; Shrestha *et al.*, 2012)
- Himalayan forests are also prone to serious ecological degradation (Ives and Messerli, 1989; Pandit *et al*., 2007)

However, an understanding of how adaptive the current Himalayan forests are, and how heterogeneity in regional vulnerabilities influence such changes to broad range of ecosystem functions and services, is lacking. This, in turn, enhances the vulnerability in the complex Himalayan landscape. Further, current management practices have decreased adaptive capacities of forests. The ever-increasing anthropogenic pressure and competition for forest-based resources leads to additional stress beyond the capacities to withstand continuity of change from nature. Under these circumstances, an amalgamation of new scientific approaches based on empirical evidence, along with traditional knowledge from communities, a holistic approach for forest resource utilization needs to be implemented. The anticipated future impacts of climate change, identified by the Government of India (GOI) in its Initial National Communication to the United Nations Framework Convention on Climate Change (UNFCCC) mention that over 50 per cent of India's forests are likely to experience a shift in forest types, adversely impacting associated biodiversity and regional climate dynamics, as well as livelihoods based on forest products (GOI, 2004).

5. Impacts of Climate Change on FGRs

Temperature and precipitation are the twomain climate drivers for forest ecosystems; anysignificant changes in either of these will have animpact on species composition and forest cover.Impacts can range from extreme disturbancessuch as forest fires or pest outbreaks to effects onphysiological processes from more subtle changesin temperature.

It has been reported in the literature that many trees have sufficient phenotypic plasticity and genetic diversity at the population level to significantly reduce the negative effects of climate change. Climate change impacts are expected to be severe in dry and high temperature regions where trees at their adaptive limit (Lindner *et al*., 2010).

Based on the data available to date, expected impacts of climate change on FGR will be experienced through demographic , physiological and genetic process, like high mortality due to extreme climatic events in combination with regeneration failure will result in local population extinction and the loss of FGR, pest and disease attack may be more severe, asynchronous flowering resulting low seed production,new species invasions, altered patterns of gene flow and the hybridization of species and populations(Loo *et al.*, 2011). High mortality reduces the size of available gene pool, may increase inbreeding among survivors, resulting reduction in products and services to people.

In Asia, where key biodiversity hotspots are found, endemic species are predicted to decline, with changes in ecosystem structure and function (FAO, 2010). Changes in precipitation may have a greater influence than temperature for these species (Dawson *et al*., 2011). Changes in water availability are a major emerging threat to FGR; they will be a key factor for the survival and growth of tree species. The response to prolonged droughts will vary among tree species and within genotypes of the same species (Lucier *et al*., 2009). In arid and semi-arid lands, increased duration and severity of drought has increased tree mortality, resulted in degradation, and reduced distribution of forest ecosystems, including Cedrusatlantica forests in Algeria and Morocco (Bernier and Schoene, 2009). The indirect impacts also need addressing. When drought becomes a limiting factor for agriculture, there will be a tendency to shift to forests for crop cultivation, grazing and illicit harvesting of wood and other forest products, aggravating the loss of FGR (Bernier and Schoene, 2009).

Even small changes in climate are likely toaffect the timing and intensity of floweringand seeding events, which would in turn havenegative impact on forest biodiversity andecosystem services. Increased frequency andintensity of extreme events, such as cyclones,may result in shifts in species composition.Mangrove ecosystems are especially vulnerable,A projected sea-level rise poses great threat to the mangrove ecosystems.They could potentially move inlandto cope with sea-level rise, but anthropogenic pressures or the lackof necessary sediment would restrict their spread. Temperaturestress will also affect the photosynthetic andgrowth rates of mangroves (McLeod and Salm,2006). Climate change impacts are expected tobe severe in dry, high-temperature regions wheretrees are at their adaptive limit (Lindner *et al*., 2010) and in confined islands ofmoist forest that are surrounded by drier land (Williams *et al.*, 2003).

Choat *et al.* (2012) found that of 226 forest treespecies from 81 sites worldwide, 70 percent havenarrow safety margins in the event of injuriouslevels of drought stress and therefore couldface long-term reductions in productivity andsurvival if temperature and aridity increase aspredicted. While gymnosperms were found to bemore tolerant of reduced hydraulic conductivitythan angiosperms, safety margins were seento be largely independent of mean annualprecipitation, with all forest biomes equallyvulnerable to hydraulic failure and drought-inducedforest decline. These findings help toexplain why drought and increased heat areresulting in forest dieback across a broad rangeof forest and woodland types around the world (Allen, 2009). These dieback problems haveoccurred at a time when increases in temperaturehave been relatively modest, which does notbode well for forests given future temperaturepredictions. Under a scenario of a 4^{o}C increasein global temperature, greater mortality ratescan be expected as well as significant long-termregional drying in some areas.

Plasticity: Changed hydrological conditions associatedwith climate change include increases inseverity and duration of flooding, which can killwhole stands of trees. Even inundation-tolerant species, such as *Eucalyptus camaldulensis* and *Cocosnucifera*, are killed by water-logging ifthe trees have not been regularly exposed towater-logging and inundation through theirdevelopment. Inundation due to sea-level rise isbeginning to kill vegetation in coastal areas.In temperate and boreal regions, reduced snowcover, changed timing of snowmelt and shorterfrost periods are contributing to forest changesand stresses.

Changes in phenology: In FGR, changesin the climate could have an impact on seedproduction; asynchronous timing betweenflower development and the availability ofpollinators could result in low seed productionfor out-breeding species that depend on animalvectors. Pollinators worldwide are being affectedby climate change, and this will likely have a majordetrimental impact on breeding systems and seedproduction, with consequences for forest healthand regeneration.

Invasives: A changing climate also provides theopportunity for some plant species moresuited to a wide range of climate conditionsto invade new areas (Dukes, 2003). The spreadof *Leucaena* spp. and *Eupatorium* spp. is known to have adverseimpacts on biodiversity in subtropical forests inIndia. In addition to new species invasions,changing climates will result in altered patternsof gene flow and the hybridization of speciesand populations. Shifting ecological niches willincrease the risk of invasion by more competitivetree species that are more precocious or can movemore quickly than the present species. Invasionsof new genes via pollen and seed dispersal maydisrupt local evolutionary processes, but couldalso be a welcome source of new adaptive traits (Hoffmann and Sgro, 2011).

Changes in tree physiology: Teak (*Tectona grandis*), which is native to south and southeast Asia, but is now grown throughout the tropics for its valuable wood, is especially sensitive to changes in temperature and moisture. This sensitivity is reflected in the development of wood and tree rings, and has led to teak's widespread use in dendrochronology for the reconstruction of past climate, particularly rainfall, throughout south Asia (Jacoby and D'Arrigo 1990; Sinha 2012). Changes in rainfall and moisture availability may therefore affect the development of cambium and the quality or grain of teak wood. Teak is also grows faster than other hardwoods and has been estimated to store 2 MgCha^{-1} yr^{-1} of atmospheric carbon (Kaul *et al.*, 2010).

Shift in ranges: Bamboos are also increasingly important plants to the global economy. However, with a warming global climate the natural limit of bamboo forests is expected to move northward (Rui 2002), which may open up new areas for the cultivation of these unique grasses. Although bamboo can form dense tall stands throughout much of the Asia Pacific, bamboo forests do not store carbon effectively. Rather mature stands are in equilibrium between carbon taken up for growth, and carbon released from stem death and decomposition (Düking *et al.*, 2011).

6. Adaptations of FGRs to Climate Change

Climate change adaptation includes carbon management as a part of the forest management paradigm. Kaul et al. (2010) found that in the teak and sal (*Shorearobusta*) forests of India, the length of rotation and the thinning regime utilised by forest managers can influence the carbon stored by forests and the value of timber harvested. For instance maximum primary productivity was seen at 60-year rotations, but declined as the rotation length was extended. However average carbon stock increased by approximately 12% when rotation length was increased from 120 years to 150 years.

The ability of a tree species to survive the current rapid climate changes will depend on its capacity to adapt quickly to new conditions at existing sites, to survive changing conditions through a high degree of phenotypic plasticity without any genetic change, and/or to migrate to an environment with the desired conditions for that species.

A number of climate-related traits, such as the timing of bud break in spring, leader shoot growth cessation in summer, bud set in autumn and annual ring lignification, are regulated by temperature during female reproduction; temperature-induced regulation of the level of gene expression in the developing embryos is apparently maintained in the developing trees as an "epigenetic memory". Many such epigenetic responses have been documented in plants exposed to environmental stresses (Madlung and Comai, 2004), but the mechanisms involved are not fully understood.

7. Gaps in knowledge (FAO, 2011)

- Adaptive potential of traits of importance under climate change and the underlying genetic mechanisms: Field and nursery experiments to understand patterns of variation; harness genomic tools to improve understanding of genes that are important in drought tolerance and resistance, flood tolerance, phenology, response to elevated CO_2 levels, etc. Transfer of knowledge obtained from model species in temperate regions to less known "local" species that are of high importance to people in the developing world.
- The degree of phenotypic plasticity and its underlying genetic and epigenetic basis: Phenotypic characterization through more field trials designed to understand impacts and responses to environmental changes.
- Effect of changes in interspecific competition and reproductive potential in relation to changing growth rhythms as temperature changes but photoperiod stays constant. Small-scale assisted migration operations should be carried out and monitored to determine whether the expected disconnect between temperature regimes and photoperiod can be mitigated by mixing genetic sources and allowing natural selection
- Population dynamics and environmental limits for pollinator species: In all areas where trees depend on pollinator species, action is needed to understand and respond to threats.
- Species distributions and effects of fragmentation on gene flow: Map species distributions, accounting for rapidly expanding agricultural land and other developments, and considering historical data; develop predictive models that take into account life-history characteristics, the effects of fragmentation and levels of gene flow, in different parts of a species range.

- Requirements for maximizing productivity of trees in agricultural landscapes under changing climate: Develop a portfolio of varieties that have phenotypic plasticity and that perform well across a range of environments (national/ regional level)
- Past and current flows of germplasm, including quantities, origin of material and survival at the destination: Improve documentation of germplasm flows, molecular typing of origin.
- Design of effective germplasm delivery systems for large-scale plantation establishers and smallholders: Improve international transfer of germplasm to make available high-quality site-matched planting material of high-value trees to planters, with a broad genetic base to ensure adaptive potential. Improve linkages between international exchange and smallholders through revitalizing the role of national tree seed centres in developing countries
- Cultivation requirements of currently or potentially useful species: Improve access to information through education and training.
- Regions where high genetic diversity and significant threats coincide: Implement risk assessments and threat analyses to identify coincidence. Prioritize conservation of populations on the basis of importance to people, high diversity and significant threat.
- Most effective mix of *in situ, circa situ* and *ex situ* approaches to ensure conservation and maintain evolutionary processes: Increase population representation and genetic diversity of important and threatened species in conservation areas, in farmland and in seed collections.
- Seed storage behaviour and germination requirements for many important species: New approaches for “gene-banking” for many tropical species through seed physiology research, cryopreservation, pollen storage, etc. Active conservation measures are needed for species that are important for human well-being and are seriously threatened.
- Costs and benefits of FGR conservation: Application of economic valuation approaches developed for other sectors to FGR, with an emphasis on high-value species for foresters and small-scale farmers.

8. Approaches to develop resilient FGRs

Under changing environmental conditions, trees must first survive and then reproduce. To be useful to humans, they must also continue to produce the products and services for which they are valued. Some important traits needed for adaptation to different climatic conditions, but which are not often considered in breeding programmes include the following:

Drought resistance: This is a complex trait that may include deep rooting systems, water use efficiency and deciduous habit. For many tree species, altered moisture regimes will be of greater concern than temperature changes. Information on these aspects would prove useful.

Pest resistance: Pest and disease resistance has received little attention in tree breeding. Climate-change mediated changes in pest and disease attacks are becoming a crucial issue in plantation forestry (Yanchuk and Allard, 2009).

Fire resistance/tolerance: Increased fire frequency results from decreased precipitation and elevated temperatures combined with human activities such as forest clearance (Malhi *et al.*, 2009). Many tree species growing in semi-arid regions have developed mechanisms to confer a degree of resistance to periodic fires, but this may not be the case in more humid forest. Increased fire frequency will require adaptations such as thicker bark.

Cyclone resistance/salt tolerance: The combined effects of a rising sea level and increased storm frequency have the potential to wreak heavy damage on coastal forests. A differential ability to withstand storms and salt may be found more commonly among species than within, but the possibility of selection for suitable types within species needs to be explored.

Phenotypic plasticity: This information is vital for an adaptive response to changing climate and can vary at intraspecific level.

Conclusion

The forest departments, research organizations and other stakeholders handling the forest genetic resources in association with other government departments have to contribute to management and conservation of FGRs through an integrated approach (MoEF, 2009). The areas that need urgent attention in FGR conservation and management are:

i) Integrated database development at all organizational and management levels, to effectively utilize the data for decision making and establishment of a national information system
ii) skill development at all levels,especially related to new biotechnologies, benefit sharing mechanisms, tools in monitoring FGR diversity
iii) Develop modelling for economically important and threatened species due to climate change
iv) monitoring and assessing biodiversity for representative landscapes on long term continuous basis
v) Study genetic diversity, gene flow, seed characteristics and regeneration
vi) Establish tree species with mixed mating system
vii) Develop *ex situ* conservation stands, seed bank, field gene bank etc for FGR prioritized species
viii) elimination of invasive alien species, that threaten the diversity
ix) incentives for sustainable utilization of resources
x) sustained research on genetic diversity

Forestry is one of the biological sciences whose study can contribute to a better understanding of the role of forests in climate change mitigation. There is a need for an integrated approach to study the problem cutting across disciplines of physical, social, biological, health and engineering sciences for sustaining the FGRs for posterity.

Summary

Broadly, the climate change research on FGRs can be grouped into Climate change modeling, mitigation and adaptation.

i. Climate change modelling

- In addition to global models, development of regional models are required at finer spatial resolutions for decisions at micro-level. Besides the primary variables of temperature and precipitation, information on secondary variables like heating degree days, heat index, starting and ending days of seasonal monsoon rainfall, storm surge, need to be incorporated in the model.
- In order to tackle natural hazards, physico-chemical stresses faced by plants, pest and disease spectrum, species migration, there is a necessity for GIS based framework for risk assessment and to assist in decision making on spatio-temporal scale.
- Impact assessment and modeling taking all relevant factors including socio-economic impact assessment is essential to take the required measures for mitigation.

ii. Mitigation

- Integration of low-rainfall species into farming systems will provide green cover as well as insurance in case of failure of agriculture.
- Production of electricity using woody biomass, will help in reducing the use of fossil fuels. The plantation that is cut for production of biomass can again be regenerated for sequestration of more carbon. Species suitable for high-density plantation can be raised as energy plantations for providing the feedstock for power generation.
- Quantification of impacts of management practices on soil carbon dynamics due to agronomic practices and irrigation are required for optimizing the management practices for efficient carbon sequestration in soils.
- Development of improved models of sequestration is required on the basis of carbon sequestered, with a view to enhance the sequestration potential.
- Quantification carbon fixed in timber and timber products that are maintained for longer durations is essential.
- Methods have to be developed for inclusion of wood products in carbon trading.

iii. Adaptation

- New varieties that are climate change ready have to be developed through conventional breeding or molecular breeding. Breeding for increased tolerance to water stress, improved nutrient use efficiency is the ‘need of the hour’.
- Selection of broad leaved species tolerant to high temperature for CO_2 exchange and other physiological mechanism is important.
- Breeding for tolerance/ resistance to pests and diseases may also become necessary. As there may be an increase in intensity and distribution range of pests and diseases.
- Interactive effects of increased carbon dioxide and water/ nutrient deficiency need further study with changing climate.
- The anticipated beneficial effects of elevated carbon levels on grass land productivity may increase the population of herbivores, which can pose a threat to the regeneration of forests. The weeds showing phenotypic plasticity may increase in their invasive potential and expand the range. These are required to be studied for appropriate remedial action.

B. Forest Health Towards Climate Resilience

Introduction

Forests are subjected to a variety of disturbances that are themselves strongly influenced by climate. Disturbances such as fire, drought, landslides, species invasions, insect and disease outbreaks, and storms such as hurricanes, windstorms and ice storms influence the composition, structure and function of forests (Dale *et al.*, 2001). Climate change is expected to impact the susceptibility of forests to disturbances and also affect the frequency, intensity, duration, and timing of such disturbances. Increased temperatures and high levels of carbon dioxide in the atmosphere along with changes in precipitation are having notable impacts on the condition of the world's forests, They affect the frequency and severity of extreme weather events by making winters warmer or affecting the length of growing seasons. Such climate change events can affect forest pests and the damage they cause by directly impacting their development, survival, reproduction and spread; altering host defences and susceptibility; and indirectly impacting ecological relationships such as changing the abundance of competitors, parasites and predators. Insects and diseases may be the first indicators of climate change.

All of these impacts on trees and forests will inevitably have widespread impacts on the forest sector. Changes in the structure and functioning of natural ecosystems and planted forests due to climate changes will have negative impacts on the productive function of forest ecosystems which in turn will affect local economies (FAO, 2005). Decreased forest ecosystem services, especially water cycle regulation, soil protection and conservation of biological diversity, as a result of climate change may imply increased social and environmental vulnerability. While climate change is likely to increase timber production and lower market prices in general, the increases in production will certainly not be evenly distributed throughout the world; some areas will experience better conditions than others (Pérez-García *et al.*, 2002). For example, forests with low productivity due to drought will likely face further decreases in productivity, while areas where temperature limits productivity may benefit from rising temperatures.

Research has suggested that insect outbreaks can significantly affect the carbon sink or source status of a large landscape. Thus preventing and reducing pest impacts on forests would provide an opportunity to mitigate climate change. Management of pests and prevention of their spread ensure that forests remain healthy, reducing the risk of forest degradation and increasing resilience to climate change.

As forests are very stable ecosystems in time, a study of the evolution of the forests could help to understand the effects of climate change. Holling (2001) notes that an adaptive capability to climate change is a necessary component of sustainability, whereas other researchers have determined that forest health is mainly affected by environmental stress, as critical ozone levels, meteorological stress factor, air pollution stress,critical deposition level or nutrient deficiencies (Garcia *et al.,* 2001). Indicators of sustainable forest management and forest health indicators could be used for climate change assessment (Ferretti, 1997).

Increased fuel loads, longer fire seasons and the occurrence of more extreme fire weather conditions as a consequence of a changing climate are expected to result in increased forest fire activity (Mortsch, 2006). A changing climate will also alter the disturbance dynamics of native forest insect pests and pathogens, as well as facilitating the establishment and spread of non indigenous species. Such changes in disturbance dynamics, in addition to the direct impacts of climate change on trees and forest ecosystems, can have devastating impacts particularly because of the complex relationships between climate, disturbance agents and forests. Any of these disturbances can increase forest susceptibility to other disturbances.

1. Impacts of climate change on forest pests

Changes in the patterns of disturbance by forest pests (insects, pathogens and other pests) are expected under a changing climate as a result of warmer temperatures, changes in precipitation, increased drought frequency and higher carbon dioxide concentrations. These changes will play a major role in shaping the world's forests and forest sector.

Climate change can exacerbate invasions of forest pests as well as impacts of native pests. For example, climate change can facilitate the range expansion of both native and exotic pests (insects and pathogens), or affect tree resistance to pests (Jactel *et al*., 2012a), and there is increasing evidence that this is a widespread phenomenon (Anderegg *et al.*, 2015). There is evidence in the fossil record that previous episodes of rapid global warming were accompanied by increased levels of insect herbivory (Currano *et al.*, 2008).

Insects and pathogens have been noted to respond to warming in all the expected ways, from changes in phenology and distribution to influencing community dynamics and composition (Menéndez, 2007). While some impacts of climate change may be beneficial in terms of protecting forest health (e.g. increase winter mortality of some insect pests due to thin snow cover; slower larval development and increased mortality during droughts), many impacts will be quite detrimental (e.g. accelerated insect development rate; range expansions of pests) (Ayres and Lombardero, 2000).

Climate change can affect forest pests and the damage they cause by: directly impacting their development, survival, reproduction, distribution and spread; altering host physiology and defences; and impacting the relationships between pests, their environment and other species such as natural enemies, competitors and mutualists.

2. Direct impacts

Climate, temperature and precipitation in particular, have a very strong influence on the development, reproduction and survival of insect pests and pathogens and as a result it is highly likely that these organisms will be affected by any changes in climate. Because they are cold-blooded organisms, forest insects and pathogens can respond rapidly to their climatic environment impacting directly on their development, survival, reproduction and spread. With their short generation times, high mobility and high reproductive rates it is also likely that they will respond more quickly to climate change than long-lived organisms, such as higher plants and mammals (Menéndez, 2007) and thereby may be the first predictors of climate change.

Physiology: Climate influence on insects can be direct, as a mortality factor, or indirect, by influencing the rate of growth and development. Some information on the impacts of increased CO_2, and O_3, is becoming available but only for specific environments (Karnosky *et al.*, 2008) and only very partial information is available on changing UVB levels and altered precipitation regimes.

Temperature is considered to be the more important factor of climate change influencing the physiology of insect pests (Bale *et al.*, 2002). Precipitation however can be a very important factor in the epidemiology of many pathogens that depend on moisture for dispersal. Flexible species that are polyphagous, occupy different habitat types across a range of latitudes and altitudes, and show high phenotypic and genotypic plasticity are less likely to be adversely affected by climate change than specialist species occupying narrow niches in extreme environments (Bale *et al.*, 2002).

Increases in summer temperature will generally accelerate the rate of development in insects and increase their reproductive capacity while warmer winter temperatures may increase over winter survival (Ayres and Lombardero, 2000).Decreased snow depth associated with warmer winter temperatures may also decrease the winter survival of many forest insects that overwinter in the forest litter where they are protected by snow cover from potentially lethal low temperatures (Ayres and Lombardero, 2000).The impact of a change in temperature will vary depending on the climatic zone. In temperate regions, increasing temperatures are expected to decrease winter survival while in more northern regions, higher temperatures will extend the summer season thereby increasing growth and reproduction (Bale *et al.*, 2002).

However, Deutsch *et al.* (2008) suggested that, in the absence of ameliorating factors such as migration and adaptation, the greatest extinction risks from global warming may be in the tropics. Warming in the tropics, though proportionately smaller in magnitude, could have the most deleterious impacts because tropical insects have very narrow ranges of climatic suitability compared to higher latitude species, and are already living very close to their optimal temperature.

Some important forest insect pests have critical associations with symbiotic fungi but limited information is available on how temperature changes may affect these symbionts and thus indirectly affect host population dynamics. In some cases insect hosts and their symbionts may be similarly affected by climatic change while in other cases, hosts and symbionts maybe affected asymmetrically, effectively decoupling the symbiosis (Six, 2007).

Species Distribution**:** Climate plays a major role in defining the distribution limits of insect species. With changes in climate, these limits are shifting as species expand into higher latitudes and altitudes and disappear from areas that have become climatically unsuitable (Menéndez,2007). Such shifts are occurring in species whose distributions are limited by temperature such as many temperate and northern species. It is now clear that poleward and upward shifts of species ranges have occurred across many taxonomic groups and in a large diversity of geographical locations during the 20th century.

Parmesan and Yohe (2003) reported that more than 1700 Northern Hemisphere species have exhibited significant range shifts averaging 6.1 km per decade towards the poles (or 6.1 m perdecade upward).Climate change may also weaken the association between climatic and habitat suitability. Forest pests are also occurring outside historic infestation ranges and at intensities not previously observed. There is increasing evidence in the literature that insect species are changing their genetic makeup in response to climate change.

Some examples of forest pest species that have responded or are predicted to respond to climate change by altering distribution include the following.

- The outbreak of *Leptocybeinvasa*, gall infestation in eucalypts species in India is a befitting example of this.
- Climate change, which is clearly felt in the traditional rubber growing regions of India, may possibly alter the host-pathogen interactions leading to epidemics of otherwise minor diseases (Narayanan and Mydin, 2012).
- A major epidemic of the mountain pine beetle (*Dendroctonusponderosae*) has been spreading northwards and upwards in altitude in western Canada (British Colombia andmore recently, Alberta) for several years.
- Jepsen *et al*. (2008) give ample evidence of northward outbreak range expansions of twogeometrids (winter moth, *Operophterabrumata*, and autumnal moth, *Epirritaautumnata*)in Scandinavia.

- The pine caterpillar (*Thaumetopoeapityocampa*) has significantly expandedits latitudinal and altitudinal distribution in Europe.
- The European rust pathogen *Melampsoraallii-populina*is likely to spread northwards with increased summer temperatures.

The ability of a species to respond to global warming and expand its range will depend on a number of life history characteristics, making the possible responses quite variable among species. Range-restricted species show more severe range contractions than other groups and are considered most at risk of extinction due to recent climate change (Parmesan, 2006). Range shifts may be limited by factors such as day length or the presence of competitors, predators or parasitoids (Walther *et al.*, 2002).

Phenology

Phenology is the timing of seasonal activities of plants and animals such as flowering or breeding. It is mostly temperature dependent; hence phenology can be expected to be influenced by climate change. It is one of the easiest impacts of climate change to monitor (Gordo and Sanz, 2006) and by far the most documented for a wide range of organisms (Root *et al.*, 2003). Common activities to monitor include earlier breeding or first singing of birds, earlier arrival of migrant birds, earlier appearance of butterflies, earlier choruses and spawning in amphibians and earlier shooting and flowering of plants (Walther *et al.*, 2002).Evidence of phenological changes in plants as a consequence of climate change is abundant and growing (Menzel*et al.*, 2008).

In a review of phenological changes of interacting species, Visser and Both (2005) noted that insects have advanced their phenology faster (early eggs hatching and early migration return date) than their hosts (bud burst and flowering). They have also advanced their period of peak abundance more than their predators (laying date and migration arrival of birds). The disruption of synchrony between the winter moth (*Operophterabrumata*) hatching and bud burst of its host oak trees has in turn resulted in an asynchrony between the pest and one of its predators, the great tit (*Parus major*), which relies on the caterpillars to feed their young (van Asch *et al.*, 2007). Such climate induced phenological changes are clearly resulting in a great deal of asynchrony between interacting species which will ultimately influence community structure, composition and diversity.

Where insect life cycle events are temperature-dependent, they may occur earlier and increased temperatures are likely to facilitate extended periods of activity (Harrington, *et al.*, 2001). With increased temperatures, it is expected that insects will pass through their larval stages faster and become adults earlier. Therefore expected responses in insects could include an advance in the timing of larval and adult emergence and an increase in the length of the flight period (Menéndez, 2007). Members of the order Lepidoptera again provide the best examples of such phenological changes. Gordo and Sanz (2005) investigated climate impacts on four Mediterranean insect species (a butterfly, abee, a fly and a beetle) and noted that all species exhibited changes in their first appearance date over the last 50 years which was correlated with increases in spring temperature.

Parmesan and Yohe (2003) estimated that more than half (59 percent) of 1598 species investigated exhibited measurable changes in their phenologies and/or distributions over the past 20 to 140 years. They also estimated a mean advancement of spring events by 2.3days/decade based on the quantitative analyses of phenological responses for these species. Root *et al.* (2003), in a similar quantitative study, estimated an advancement of 5.1 days per decade. Parmesan (2007) investigated the discrepancy between these two estimates and noted that once the differences between the studies in selection criteria for incorporating data was accounted for, the two studies supported each other, with an overall spring advancement of 2.3 to 2.8 days/decade found in the resulting analysis.

***Activity and abundance of natural enemies*:** Relationships between insect pests and their natural enemies will change as a result of global warming, resulting in both increases and decreases in the status of individual pest species. Changes in temperature will also alter the timing of diurnal activity patterns of different groups of insects, and changes in inter-specific interactions could also alter the effectiveness of natural enemies for pest management (Hill and Dymock 1989).

Quantifying the effect of climate change on the activity and effectiveness of natural enemies will be a major concern in future pest management programs. The majority of insects are benign to agro-ecosystems, and there is much evidence to suggest that it is due to population control through interspecific interactions among insect pests and their natural enemies (pathogens, parasites, and predators). Oriental armyworm, *Mythimnaseparata* (Walk.) populations increase during extended periods of drought (which is detrimental to the natural enemies), followed by heavy rainfall (Sharma *et al.*, 2002). Aphid abundance increases with an increase in CO_2 and temperature, however, the parasitism rates remain unchanged in elevated CO_2. Temperature not only affects the rate of insect development, but also has a profound effect on fecundity and sex ratio of parasitoids (Dhillon and Sharma 2009). The interactions between insect pests and their natural enemies need to be studied carefully to devise appropriate methods for using natural enemies in pest management.

Plant–pollinator interactions under climate change

Tree-pollinator interactions are important ecosystem services that are threatened by global warming and climate change. Pollinators such as birds, bees, butterflies, moths, flies, wasps, beetles bats and even mosquitoes are essential for food production because they transfer pollen between seed plants-impacting 35% of the world's crops. Among the pollinator groups, bees have been considered a priority group. Bees are synonymous with insect pollinators and they are publicly shared assets, most species and populations belonging to nobody, yet benefiting all of us through pollination – a perfect example of 'positive externality', in economic parlance (Batra, 1995). According to Gallai *et al*., 2009, more than 40 % of honey bees have been disappeared during last 25 years in India.Solitary bees and other insect pollinators play a great role in the pollination of wild plants. They also pollinate many cultivated plants. There is a lack of data on many invertebrate species that act as pollination agents. Many pollinator species that were relatively rare in the past are becoming rarer, while more common species have become widespread. The loss of bee pollinators is becoming a reality as reports all over the world have pointed out that most pollinator populations have declined to levels that cannot sustain their pollination services in both agro-ecosystems and natural habitats. European honeybees in North America have suffered dramatic declines (up to 50% of managed colonies) (Kraus and Page, 1995).

Research activities in India on bees or on other pollinators are in a state of neglect. Despite the global worry, no study had been done to assess directly the scale of the decline in natural pollinators. In India at present, one hundred and fifty million colonies are needed to meet the pollination requirement of around 50 million hectare bee dependant crops but there are only 1.2 million colonies present (TNAU agritech portal). On a global level, the Convention on Biological Diversity has identified the importance of pollinators with the establishment of the International Initiative for the Conservation and Sustainable Use of Pollinators (also known as the International Pollinators Initiative-IPI) in 2000, facilitated and coordinated by FAO.

International Pollinators Initiative includes a project involving seven nations (including India) with the aim of identifying practices and building capacity in the management of pollination services.

3. Indirect impacts

Changes in temperature, precipitation, atmospheric CO_2 concentrations and other climatic factors can alter tree physiology in ways that affect their resistance to herbivores andpathogens (Ayres and Lombardero, 2000).

Elevated CO_2 levels can also result in changed plant structure such as increased leaf area and thickness, greater numbers of leaves, higher total leaf area per plant, and larger diameter stems and branches (Garrett *et al.*, 2006). An increase in defensive chemicals may also result under such conditions (van Asch and Visser, 2007). Either of these changes to host physiology would influence palatability to insects, though the impacts on pests differ by species. Under increased CO_2 levels the winter moth (*Operophterabrumata*) consumes more oak (*Quercusrobur*) leaves due to a reduction in leaf toughness, while the gypsy moth (*Lymantriadispar*) exhibits normal pupation weight but requires a longer time to develop as a result of an increase in tannin concentrations (van Asch and Visser, 2007).

Drought: Drought is one of the most important climate-related events through which rapid ecosystem changes can occur as it affects the very survival of existing tree populations. Long-term drought can result in reduced tree growth and health thereby increasing their susceptibility toinsect pests and pathogens. A number of insect pests and pathogens are associated with stressed trees, such as *Agrilus*beetles and the common and widespread *Armillaria* species which have been linked to oak decline (Evans, 2008).

Drought can also elicit changes in plant and tree physiology which will impact pest disturbance dynamics. Leaves may change colour or become thicker or waxier which could affect their palatability to insects (Harrington et. al., 2001). The concentration of a variety of secondary plant compounds tends to increase under drought stress which would also lead to changes in the attraction of plants to insect pests. Moderate drought however may actually increase production of defense compounds in plants and trees possibly providing increased protection against pests.

Sugar concentrations in foliage can increase under drought conditions making it more palatable to herbivores and therefore resulting in increased levels of damage (Harrington *et. al.*, 2001). Increases in the sugar content in drought-stressed balsam fir for example have been known to stimulate the feeding of certain stages of spruce bud worm(*Choristoneura fumiferana*) and accelerate their growth (Mortsch, 2006). Another advantage for forest pests is the increased temperature of drought-stressed trees, which can be 2 to 4 °C warmer, which can benefit the fecundity and survival of insects (Mortsch, 2006).

The impacts of such changes to host tree physiology and susceptibility provoke different responses from pest species. Rouault *et al.* (2006) investigated the impacts of drought and high temperatures on forest insects and noted that woodborers were positively influenced by the high temperatures which increased their development rates and the prolonged water stress that lowered host tree resistance while defoliators benefited from the increased nitrogen in plant tissues linked to moderate or intermittent water stress. The large natural spatial and temporal variability in forest processes makes it difficult to positively relate drought-related tree mortality to a greater incidence of insect pest or fungal pathogen damage.

Elevated levels of atmospheric carbon dioxide result in improved growth rates and water use efficiency of plants and trees. This increased productivity leads to lower nitrogen concentrations in trees and plants as carbon-nitrogen (C: N) ratios rise and thus reduces the nutritional value of vegetation to insects (Mortsch, 2006). In response insects may increase their feeding (and consequently tree damage) in an attempt to compensate for the reduced quality and gain the necessary nitrogen (Ayres and Lombardero, 2000). In many cases the increased feeding does enable the insect to meet its nutritional needs but most often it does not and results in poor performance, reduced growth rates and increased mortality (Harrington *et al.*, 2001). Suchan effect, however, is not consistently observed, and increased growth due to enhanced CO_2 may in fact more than compensate for the defoliation in some cases (Kopper and Lindroth, 2003).

Extreme events**:** Besides drought, climate change may affect the frequency and intensity of other extreme climate-related events, with subsequent impacts on forest health. Direct damage to trees or alterations in the ecosystem may increase their susceptibility to pest outbreaks. Climate change also being associated with increased warm air mass movements towards high latitudes, the frequency and extent of long-distance windborne dispersal events are likely to increase, as was observed in a recent influx of diamondback moths on Svalbard Island in Norway, 800 km north of the likely source population in the Russian Federation (Coulson *et al.*, 2002).

Impacts on community ecology: Distributional changes and range shifts interfere with community relationships as expanding species will begin to interact with other species in new environments with which previous interaction may have been limited or non-existent (Menéndez, 2007).Species capable of responding to climate change by increasing their range will also benefit from the lack of competitors and natural enemies in their new environment. Species expansions may not be promptly followed by that of its natural enemies (Battisti, 2004).Some pathogens may benefit from the improved survival and spread of their insect vectors.

Conclusion

It is likely that changing temperature and precipitation pattern due to climate change will produce a strong direct impact on the health of both natural and man modified forests. The climate change-induced modifications of frequency and intensity of forest wildfires, outbreaks of insects and pathogens, and extreme events such as high winds, may be more important than the direct impact of higher temperatures and elevated CO_2. Increased tree cultivation in private lands and development of urban forests are on the rise and therefore, there is a clear need for extensive research in India in the following line in future,

- Behavioural assessments of forest health agents (Insect pests, pathogens both native and invasive species, natural enemies, pollinators, litter inhabiting fauna and flora) in forests and plantations of economically important tress species.
- Development of pest management strategies for dealing with future pest adaptations to climate change.
- Strengthening Plant Quarantine to meet the new challenges emerging due to the increased risk and frequency of global trade-driven international pest movement with changing climatic situations.
- Development of pest/disease tolerant trees identified through breeding programmes as an alternative management practices to reduce subsequent vulnerability of plantation trees due to climate change.

Summary

- The challenge to understanding climate change impacts is not just in obtaining information on the impacts of temperature, precipitation and other climatic factors on forests and pests but also acquiring knowledge on the interaction between the different climate change factors, and how climate change impacts disturbances and *vice versa*.
- Knowledge derived from the pests' ability to adapt to climate shifts in their area of origin may be a useful management tool but it is considered that increased opportunities for pests to encounter new and suitable eco-climatic zones for establishment will result in many new infestations and challenges in forest pest management. The forest sector needs effective monitoring and detection activities to allow for quick action in the face of changing or increasing pest outbreaks including continual pest risk assessments. There is also a need for alternative practices to reduce subsequent vulnerability of forests, such as planting pest tolerant trees identified through breeding programmes; noting however that it is unlikely that such programmes can predict new pest risks in a timely fashion due to shifting species adapting to new environments. Comprehensive risk assessments as well as enhanced knowledge management systems using a variety of information technologies such as simulation models, geographic information systems (GIS) and remote sensing could also play a role in protecting forest health from the impacts of climate change and forest pests.
- While a fair amount of information is already available concerning the impacts of climate change on the world's species and ecosystems, from the perspective of forests, considerably more information is needed on the impacts on forests, forest pests and the complex relationships relating to climate change. Much of the information available comes from Europe and America. India is yet to generate reports on this aspect. There is also scant information available on the effect of climate change on symbionts and host dynamics. Further detailed studies of important forest pests would allow for the development of pest management strategies for the future and assist forest managers and policy-makers to better prepare for the challenge of dealing with climate change and provide insights into future pest adaptations to climate change.

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Climate Change and Forest Genetic Resources

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Introduction

Forest genetic resources (FGRs) refer to the heritable materials maintained within and among tree and other woody plant species that are of actual or potential economic, environmental, scientific or societal value. A population of a particular tree species comprises all the individuals of that species in the same geographical area and genetically isolated from other populations of the same species. Trees and other woody species differ from other organisms in several key respects. Forest tree species are generally perennial, long-lived and have developed natural mechanisms to maintain high levels of genetic variation within species. They include high rates of outcrossing and often long-distance dispersal of pollen and seed. These mechanisms, combined with native environments that are often variable, have enabled forest tree species to develop into some of the most genetically diverse organisms in existence. For long-term survival at a particular site, they need to be able to endure environmental extremes and changes and/or to persist in the soil seed bank or regrow from root suckers and coppice. The high genetic diversity that characterizes tree populations and individuals, and associated stress tolerance and disease resistance mechanisms, help explain their capacity to persist and thrive for long periods. Trees are notable for their diverse breeding and reproductive systems, which are in turn major determinants of spatial patterns of tree species genetic diversity. Most tree species reproduce sexually, although many have a combination of sexual and asexual reproductive means, while a few have lost the ability to reproduce sexually and are maintained as sterile, root-suckering clones in certain parts of their range. Climate change poses a major threat to forestry, biodiversity, agriculture and food security through extreme climatic events, droughts, increases in temperature, more frequent and intense wildfires, and increased activity of pests and alien invasive weeds. It will be increasingly vital to provide the deepest possible reservoir of genetic variability on which natural and artificial selection can act, facilitating adaptation to changed conditions.

Globally, deforestation has contributed significantly to climate change by releasing carbon dioxide into the atmosphere and reducing the production of oxygen. Several countries have taken significant steps in conserving the genetic resources of forest trees. However, they have rarely taken into account the implications of climate change for the conservation of forest genetic resources. Climate change poses unique conservation challenges that require specific responses. Globally forests have been expanding in terms of area and timber stock and subsequently they have acted as a carbon sink while they have been recovering from previous eras of deforestation. The impacts of climate change on forests, and especially on their genetic diversity have not been given proper consideration in forest management policies. Several recommendations for action have been put forth. These focus on establishing additional genetic conservation units specifically to respond to climate change, enhancing cooperation among countries and enlarging collaboration on the conservation of forest genetic resources, the need for continued and expanded monitoring and sharing of data, including the development of decision tools and red lists within each nation, and further research on aspects of assisted migration and on marginal and peripheral tree populations.

Genetic diversity is a key component of resilience and adaptability. Overall, forest tree populations are genetically very diverse, conferring them an enormous potential for genetic adaptation via the processes of gene flow and natural selection. Recent progress in genetics can contribute to the development of appropriate practical actions that forest managers and policy makers can adopt to promote forest resilience to climate change. Gaps in our knowledge remain, and we identify where additional information is needed (e.g., the adaptive value of peripheral populations or the genetic determinism of key adaptive traits) and the types of studies that are required to provide this key understanding.

No worthwhile paper could be seen on forest genetic resources in relation to climate change or resilience in the Indian context. Majority of papers involved assessment of climate change impacts or the sensitivity or vulnerability of forests to climate change and some considered adaptation. This paper attempts to focus on forest genetic resources (FGRs), and it does so in the context of trees in natural forests, plantations and agroforestry systems (Rodney, 2015).

The context

Forest trees are long-lived species that are genetically very diverse. Trees have developed natural mechanisms to maintain high levels of genetic variation and reduce inbreeding, e.g. through long-distance dispersal of pollen and reproduction among unrelated distant individuals. Because native tree individuals with a particular genetic make-up occupy very diverse environments, these mechanisms have maintained high levels of genetic variability within forest trees despite strong selection. Climate change is expected to have a significant impact on forests, causing changes in the geographic distribution of species, ecosystem functioning and interactions between species. Given the long lifespan of trees, fast local adaptation will largely depend on the genetic variability available within and among tree stands and populations. High levels of genetic diversity are thus beneficial as they allow individual trees and populations to adapt more easily to environmental changes.

Challenges facing Indian forests

Forests face major challenges from climate change and various native and exotic pests. In particular, it is the uncertainty in predicting the nature and impacts of these threats that is hampering efforts to plan mitigation. Despite a huge amount of modelling aimed at predicting the likely pattern, speed and intensity of climate change, there is still great uncertainty in forecasts of the magnitude of change at specific locations and the ability of our forest resources to cope with them. Similarly, whilst many new disease causing pests have been identified as present in India, perhaps the greater threat lies in those that are present but have not yet been identified and those that have yet to arrive. There are numerous examples where introduced pathogens have led to mass destruction of tree species elsewhere in the world, e.g. chestnut blight (Jacobs et al., 2013) and white pine blister rust (Kinloch, 2003) in North America.

The interaction of virulent exotic pests with native trees coupled with climate change could operate in several ways. This can induce maladaptation to changing future conditions. Trees that are stressed may be more likely to succumb to both native and introduced pests and diseases.

There will be altered balance between tree host and existing pests. For example, rising temperatures may affect the synchrony between herbivore emergence and bud burst. Changed climates cause species that were not previously damaging to develop into threats or facilitate the establishment of new species from other warmer countries.

Genetic variation and the phenotypic plasticity found in forest tree populations provide the means to cope with the new challenging conditions. Most genetic studies to date indicate that there is a large amount of heritable adaptive variation available in tree species on which natural selection can operate. Thus, the rather dramatic predictions made by climate envelope models of large-scale changes in forest distribution within the coming decades require reassessment and refinement to include genetic processes. However, adaptive potential depends on the species and local ecological conditions and demographic constraints could severely limit the capacity of populations to develop under the most severe climate changes. Thus, although usually appropriate, management scenarios based solely on locally existing forest material and genetic resources may be hazardous particularly at range and ecological edges (Bruno Fady et al., 2015). The task of monitoring to determine whether the native species in natural woodlands are currently at risk under climate change is vital. A lack of genetic adaptation and demographic collapse can drive populations to extinction. Determining which genetic and demographic thresholds will lead to maladaptation is crucial to make informed management decisions, particularly in forests where, despite predictions, evidence of decline due to climate change is not yet strong. This can be achieved by genetic monitoring. Monitoring the potential of forests to adapt genetically under climate change is necessary over broad areas to inform management. Monitoring based on parameters used in classical forest management (such as adult age classes, seedling density and presence of pests) can now be coupled with molecular genetics assessment methods to provide early warning signs of maladaptation risks (Bruno Fady et al., 2015). Assisted migration can be the answer for managing forests and their habitats under climate change. When sound evidence suggests that current genetic resources at a site will cease to offer an appropriate option under future climate, and introduction of non-local resources is being considered. One type of assisted migration concerns the sourcing of seed and planting stock and can take two forms: the use of exotic species (i.e., species that do not naturally occur at the planting location or, more generally, within the country) or the use of non-local genetic resources (i.e., populations of naturally occurring species which originate from other parts of the species distribution range). Assisted migration and assisted gene flow programs can disrupt local genetic adaptation and affect the present and future dynamics of forest genetic resources. We can take advantage of past experiences in the introduction of species and provenances, but these are not real experiments to test the effectiveness of present-day-assisted migration programs. Caution is needed in the use of extensive assisted migration as the responses will likely affect not only trees but also the whole forest community in which they are established (Bruno Fady et al., 2015). Natural regeneration is the most appropriate management technique for promoting the adaptation of natural forests to climate change. Natural regeneration is being promoted in the context of close-to-nature forest management for several reasons including those that relate to cost reduction, decreased disturbance, better selection potential due to larger seedling density and conservation and continuous natural development of the local gene pool. To provide sufficient material on which natural selection can operate to bring about developmental change, the option of natural regeneration is likely to be the most appropriate as it typically provides a much larger base population than is the case for plantations. Forestry will need to rethink its strategies for long rotation species to make it possible for selection to occur in those areas where climate change is expected to have its strongest impacts (Bruno Fady et al., 2015). The conservation of genetic diversity has to be included as a component of habitat and species conservation strategies. Foresters tend to give much less consideration to the conservation of genetic resources (gene conservation) than to that of species and habitats. Gene conservation of forest tree species should be viewed as an integral part of biodiversity conservation, alongside that for species and habitats. Protected forest areas in which there is little or no active management can sometimes directly contribute to the conservation of forest genetic resources, and genetic diversity monitoring should become a priority concern there for the most relevant species (Bruno Fady et al., 2015). Tree breeding involves selecting individuals that have particularly desirable traits and crossing these individuals to improve that trait or traits of interest within populations. Breeding programs can therefore produce genetic resources which are valuable in enabling forests to adapt to climate change and to provide more and/or better ecosystem services. Whether based on a high- or a low-input strategy, breeding programs should include the assessment of phenotypic traits that are likely to be important in conferring genetic adaptation to climate change (which may well be found outside the usually investigated resources and will require well-organized international collaboration). Low-input breeding strategies represent an opportunity to do so for species that are traditionally under-represented in breeding programs because of their low market value. This may be useful, as in the future, such species (e.g., Mediterranean trees) may become increasingly important under climate change (Bruno Fady et al., 2015). In addition to changing perceptions of the importance of genetic resources for better coping with increased disturbances, the views of society are also shifting regarding the role of genetic resources in meeting the demands for forest goods and services. The two main current drivers of this shifting perception are climate change and expected future demands by end-users. Increasing the societal perception of the value of genetic diversity in managed forest ecosystems should be a priority. Raising awareness among forest managers, policy makers and conservationists of the essential role of genetic diversity on biodiversity dynamics and adaptability of forests to future conditions is urgently needed. Improvements in knowledge transfer beyond academia are required (Bruno Fady et al., 2015).

Need for resilience

Recently, attention has begun to focus on identifying and quantifying ways to bolster the resilience of ecosystems (Folke et al., 2004; Batt et al., 2013), in a move from prevention to mitigation of disturbances such as climate change. Now that both climate change and globalized trade are realities, there is a need to find ways to ensure the persistence of essential ecosystems in the face of new conditions, in other words, to maximize their potential to adapt to a changed environment. All these aspects are difficult to measure and, even where clear negative effects are expected, results have, on occasions, been counterintuitive. For example, some systems have shown unexpected resilience even in the face of pressures that had been expected to cause ecosystem change (Bestelmeyer et al., 2013; Ponce Campos et al., 2013). The policy shift towards resilience appears to be emerging from a combination of increasingly visible change and the lack of progress in international efforts to address these issues. Therefore, to find ways to meet policy goals and to ensure the long-term persistence of the ecosystems we value, it is essential to reach a working understanding of what resilience means and how it can be optimized via appropriate management (Cavers and Cottrell, 2015).

Resilience in theory

Resilience is defined as the extent of perturbation that a system can experience before it undergoes a shift to an alternative state (Holling, 1973; Scheffer et al., 2001) or, more subtly, 'the capacity of a system to reorganize whilst undergoing change so as to retain the same function, structure, identity and feedbacks' (Folke et al., 2004). Resilience can also be defined in the case of an ecological network as its 'capability to absorb, resist or recover from disturbances and damage at the same time continuing to meet its overall objectives of supporting biodiversity and providing ecosystem services'. Originating from engineering theory, these concepts of resilience developed for the purposes of predicting how and when systems shift from one stable state to another and are perhaps most advanced in the study of lakes, where the essentially closed nature of the system makes them more amenable to model development. State shifts may be complicated by hysteresis, where forward and reverse tipping points occur at different levels of pressure, such that restoring the original state is not simply a case of reversing the initial disturbance (Cote and Darling, 2010). A key element in resilience theory is the relationship between diversity and resilience. Although positive relationships have been shown between biodiversity and stability of ecosystem function (Laliberte et al., 2010), in theory it is the functional redundancy associated with higher diversity that confers stability. However, measuring the extent of functional redundancy is difficult, and this becomes more complicated when applied to heterogeneous environments, where functional roles may alter with context (Wellnitz and LeRoy Poff, 2001). Furthermore, depending on whether ecosystem resilience (resilience of the ecosystem as a whole) or species resilience (the resilience of individual species) or genotypic resilience is being considered, stability may depend on either species diversity or intraspecific genetic diversity, respectively, and the processes governing their maintenance. If one tree species within that forest becomes the focus of a severe threat, it might best be managed by complete removal of that species and replacement with an alternative species or with natural recruitment. In contrast, if the forest type is important, for example, if it is a priority habitat, then the resilience of particular tree species within that woodland is essential. Exposure of that key species to severe threat risks the delivery of the ecosystem service, and the internal diversity of the species consequently becomes important. Direct evidence for the relationship between diversity and resilience is typically experimental but has been shown for ecosystem resilience in many systems (Norden et al., 2009; Batt et al., 2013; McGovern, 2013;Prober et al., 2013). However, in the case of single species resilience, the evidence base is much poorer, with well cited studies of eelgrass (Reusch et al., 2005) and model organisms such as yeast (Bell and Gonzalez, 2009), *Drosophila* (Bakker et al., 2010) and *Daphnia* (Latta et al., 2010) providing the best demonstrations. Such studies indicate that the level of intraspecific genetic diversity, the integrity of gene flow mechanisms and population size all play key roles in delivering the potential for 'variability rescue'. The mechanism of variability rescue involves initial population decline followed by recovery as genotypes adapted to the new conditions prosper via natural selection (Cavers and Cottrell, 2015).

Salt tolerance to survive sea water incursion into coastal terrestrial environments

One way to address impacts of sea-level rise on coastal forests is to identify salt tolerance in plants/trees. In Kiribati, a single king tide can kill established *Artocarpus altilis* (breadfruit) trees. As these trees harbour seabirds such as terns which are used by local fishermen to locate schools of fish, their loss has a major impact on food security and livelihoods. Given the impacts of sea-level rise in Kiribati, Tuvalu, and other atoll island nations in Oceania, development of salt-tolerant breadfruit is an urgent task. Studies with salt-tolerant non-halophyte trees (Thomson et al.,1987; Marcar et al., 1999) have frequently demonstrated considerable genetically based resistance to salinity. Given the substantial genetic diversity in breadfruit, including putative salt tolerance in particular varieties and natural hybrids between *A. altilis* and *A. mariannensis* (Morton, 1987; Ragone, 1997), it is almost certain that salt-tolerant breadfruit can be selected and further developed, illustrating the need to conserve and make use of genetic diversity in multipurpose tree species.

Rapid transition from fire-sensitive to fire-resistant variability

Severe fire may have the same effect as clearing a forest, especially where fire creates large patchy openings. The pattern and size of such openings in relation to the forest cover influence genetic diversity. Where mortality among burnt species is heavy, it results in reduced population sizes and increased genetic drift. For isolated populations, the migration rates of seed and pollen exchange are therefore affected. Sources of migration could even be cut off, thus reducing the effectiveness of pollinators (Kigomo, 2001). Adverse fire may directly affect biotic dispersal agents, and this may decrease migration of genes between populations. Migration may increase if the migration vectors are abiotic. A devastating fire may affect traits that could have a direct bearing on fire-resistant species, resulting in direct selection that indiscriminately removes all such genotypes (FAO, 2010). The cumulative impact of interacting disturbances can increase fire risk. For example, drought often reduces tree vigour, increasing vulnerability to insect infestations and diseases. Insect infestations and diseases add to the fuel available and therefore increase the opportunity for forest fires, which in turn can support future infestations by weakening tree defence systems (Dale et al., 2001).

Invasive species

Invasive species, including plants, insect pests and microbial pathogens, are increasingly being identified and noted as major threats to ecosystem integrity and individual species, including trees. The main invasive plant threat comes from “transformer” plant species which have the capacity to invade natural or slightly disturbed forest associations, becoming the dominant canopy species and completely modifying or displacing entire ecosystems, with the loss of displacing entire ecosystems, with the loss of many of the existing species (trees and others). An example is the introduced tropical American tree *Prosopis juliflora* in East Africa, which is taking over large swathes of natural forest and woodlands, with considerable negative impacts on native tree populations (in terms of both species and genetic diversity). It is also damaging local livelihoods in the process (Mwangi and Swallow, 2005). In island countries and territories of Oceania, excessive opening of the forest canopy through intensive timber harvesting, coupled with major cyclones, has greatly favoured the spread of light-loving vines such as *Merremia peltata* and *Mikania scandens*; these vines and creepers have now taken over large swathes of forest ecosystems, thickly draping all trees and shrubs (Maturin, 2013; Kamusoko, 2014).

Drought and heat-induced tree mortality reveals emerging climate change risks for forests

Greenhouse gas emissions have significantly altered global climate, and will continue to do so in the future. Increases in the frequency, duration, and/or severity of drought and heat stress associated with climate change could fundamentally alter the composition, structure, and biogeography of forests in many regions including the forest genetic resources. Of particular concern are potential increases in tree mortality associated with climate-induced physiological stress and interactions with other climate-mediated processes such as insect outbreaks and wildfire. Episodic mortality occurs in the absence of climate change, studies suggest that at least some of the world’s forested ecosystems already may be responding to climate change and raise concern that forests may become increasingly vulnerable to higher background tree mortality rates and die-off in response to future warming and drought, even in environments that are not normally considered water limited. This further suggests risks to ecosystem services, including the loss of sequestered forest carbon and associated atmospheric feedbacks. Key information gaps and scientific uncertainties that currently hinder our ability to predict tree mortality in response to climate change which emphasise the need for a globally coordinated observation system. The potential for amplified tree mortality due to drought and heat in forests worldwide has been revealed (Allen et al., 2010).

Importance of forest genetic resources or intraspecific variability

Natural forests are reservoirs of genetic diversity for tree species or intraspecific variability within species, essential to the adaptation of forests, and thus of the forestry sector to climate change. Trees are long-lived, and maintaining resilient forest ecosystems requires more than planting new tree varieties and species. Persistence will largely depend on the ability of existing trees and populations to adapt locally. In particular, the existence of a high level of genetic diversity within stands is a key prerequisite for forest trees to adapt and be resilient to the unpredictable effects of climate change. There is need to examine genetic variation within forest tree populations in India, and assess how this variability and its management could help forests adapt to environmental changes. Tree species within (semi-)natural forests contain significant genetic variation. Variable environmental conditions, such as temperature, light availability and drought intensity maintain and promote genetic diversity within and between (semi-)natural forests, even at short spatial scales. High genetic variation in forest tree populations allows for more rapid adaptation to climate change. Genes associated with key adaptive traits (such as trees' resistance to drought, cold or forest fires) can vary in their frequency spatially and geographically. This type of information is now easily accessible and should be included, along with neutral genetic diversity, in the adaptive forest management toolkit. Forestry practices can significantly modify the genetic composition and structure of forest trees and the development of their genetic diversity.

Genetic variability and adaptation to environmental changes at local spatial scales

Earlier research has confirmed that within-species genetic diversity can be very high with significant differentiation even among neighboring trees within the same forest. With sufficient genetic variation, trees in forests can adapt rapidly to environmental changes. Researchers identified genes associated with individual tree response to major environmental threats such as drought, cold, heat, and recurrent forest fires. Within populations, genes associated with the seasonality of new leaf emergence in spring, flowering time, and resistance to drought and cold varied significantly along environmental gradients at small spatial scales. Experimentally it is showed that the variability found for these genes is associated not just with migration and population foundation, but also with varying environmental conditions, such as altitudinal and latitudinal gradients, and is thus affected by natural selection. They also found that up to 80-90 percent of the genetic diversity underlying adaptive genes remains within populations, suggesting that local environmental conditions can promote and maintain genetic diversity within and among tree populations. They also found that genetic diversity for key traits can develop within just a few generations, allowing rapid adaptation to a changing environment. Knowledge of how genetic variability is partitioned in space for such important genes can thus help improve models of future range distributions, and better inform the choice of trees in reforestation projects.

Other results point to the existence of significant genetic variability affecting tree survival and reproductive output (fitness) in small forests. These studies revealed that the pollen output of male trees is highly dependent on the microenvironment in which each tree is growing (e.g. soil humidity, fertility and texture). Similarly, studies of three maritime pine forests located in the Mediterranean region indicate that altitude has a measurable effect on genetic diversity at the scale of a few hectares. They also showed that the local environment is very important for the survival of transplanted trees. Indigenous trees showed a higher fitness than transplanted trees only under certain microenvironmental conditions. This suggests that the difference in fitness between populations depends strongly on the environmental context, and that it is affected not only by regional climate but also by the local environment at very small scales. Consequently, local genetic resources are not always best for all environmental conditions, such as in sites with full sun exposure.

Genetic resources for forest management in a changing environment

To make forests more resilient to an unpredictable future, development of highly efficient sequencing and genotyping methods previously restricted to model organisms only has added to our knowledge of this aspect. These methods provide better information on the genetic make-up of trees and their adaptative potential, thus helping them to sustainably manage forests in a changing environment. As a short term perspective, it is conceivable that foresters will target the collection of reproductive material for conservation, direct use and breeding programs for trees carrying particular gene variants of interest for managed forests. In the longer term, surveying changes in occurrence of different genotypes will considerably improve monitoring, allowing predictions of whether or not particular stands have a good ability to withstand strong environmental changes.

Water is a natural resource of vital importance in agriculture. This makes it also a limiting factor for growing sufficient crops or commercial plantations or agroforestry stands to ensure food and wood supplies for the world’s growing population. For harnessing genetic resources for improving drought stress tolerance in crops, there is an urgent need for the genotyping of gene bank accessions to benefit from the genetic diversity of gene bank material worldwide, and the reliable phenotyping for drought stress tolerance. Thus genotyping and phenotyping of forest genetic resources are vital. Adaptation to climate change involves monitoring and anticipating change and undertaking actions to avoid the negative consequences and to take advantage of potential benefits of those changes.

Managing climate change and forests in the face of uncertain future

Forest genetic resources managers will be challenged to integrate adaptation strategies (actions that help ecosystems accommodate changes adaptively) and mitigation strategies (actions that enable ecosystems to reduce anthropogenic influences on global climate) into overall plans. Adaptive strategies include resistance options (forestall impacts and protect highly valued resources), resilience options (improve the capacity of ecosystems to return to desired conditions after disturbance), and response options (facilitate transition of ecosystems from current to new conditions). Mitigation strategies include options to sequester carbon and reduce overall greenhouse gas emissions (Millar et al., 2007).

Climate change increases the drought risk

In the case of the projected drought exposure of various regions of India, the anticipated dynamics of the regional forests facilitate the adaptation of forests to climate change-induced drought risk. On the basis of an ensemble of climate change scenarios we expect substantial drying in various parts of India due to temperature rise, while such trends were found to be less pronounced during the past. In response to these climate trajectories, a change in species composition towards a higher share of drought tolerant species as well as the use of drought resistant provenances or variability are to be identified as paramount actions in forest adaptation in the drier warm regions. Adaptation to aggravating climate change may need to use artificial regeneration to enrich local gene pools and increase the drought tolerance of stands. Increasing risks from pests and other disturbances are expected as a result of more frequent and severe droughts, underlining the need to put a stronger focus on risk management principles rather than on indicators of productivity in silviculture and forest planning. A consolidation of disturbance monitoring systems and a broader use of pest dynamics and hazard rating models are paramount tools to facilitate this adaptation process in forest management. Systematic and long-term implementation of the presented measures should increase forest stability and resilience, and further secure the sustainable provision of ecosystem services under climate change.

In regions where climate change is expected to be extensive and rapid, many tree species are predicted to experience severe stress in their native ranges. Survival will then depend on the capacity to undertake at least one of the following: (1) quickly adapt genetically to new conditions at existing sites; (2) survive changing conditions through a high degree of phenotypic plasticity without genetic change; and/or (3) migrate rapidly to newly found suitable environments that match basic physiological requirements. The expected impacts of climate change – and hence strategies for responding to it – differ among these environments. Assisted migration and artificial selection for appropriate traits are approaches that can be applied to planted trees, whether in commercial plantations or farms, but are less appropriate for natural forests. Adapting to climate change poses a greater problem for naturally regenerating populations where the potential for natural migration is hindered by forest fragmentation and agricultural expansion, and when confounding factors for adaption include pests and diseases, reduced population sizes, and simplified forest structures and species compositions. Lack of information on the following hinders our ability to manage climate change impacts better: (1) little is known about the sequences and functions of the genes conferring adaptation; (2) the genetic and epigenetic basis of phenotypic plasticity and its role in producing responses to environmental alterations is unclear; (3) the basic life-history characteristics, ecological determinants and geographic distributions of many trees are not well studied; and (4) meaningful syntheses of such information into predictive models of change and response are poorly developed.

Trees harness the power of microbes to survive climate change

Microorganisms are the most abundant and diverse taxa on earth. They have the ability to tolerate extreme environments, catalyze a range of metabolic functions, and rapidly develop in response to changing environmental conditions. Imagine if plants and animals could harness these powers. In fact, microorganisms confer numerous benefits to plants and animals. For example, microorganisms in the mammalian gut improve nutrition, reduce susceptibility to disease, and even alter host behaviour (Diaz et al., 2011). Some of the most complex microbiomes are found in soils, where they are responsible for nutrient cycling, crop yield, and carbon sequestration (Bender et al., 2016). In some cases, soil microbes can even rescue plants from the negative consequences of climate change (Lau and Lennon, 2012). If plants and animals can build associations with specific microbial members that maximize benefits, then harnessing microbial powers may provide rapid and efficient solutions to the challenges resulting from global change. Gehring et al. (2017) showed that the relationship between soil microbial communities and plants is not a fortunate coincidence. Instead, some pinyon pine genotypes form associations with different belowground ectomycorrhizal fungal (EMF) communities that help them contend with drought. These EMF communities were responsible for the observed difference in drought tolerance between host tree genotypes. Because these microbial communities are, at least partially, under plant genetic control, EMF community composition is an extended phenotype of the host tree and potentially a mode of adaptation to the increased drought stress pinyon pines face in a changing climate. Given the vast array of biogeochemical and metabolic functions in the microbial arsenal, if similarly tight linkages occur between diverse soil bacterial and fungal communities and host plant genotypes, then host plants may possess a powerful tactic for adapting to environmental change. Gehring et al. (2017) provide important advances for the idea that host-associated microbial communities may underlie adaptation (Zilber-Rosenberg and Rosenberg, 2008). They piece together evidence showing that the pinyon pine genotypes differ in their EMF microbial associates (even when they are grown in the same soil), and that these divergent EMF communities influence host performance and fitness in response to drought. Such findings support the view that plant-associated microbiomes represent a heritable extended phenotype of the host genome, that microbial communities influence fitness, and that the host traits controlling these associations can serve as adaptations to changing environments. Although genetically based differences in plant colonization by microbial partners are well known in other symbioses (Heath and Tiffin, 2009; Grillo et al., 2016), rarely are connections between specific plant-controlled symbiotic associations and fitness made. This critical link is necessary to show that these associations are adaptive. Gehring et al. (2017) establish this link, between host-determined EMF communities and host fitness variation, by carefully building evidence from a combination of long-term observational field studies, manipulative greenhouse studies, and microbial community sequencing. They characterize EMF communities associated with drought-tolerant and drought-sensitive trees in both the field and greenhouse, while demonstrating how those microbial communities influence tree fitness responses to drought. The mutualistic association between plants and EMF communities is an ancient symbiosis in which hosts provide fixed carbon (from photosynthesis) to their root symbionts in exchange for increased nutrient acquisition via the fungus. However, EMF species can provide other benefits (e.g., stress tolerance) and can vary widely in the levels of host benefits provided (Pena and Polle, 2014). Gehring et al. (2017) found that drought-tolerant genotypes were colonized by EMF species in the genus *Geospora* at much higher rates. Indeed, even drought-intolerant individuals that had higher colonization by *Geospora* showed higher drought tolerance compared with other drought-intolerant individuals that failed to form associations with *Geospora*. In the absence of EMF species (when soil was sterile), differences between tree genotypes in drought tolerance disappeared. Given that plant genotypes also influence diverse soil bacterial and fungal communities that perform a plethora of metabolic and biogeochemical functions (Wagner et al. 2016; Edwards et al. 2015), the adaptive potential of host traits underlying plant–microbe interactions could be extensive. Gehring et al. (2017) also stimulate many new questions at the intersection of emerging fields in the biological sciences. For example, perhaps the wealth of knowledge on plant–microbe interactions at the biochemical level and, more recently, at the genomic level can someday inform our understanding of global change ecology and lead to better models of plant community responses to climate change. Perhaps the recognition that genotypes vary in their associations with aboveground and belowground microorganisms will change how we breed agronomic crops to feed the planet in the face of the global changes dominating us.

Recommendations for future forest managers and researchers

The nation would benefit from incorporating measures to maintain and if necessary increase genetic variation within tree populations and stands to ensure the ability of forests to adapt to climate change. The conservation of tree genetic resources should be promoted accordingly. Management of different ecosystems should take into account that protected forests can act as gene banks.

New knowledge from molecular genetics provides insights into the processes through which forests adapt to changing conditions. Such knowledge is important for guiding forest management decisions, and thus avoiding costly mistakes. The new knowledge highlights the key role of genetic diversity of trees in determining forest resilience. All stakeholders in the forestry sector should strengthen forest genetics conservation with support from ICFRE. However, the conservation of forest genetic resources currently does not seem sufficiently emphasized to ensure that agreed biodiversity targets are met.

Genetic adaptation of forest trees to climate change ultimately depends on specific genes, which underlines the importance of studying and valuing the genetic variability stored in trees and to identify genes involved in local adaptation. We can benefit from including such knowledge in models forecasting climate-induced range shifts. In fact, the inclusion of genetic diversity in such models may considerably modify the expected range shift of forest tree species.

The strategy should aim at increasing the contribution of agriculture and forestry to maintenance and enhancement of biodiversity, and it is expected that by 2030, State-wise Forest Genetic Resource Management Plans should be in place throughout India. Increasing the genetic diversity of trees increases the species diversity of the forest community they harbour.

The marketing of forest reproductive materials should be improved with requirements on how to maintain a high level of genetic diversity within traded seed lots. Requirements should address the minimum number of seed trees to collect from a natural stand (typically more than 100), the necessity to sample seed trees from ecologically variable microenvironments within stands, and the importance of mixing seed lots collected within a region of provenance. Traded seed lots should eventually be made of collections sampled from hundreds of seed trees. It is suggested that such recommendations go beyond reforestation and afforestation projects and address all ecological restoration efforts.

Forest management practices that maintain genetic developmental processes in naturally regenerated forests should be promoted. If needed, forest adaptation potential can be accelerated through tree breeding practices and transfer of suitable forest reproductive material.

Connectivity between protected areas facilitates gene flow and is important for the maintenance of genetic variation and adaptive potential of species.

Experimental work is needed to test the extent to which intraspecific genetic diversity underpins stability. This should encompass testing of multiple genotypes, but also multiple pressures. For this, a decision-making framework should be developed, to let forest policymakers identify the most appropriate action in specific pest threat situations. This should define a minimum set of parameters for a host tree species, such as its ecology, distribution and diversity; those of the threat organism(s) and likely future environments. Model-based testing could then be used first to evaluate potential developmental rates in tree populations, taking into account genetic diversity, adaptive potential and variations in demographic turnover, and secondly, to explore and prioritize different management scenarios using both idealized populations and spatially explicit simulations reflecting the known distribution of species in the Indian context.

New information on genetic and adaptive variation for tree species should be collected at a fine spatial scale. Detailed assessments of phenotypic variation in existing trials should be made, including development of high-throughput methods for gathering such data. New, large-scale trials should be established to test resistance related trait variation and to maximize the impact of advanced genomic approaches. The coordination and collation of existing data sets on intraspecific diversity in Indian tree species should be carried out as a priority, particularly for those species as yet unaffected but with imminent serious threats, and encompassing both molecular and phenotypic variation (Cavers and Cottrell, 2015).

Conclusion

Forests in India exist in many forms and composition, which include native woodlands with very low levels of intervention, low impact silviculture plantations and woodlands of native and exotic species in a mixture of man-made plantations composed of fast-growing exotic conifer species. All are subject to biotic and abiotic change in the form of pests, climate change and increasing frequency of weather extremes. Their ability to adapt to these challenges is dependent on a number of factors including inter- and intra-specific diversity. The main factor influencing adaptedness is the balance between natural selection and gene flow, and therefore, consideration needs to be given to the best means of conserving the developmental process rather than the genetic structure present at a given point in time. The importance of integrating developmental considerations into adaptive forestry is being stressed in cases, where, more extreme climate change is predicted (Lefe`vre et al., 2013).

Research to support adaptation to climate change is still heavily focused on assessing impacts and vulnerability. However, more refined impact assessments are not necessarily leading to better management decisions. Multi-disciplinary research approaches are emerging that integrate traditional forest ecosystem sciences with social, economic and behavioural sciences to improve decision making. Implementing adaptation options is best achieved by building a shared understanding of future challenges among different institutions, agencies, forest owners and stakeholders. Research-policy-practice partnerships that recognise local management needs and indigenous knowledge and integrate these with climate and ecosystem science can facilitate improved decision making (Rodney, 2015).

Summary

Forest ecosystems can face a range of challenges in the coming decades, of which climate change and pests are the most serious. These challenges will be overlaid on a background of historically modified and fragmented forests managed in a wide range of ways for different objectives over the years. As Indian forests are species rich in the global context, their resilience to these challenges is fundamentally dependent on the expression of resilience of the variability within individual species or their genetic resources. A better strategy for establishing long-term resilience would be to harness natural developmental processes, to maximize the capability of individuals of tree species to respond to new threats by the reorganization of populations via natural selection or in other words, to be resilient. Such processes depend on the internal variability of the species, their mechanisms of dispersal and their ability to recruit new genotypes to a population. In this paper, a review of the theoretical concept of resilience will be presented. In addition, it will examine how it might be applied to tree populations comprising of intraspecific variability and assess the state of knowledge of forests from this perspective.

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Harnessing Forest Genetic Resources for Climate Resilience and Forest Health

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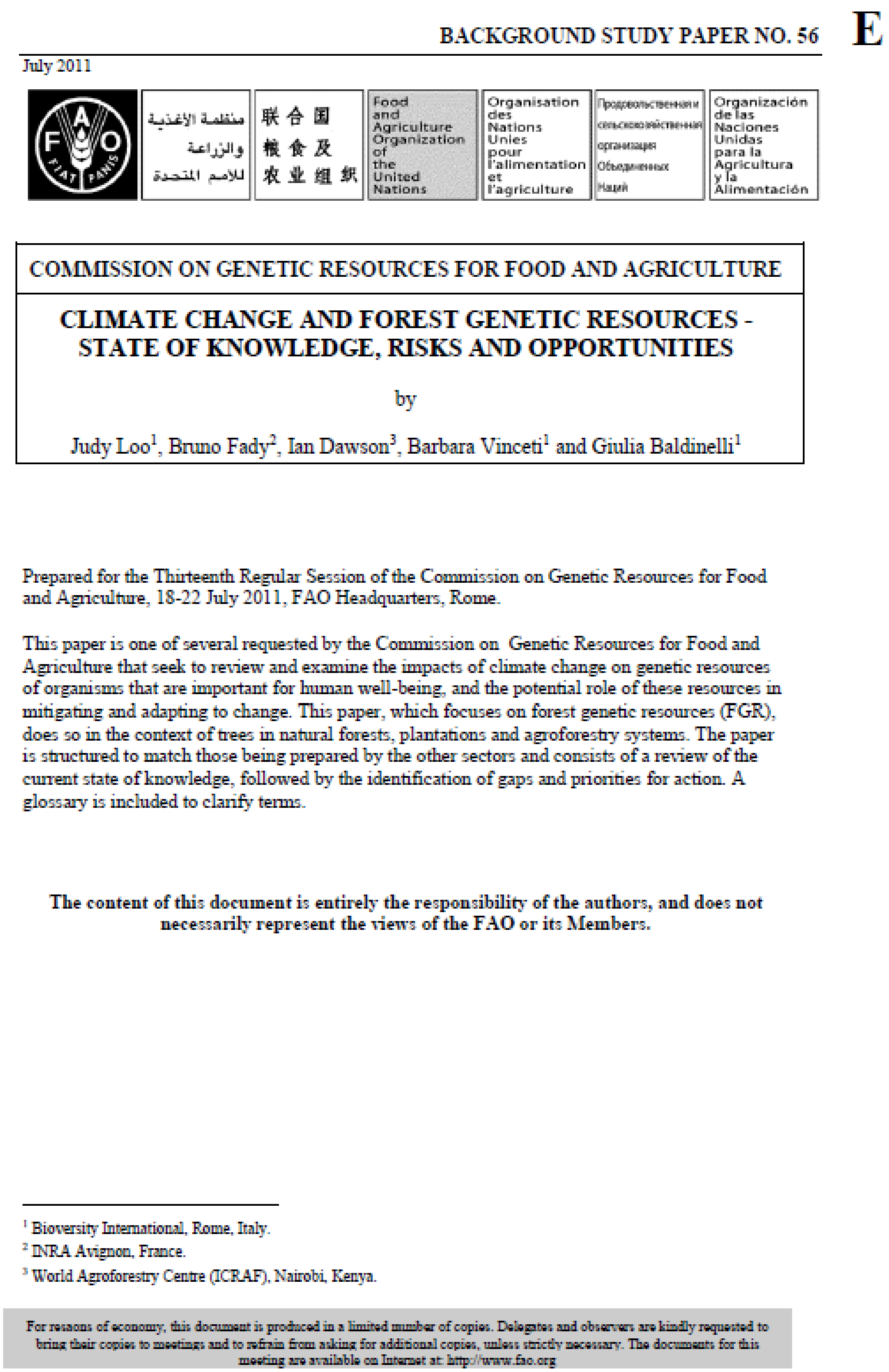
Forests are considered to be the richest storehouse of genetic resources which functions as the repository on which agriculture, medicine and diverse array of ecosystem services rely on. However, climate change has induced a myriad of direct and indirect challenges which necessitates a relook at the function of forests and its ability to conserve genetic resources. This paper looks at the climate resilience of tropical forests in the context of forest health. Although forests have proved to be resilient to changes in the past, in recent times the quality of forests has deteriorated mainly due to degradation and fragmentation. Large expanse of bamboo forests undergo mass flowering and perish at the same time with grave impact on the food availability of large mammals like elephants forcing them to move out of forests resulting in human-wildlife conflicts. We need to have a wider genetic pool for our bamboo forests to ensure that the flowering is evenly spaced and that the resources do not dwindle all at once. Teak is another species which needs urgent consideration from the point of view of genetic variability. Starting from the 1970s, the productivity of teak is on a sharp decline which has multiple reasons to it. Decline in soil fertility in subsequent rotations, absence of good quality planting stock, impact of pests like the Teak defoliator which can substantially reduce the volume increment and the Teak trunk borer which can kill older trees are of much concern. A recent study has demonstrated the possibility of increased outbreaks of the teak defoliator which can nullify the productivity enhancement predicted under higher CO_2 levels. Increased temperatures have also been correlated with the higher incidence heart rot in young teak stands. From the forest health perspective a high impact problem and which is not well addressed is the impact of exotic species in the natural forests. For example, a total of 89 invasive alien species have been recorded in Kerala, many of which have gained entry into natural forests. In most invaded locations, the rich diversity of flora is brought down into a monoculture of the invading species. As these chosen examples show, assessing the diversity of forest genetic resources at the species, population and ecosystem levels is an immediate prerequisite to evolve conservation strategies. Inventories on wild genetic resources of cultivated crops and medicinal plants whcih can resist extreme climatic variations from the Proteced Areas are lacking. One of the key interventions needed is to enhance the area of intact forests where evolutionary processes continue unimpacted with appropriate long-term management plans. However, this is an uphill task considering the increase in the area of open forests and the possibility of our intact forests getting more and more fragmented owing to development pressures. A multisectoral approach is required to address this grave problem.



BACKGROUND STUDY PAPER NO. 56 **E**

July 2011

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COMMISSION ON GENETIC RESOURCES FOR FOOD AND AGRICULTURE

CLIMATE CHANGE AND FOREST GENETIC RESOURCES - STATE OF KNOWLEDGE, RISKS AND OPPORTUNITIES

by

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Prepared for the Thirteenth Regular Session of the Commission on Genetic Resources for Food and Agriculture, 18-22 July 2011, FAO Headquarters, Rome.

This paper is one of several requested by the Commission on Genetic Resources for Food and Agriculture that seek to review and examine the impacts of climate change on genetic resources of organisms that are important for human well-being, and the potential role of these resources in mitigating and adapting to change. This paper, which focuses on forest genetic resources (FGR), does so in the context of trees in natural forests, plantations and agroforestry systems. The paper is structured to match those being prepared by the other sectors and consists of a review of the current state of knowledge, followed by the identification of gaps and priorities for action. A glossary is included to clarify terms.

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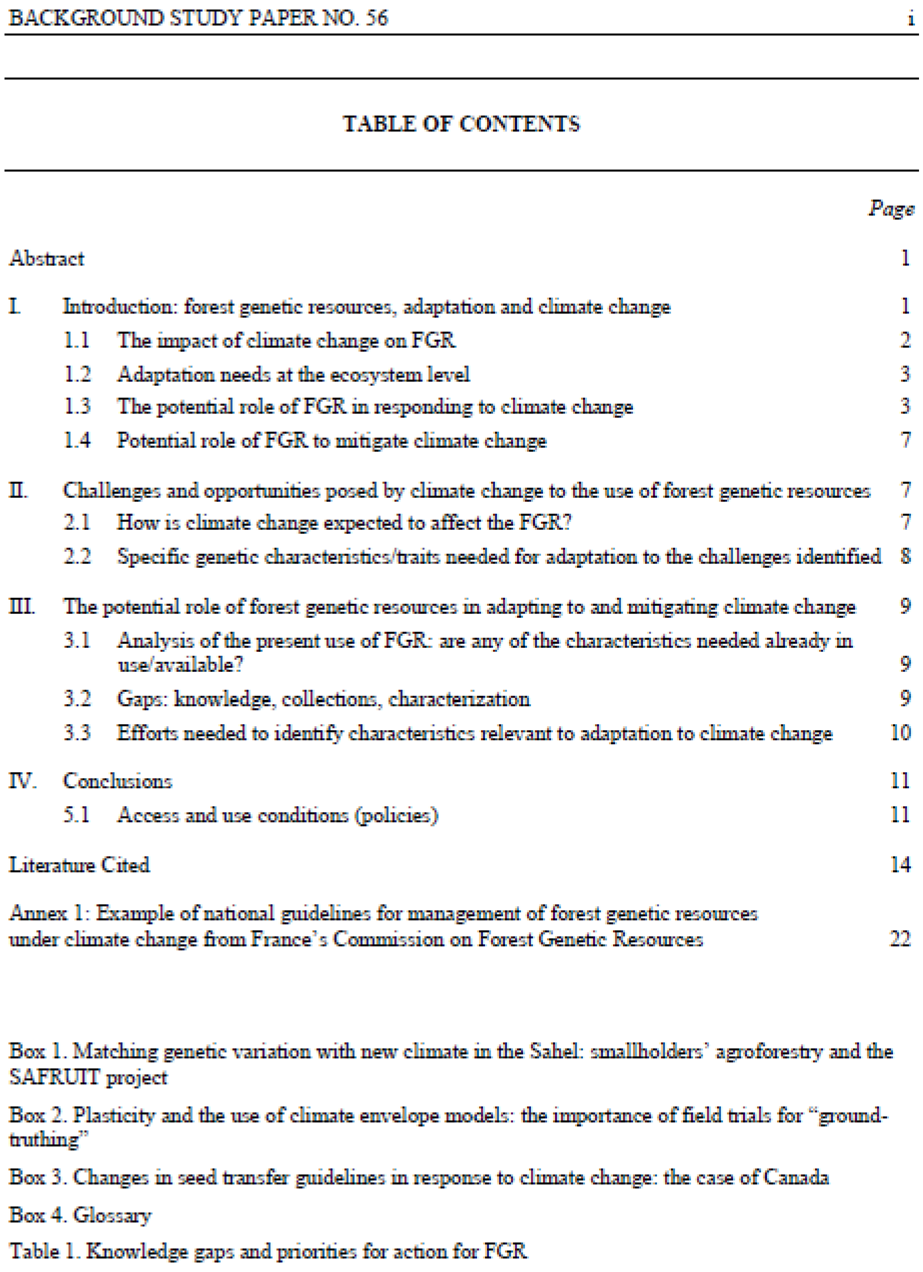

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ABSTRACT

In regions where climate change is expected to be extensive and rapid, many tree species are predicted to experience severe stress in their native ranges. Survival will then depend on the capacity to undertake at least one of the following: (1) quickly adapt genetically to new conditions at existing sites; (2) survive changing conditions through a high degree of phenotypic plasticity without genetic change; and/or (3) migrate rapidly to newly evolving environments that match basic physiological requirements. This paper considers forest genetic resources in the different settings where people depend on products and services from trees for a wide variety of purposes, including naturally regenerating forests, commercial plantations, and trees on farms (including planted trees and wild remnants left standing for various functions). The expected impacts of climate change – and hence strategies for responding to it – differ among these environments. Assisted migration and artificial selection for appropriate traits are approaches that can be applied to planted trees, whether in commercial plantations or farms, but are less appropriate for natural forests. However, management actions are confronted with serious challenges, including national and international policies that limit the movement of genetic resources among countries, and long regeneration cycles that make tree breeding time-consuming and costly. Adapting to climate change poses a greater problem for naturally regenerating populations where the potential for natural migration is hindered by forest fragmentation and agricultural expansion, and when confounding factors for adaption include pests and diseases, reduced population sizes, and simplified forest structures and species compositions. Lack of information on the following hinders our ability to manage climate change impacts better: (1) little is known about the sequences and functions of the genes conferring adaptation; (2) the genetic and epigenetic basis of phenotypic plasticity and its role in producing responses to environmental alterations is unclear; (3) the basic life-history characteristics, ecological determinants and geographic distributions of many trees are not well studied; and (4) meaningful syntheses of such information into predictive models of change and response are poorly developed.

I. INTRODUCTION: FOREST GENETIC RESOURCES, ADAPTATION AND CLIMATE CHANGE

While in the crop sector genetic improvement programmes use advanced technologies and have proceeded through many breeding cycles, in forestry there is heavy reliance on undomesticated resources. In only a few cases (mostly eucalypts, poplars, and pines and other temperate conifers) have public or private sector breeding programmes advanced beyond the third generation. In the cases where genetic improvement is taking place, a clear "use value" can be ascribed to FGR (often related to traits such as increased yield, increased stem straightness, increased lignin content or resistance to a particular pest or disease), but in other cases resources primarily present an "option value".

Different ways of estimating the value of genetic resources are available (Sarr *et al.*, 2008), but few have been applied to FGR (although see Bosselmann *et al.*, 2008; Hein and Gatzweiler, 2006). The economic valuation of biodiversity and ecosystem services is particularly challenging to undertake (e.g. Salles, 2010), and this is especially so for often uncharacterized FGR (Elsasser, 2005). Thorsen and Kjaer (2007) suggested that meaningful valuation in the context of climate change should extend beyond traditional measures such as wood production to include indicators related to societal use and ecosystem function.

In this paper, we do not attempt to provide an economic valuation of impacts in terms of the products and services of FGR under climate change, but judging by losses already experienced by the forest industry in British Columbia, Canada, for example, these will be significant. We indicate that the current portfolio of FGR used in breeding programmes, on farms and in conservation units should be increased. In the absence of appropriate mitigation and adaptation measures, there is a significant danger that climate change – together with other inter-related challenges such as high human population growth, fuel scarcity, deforestation, soil degradation and biodiversity loss – may result in catastrophic impacts in many regions of the globe.

1.1 The impact of climate change on FGR

Predictions regarding impacts on FGR in natural forests, forest plantations and on farms vary. Although some authors (e.g. Hamrick, 2004) consider that many trees have sufficient phenotypic plasticity[4] and genetic diversity at the population level (bolstered by high gene flow among natural stands) to significantly reduce the negative effects of climate change , others have taken a different viewpoint and predicted severe impacts (e.g. Mátyás 2007; Rehfeldt *et al.*, 2001). Different positions relate partly to the types of species and environments being considered. Authors who make the more pessimistic forecasts often base their views on tropical trees (Dawson *et al.*, 2011) or on marginal populations of temperate species (Mátyás *et al.*, 2009), while more optimistic authors often consider temperate and boreal taxa (Lindner *et al.*, 2010).

Climate change impacts are expected to be severe in dry, high-temperature regions where trees are at their adaptive limit (e.g. Lindner *et al.*, 2010 for Europe) and in confined islands of moist forest that are surrounded by drier land (e.g. moist forests in Australia; Williams *et al.*, 2003). Whereas the ranges of some tree species are expected to expand, others will diminish. In temperate regions, range reduction at the receding edge of distributions (low elevation and low latitude) is expected to be more rapid and of greater magnitude than expansion at the leading edge (high elevation and high latitude) because of a number of factors that limit the ability of tree species to migrate across landscapes. Thuiller *et al*. (2006) have also shown that tree species richness and functional diversity will be impacted more at low than at high latitudes in Europe. In other regions such as the tropics, changes in precipitation rather than temperature may be of key importance (Dawson *et al.*, 2011).

Based on the data available to date, expected impacts of climate change on FGR will be experienced through several demographic, physiological and genetic processes, which may include the following:

- High mortality due to extreme climatic events, in combination with regeneration failure, will result in local population extinction and the loss of FGR. This will be the case particularly at the receding edge of distributions.
- Under changing climatic conditions, pest and disease attack may become more severe in some regions, because of improved environmental conditions for the attackers and because trees experience more stress and are therefore more susceptible.
- The fecundity of trees will change due to sensitivity to spring temperatures (e.g. as observed in the southeastern United States of America; Clark *et al.*, 2011) and other factors (Restoux, 2009). For example, in central Spain, a decline in cone production in *Pinus pinea* over the last 40 years has been correlated with warming, especially with hotter summers (Mutke *et al.*, 2005).
- Changes in climate may result in asynchronous timing between the development of tree flowers and the availability of associated pollinators, leading to low seed production for outbreeding species dependent on animal vectors. Absolute population levels of some pollinators are also likely to be reduced. Many tropical tree species that are pollinated by insects, birds or bats may be affected; in some cases, functional use would be severely affected.
- Increased fire frequency may eliminate fire-sensitive species altogether from woodlands and parklands. In regions that have not regularly experienced wild fires in the past, fire may become the main driver of change, with a rapid transition from fire-sensitive to fire-resistant species.
- Changing climates will result in new species invasions, altered patterns of gene flow and the hybridization of species and populations. Shifting ecological niches will increase the risk of invasion by more competitive tree species that are more precocious or can move more quickly. Invasions of new genes via pollen and seed dispersal may disrupt local evolutionary processes, but could also be a welcome source of new adaptive traits (Hoffmann and Sgro, 2011).

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[4] A glossary of this and other terms used in this paper are given in Box 4.

1.2 Adaptation needs at the ecosystem level

At the ecosystem level, adaptation to climate change requires maintaining options at the species and intra-species levels. Species diversity is a form of insurance that should increase the resilience of natural forests and planted tree stands in the face of environmental variability if the various species present respond differently to disturbances (Kindt *et al.*, 2006). As climate changes, less well-performing species may be replaced through a process of natural selection and competition by other trees that are already present within systems and that are better-suited to new conditions, such that the relative abundance of different species in the landscape alters, although it is not desirable if one taxon alone comes to dominate (see above discussion of species invasions).

At intraspecific level, maintaining genetic diversity within and among tree populations can similarly increase the stability of ecosystems (Whitham *et al.*, 2006; Thorsen and Kjær, 2007), especially when trees are keystone or foundational species. For example, the genetic variation of keystone species has in some cases been correlated with the interspecific diversity of their associated communities (Barbour *et al.*, 2009). In addition, intraspecific diversity promotes the resilience and productivity of individual species. For instance, modelling has shown that optimum production can be attained in plantations by "composite provenancing" and/or by mixing different genotypes from within species (Bosselmann *et al.*, 2008; Hubert and Cottrell, 2007).

Genetic adaptation is a process of shifting fitness trait values over generations to track environmental change and ensure better survival. The speed of adaptive responses at the population level depends on the amount of additive genetic variation in a stand and the heritability of important traits, in combination with the size of the selection pool, the intensity of the selection pressure and generation length. Many tree species are known or believed to have high genetic variability in adaptively important traits and have high fecundity, creating a large selection pool (Petit and Hampe, 2006). Thus, if environmental change is directional and continuous, many tree species have the potential to undergo relatively rapid evolution (Hamrick, 2004). However, the magnitude and speed of climate change are often predicted to surpass the capacity of tree populations to adapt, at least at the receding edge of species distributions where local extirpation may therefore occur (Davis and Shaw, 2001).

Climate change may also be experienced as increased variability in temperature and precipitation, with an associated elevated incidence of extreme events (e.g. drought followed by flooding; IPCC, 2007). The threat posed by increasing storm frequency due to climate change in the Pacific has led to efforts to identify cyclone-resistance species, such as *Endospermum medullosum* (whitewood), for large-scale planting. In Vanuatu, for example, establishment of 20 000 hectares of plantations of the species is planned over the next 20 years, with a resultant high demand for germplasm. Natural selection may, however, not efficiently mediate adaptation in situations of increased weather variability, because at least in the short-term, the selection pressure is not directional and the required traits may be inversely correlated at the gene level (Jump and Penuelas, 2005; although some features for adaptation to, for example, drought, such as deep root systems, should also contribute to tolerance to, for example, flooding).

1.3 The potential role of FGR in responding to climate change

Standing genetic variability. This comprises the potential of populations to adapt and depends on population size and the amount of diversity expressed in traits that will influence survival and reproduction under new conditions. Many tree species that have been studied have high genetic variability and can grow under a range of conditions (Gutschick and BassiriRad, 2003; Petit and Hampe, 2006). Phenotypic traits of adaptive importance such as drought tolerance, cold-hardiness and flowering and fruiting phenology have been shown to vary within some species across ecological and geographic gradients to an extent that may be as important as the differences often observed among species (Aitken *et al.*, 2008). Similarly, recent molecular-level studies have demonstrated allelic shifts in genes related o drought and heat tolerance among populations; conversely, however, genetic variability within populations can sometimes be low (Jump *et al.*, 2006; Grivet *et al.*, 2011; Hoffmann and Sgro, 2011). Management plans can influence the genetic composition and structure of naturally regenerating forests, providing opportunities for silvicultural interventions in order to respond to change (Guariguata *et al.*, 2008; Sagnard *et al.*, 2011).

Common garden experiments have been central in demonstrating the extent and distribution of the genetic diversity of fitness-related traits, such as survival, growth, phenology, and adaptation to cold, drought, pests and diseases, in tree species. Most such experiments have been conducted on boreal, temperate or a few commercially important tropical species. Recently there has been a move to include a wider range of indigenous species important to local people (Box 1). Not only is genetic diversity in important adaptive traits expressed across regions and provenances, but it can sometimes be abundant within populations, reinforcing an optimistic view that climate change challenges may be met by standing genetic variation in such species (Hoffmann and Sgro, 2011). An example of the contrast between species is provided by *Pinus halepensis* and *Pinus brutia*, two closely related pines with extensive distributions around the Mediterranean; the amount of among-provenance variation for survival under diverse climatic conditions is greater in the former, encompassing and extending that found in the latter (Bariteau and Pommery, 1992).

Box 1. Matching genetic variation with new climate in the Sahel: smallholders' agroforestry and the SAFRUIT project

The current understanding of population-level environmental responses in indigenous tree species planted by small-scale farmers in Africa is limited. New trials have, however, been established to consider climate change effects. Under the Sahelian Fruit Tree project (SAFRUIT, see www.safruit.org), for example, trials on drought stress for important trees for smallholders, such as *Adansonia digitata* (baobab) and *Parkia biglobosa* (African locust bean), are being conducted in the semi-arid West African Sahel, a region that has become drier over the last decades (Jensen *et al.*, 2011). In nursery experiments, populations collected from locations with different rainfall levels have been exposed to a range of watering regimes (Sanou *et al.*, 2007). Characters being measured include photosynthesis, water use efficiency, water potential and chlorophyll fluorescence. The information obtained on the effects of different treatments on root development, seedling vigour and other important adaptive characteristics will inform subsequent germplasm distribution strategies.

In some cases, climate change considerations for seed distribution are already being taken into account in the region. One example is provided by *Prosopis africana*, used for wood production; based on field trials measuring growth, survival and wood density in relation to rainfall patterns across seed collection sites, Weber *et al.* (2008) recommended that germplasm transfers of the species should only be undertaken in a single direction, from drier to (currently) wetter zones. A similar strategy was adopted for a recent International Fund for Agricultural Development agroforestry project in the same region. Different global circulation models used to explain environmental changes in temperature and precipitation profiles vary in future predictions of rainfall in the Sahel, with some indicating drier (e.g. Held *et al.*, 2005) and some wetter (e.g. Shanahan *et al.*, 2009) conditions. Given current uncertainties in projections, an emphasis in the region on matching seed sources to the more limiting scenario of a drier future climate would appear to be the most risk-averse option.

Phenotypic plasticity. Plastic tree species and/or provenances are those with flexible morphology and physiology that grow at least reasonably well under a range of different environmental stresses without genetic change (Gienapp *et al.*, 2008). At least in the short term, this characteristic is likely to be more important than genetic adaptation in ensuring persistence in highly variable environments; plastic trees do not need to genetically adapt, but can instead modify their phenotype in response to new conditions. Processes related to phenotypic plasticity may thus oppose those related to genetic adaptation, in that the selection pressure is reduced if plasticity is high, although a heritable basis for plasticity means that there will be selection for genotypes with more flexible responses as the environment becomes more variable. If phenotypic plasticity supports the persistence of trees it may be a particularly desirable trait because of the time taken for trees to mature and reproduce (they need to survive for several years in order to set seed and thereby perpetuate).

A degree of phenotypic plasticity is found in most trees (Piersma and Drent, 2003; Rehfeldt *et al.*, 2001), but varies among and within species (Aitken *et al.*, 2008; Bouvarel, 1960; Skroppa and

Kohmann, 1997). It is likely to be more important in species that contain limited genetic diversity for adaptation (Le Corre and Kremer, 2003). Examples of species with little genetic variation include the rare conifer *Picea omorika* found in Central Europe (Nasri *et al*., 2008) and *Pinus pinea* found around the Mediterranean (Vendramin *et al*., 2008); *P. pinea* has in fact been shown to display strong phenotypic plasticity for growth-related traits (Mutke *et al*., 2010). Selecting "generalist" species and populations using multi-locational field trials and environmental data may be an important strategy with which to respond to climate change, especially for regions where greater variation in weather conditions is anticipated. Sometimes, trials reveal that trees can have more plastic responses than would be expected based on existing geographic distributions (Box 2).

The mechanisms underlying phenotypic plasticity remain poorly understood, but epigenetic effects, where heritable changes in phenotype are the result of the modification of DNA expression but not sequence, for example through methylation to down-regulate gene activity, may be important (Hedhly *et al*., 2008). Epigenetic effects can be inherited across several generations and be variable across populations and individuals (Bossdorf *et al*., 2008). According to Aitken *et al*. (2008), it is possible that the epigenome provides a buffer against climatic variability that provides time for the genome to "catch up" with change. Epigenetic effects have been demonstrated in the phenology of bud set in *Picea abies*, where progenies whose embryos develop in warm environments are less cold hardy than those that develop under cold conditions (Johnsen *et al*., 2005).

Box 2. Plasticity and the use of climate envelope models: the importance of field trials for "ground-truthing"

Climate envelope models, which operate on the basis that a species is optimally adapted to the habitat conditions of its current range, are frequently used to predict the impacts of climate change. As demonstrated by van Zonneveld *et al*. (2009), however, they can lead to false assumptions for a number of reasons, including inattention to the degree of phenotypic plasticity exhibited by many species, and the absence of taxa from sites with optimal abiotic conditions due to factors such as competition, barriers to migration and large-scale historical disturbances.

The best way to test the accuracy of climate envelope model predictions is through field trials. Ideally, these should include many seed sources from the entire species range and be planted on a range of sites including some outside the native distribution. Thanks to trials set up by the Central America and Mexico Coniferous Resources Cooperative (CAMCORE) over the past two decades, data from such trials were available to van Zonneveld *et al*. (2009) who found that two Central American pine species, *Pinus tecunumanii* and *P. patula* (both important globally for plantation forestry), performed well outside the ecological space defined by the climate envelopes of current distributions. Both species can thus be expected to perform better under climate change than otherwise anticipated. Unfortunately, such data do not exist for the majority of tree species and many more such field trials are needed to produce accurate predictions.

Gene flow: migration by pollen and seed. Gene flow among populations via pollen contributes to genetic variability within populations and hence to adaptive potential (Le Corre and Kremer, 2003). For trees, it is known that pollen travels very long distances, particularly in wind-dispersed social broadleaves and conifers, but also sometimes for animal pollinated species (Jha and Dick, 2010; Kramer *et al*., 2008; Liepelt *et al*., 2002; Oddou-Muratorio *et al*., 2005; Ward *et al*., 2005). Palaeoecological reconstructions of the recolonization of temperate zones in the Holocene have indicated that seeds were also capable of travelling long distances rapidly (Brewer *et al*., 2002; Nathan *et al*., 2002), but these high rates have recently been challenged by new research approaches (e.g. landscape genetics methods), which indicate slower migration (McLachlan *et al*., 2005).

For natural forests in temperate regions, it has been estimated that migration rates of more than 1 km per year may be needed for trees to overcome physiological mismatching and keep pace with current climate change, a rate around ten-fold greater than that observed in the past after glacial maxima (Pearson, 2006; data from pollen core studies and molecular marker analysis, see e.g. McLachlan *et al*., 2005; Olago, 2001; Pearson, 2006; Petit *et al*., 2008). In tropical regions, changes in precipitation may be the key factor to which species have to respond, as evidenced by molecular marker research that indicates dryness as a particular barrier to genetic exchange (e.g. see Muchugi *et al*., 2006, 2008 for discussion of the case of the dry East African Rift Valley limiting past migrations). As with temperate regions, natural migration rates in the tropics will not keep up with anthropogenic climate change except in the case of a small range of invasives that can respond very quickly to change because they are highly precocious, seed are dispersed over exceptionally long distances, and/or trees are very quick to reach maturity (Malcolm *et al*., 2002).

Rates of possible natural migration are reduced by forest degradation and deforestation, increasing vulnerability (Malcolm *et al*., 2002; Kellomäki *et al*., 2001). However, in some cases pollen-mediated gene flow can be enhanced by fragmentation (Ward *et al*., 2005) and trees planted in corridors and as stepping stones in farmland may provide opportunities for "reconnecting" forest patches, allowing forest ecosystems to respond better to environmental change (Bhagwat *et al*., 2008; Thuiller *et al*., 2008).

Due to barriers to migration, the response of trees in natural forests to climate change must generally involve adaptation and/or plasticity, at least in the short term. On the other hand, planted trees are amenable to the "facilitated translocation" of germplasm, which involves human movement of tree seed and seedlings, from existing ranges to sites expected to experience analogous environmental conditions in future years (Guariguata *et al*., 2008; McLachlan *et al*., 2007). A fundamental presumption is that the global circulation models used to explain the environmental changes in temperature and rainfall profiles that result from anthropogenic climate change can be used to predict change with some certainty at given locations; such predictions are, however, not always reliable or precise (Christensen *et al*., 2007).

Although the assisted migration of suitably adapted germplasm sources is recognized as an important response to climate change, the approach has not yet been widely implemented through policy recommendations or practice. For example, in France as in most other nations, local germplasm sourcing is often still recommended on the basis that a certain level of local adaptation can be expected (but see Annex 2), even though in a few decades from now the locations of suitable planting zones may have changed significantly. An exception from Canada is given in Box 3.

Box 3. Changes in seed transfer guidelines in response to climate change: the case of Canada

British Columbia, Canada's most westerly province, has a relatively long history of regulating tree seed movement (Ying and Yanchuk, 2006), but the current concept of "floating" seed zones was not adopted until the mid 1980s. Provenance trials were established for commercially important tree species and concurrently a hierarchical ecological classification of the province's forest land was completed on the basis of geography, climate and vegetation. The boundary of a seed zone is essentially an overlay of adaptive genetic variation onto the ecological classification of forest lands (Ying and Yanchuk, 2006). A seed zone "floats" in the sense that seedlings may be planted outside of the boundary as long as they are within a zone of adaptation based on a statistical predictive model that establishes geographic patterns of local optimality.

Increasing concern about the effects of climate change has led to a new approach in the province. Potential impacts of change were assessed using an ecosystem-based climate envelope modelling method (Hamann and Wang, 2006) and realized niche space was modelled for tree species under current and predicted future climates. The results of analyses were startling in predicting among other effects that tree species that have their northern range limit in British Columbia could gain new suitable habitat at a rate of at least 100 km per decade.

On the basis of this and similar work (Wang *et al*., 2006), seed transfer policies in the province were re-examined and British Columbia now claims to be the first jurisdiction to have modified seed transfer standards specifically in response to climate change. The modest modification allows seed of most species in most areas to be moved 100 to 200 m further upwards in elevation (British Columbia Ministry of Forests, Lands and Natural Resource Operations, 2008). This policy change constitutes an implicit recognition and acceptance of the need for assisted migration to ensure that plantations in the province will be adapted to future climates.

If assisted migration is to be widely adopted as a response strategy, it will require moving increased quantities of germplasm across national boundaries for both research and planting purposes. A recent study, however, indicated that the international transfer of tree germplasm for research purposes has become increasingly difficult and costly in recent years as nations seek to conform to their commitments under the Convention on Biological Diversity; new approaches to facilitate exchange are therefore required (Koskela *et al.*, 2009). At the same time, however, the indiscriminate movement of poorly adapted germplasm, which may be encouraged inadvertently by some regional policies designed to promote free trade in tree seed, is not advisable. In addition, during exchange it is also important to take into account the invasiveness potential of new introductions, which may be enhanced by altering environments (McLachlan *et al.*, 2007; Peterson *et al.*, 2008).

1.4 Potential role of FGR to mitigate climate change

The role of natural forests and tree planting in mitigating climate change through carbon sequestration is well recognized (see e.g. the UN-REDD program: http://new.un-redd.org/Home/tabid/565/Default.aspx). The importance of genetic variation within species for maintaining forests and ensuring productivity in cultivated trees is less often considered. However, as is evident from the discussion above, only adapted and adaptable genetic material will efficiently mitigate, and continue to be able to mitigate, global carbon emissions. For example, mitigation by planted trees will not be successful if poorly adapted seedlings are used; appropriate sourcing of genetic resources is needed with proper site matching. In the case of smallholder plantings in agroforestry systems, trees will only be established if they provide clear livelihood opportunities for local people (Lengkeek and Carsan, 2004). Since the current payment mechanisms to reward farmers for the carbon sequestration functions of agroforestry trees are generally inefficient in reaching growers and modest in value (Jack *et al.*, 2008), the main reason for farmers to plant trees will continue to be for the other products and services that they provide, which depend on quality and yield determined by genetic factors (Roshetko *et al.*, 2007).

There are numerous examples in commercial forestry where poorly-adapted genetic resources have been introduced that have led to massive failures in production. For example, 30 000 ha of *Pinus pinaster* plantations were destroyed by frost in the Landes region of France in the years 1984-5 following the introduction of non frost-resistant material from the Iberian Peninsula (Timbal *et al.*, 2005). The importance of choosing the right genetic resources for climate change mitigation is thus no different from choosing the right genetic material when undertaking assisted migration: germplasm must be appropriately adapted for growing conditions, with some prediction (see above) of how these conditions will change over the productive cycle of the species.

II. CHALLENGES AND OPPORTUNITIES POSED BY CLIMATE CHANGE TO THE USE OF FOREST GENETIC RESOURCES

2.1 How is climate change expected to affect the FGR?

Most tree species will not be able to migrate naturally at a sufficient rate to keep pace with a rapidly changing climate, resulting in elevated mortality rates (Malcolm *et al.*, 2002; Davis *et al.*, 2005; Nathan *et al.*, 2011). High mortality reduces the size of the available gene pool, may increase inbreeding among survivors, and deprives people of the products and services that an intact forest provides. High mortality will be particularly felt in marginal populations at the receding edges of distributions or in localized populations in specific, threatened environments. Tree species that have a mixed mating system (self-fertilization is possible as well as outcrossing) may be somewhat better equipped against environmental changes because inbreeding depression caused by reduced census numbers may not be as severe. The species composition of natural forest will shift with changing climate. In some cases, high-value, less common species will be replaced by "invasive" trees (Malcolm *et al.*, 2002). In these cases, the erosion of genetic resources in high-value species will likely be accelerated by competition for habitat by the invasive taxa. The modification of species composition in mixed stand forests will require changes in silvicultural practice for productive forests (Guariguata *et al.*, 2008).

In plantation forestry, the impact of climate-change mediated insect epidemics can already be observed in western Canada where the mountain pine beetle (*Dendroctonus ponderosae*) has devastated the forest industry throughout much of the interior of the province of British Columbia (Konkin and Hopkins, 2009). The beetle is now attacking more than 13 million hectares of forest in the province. The sustained outbreak is blamed on a long series of unusually warm winters. In addition to the loss of hundreds of thousands of hectares of plantation (and natural) forest, many genetic trials that constituted important sources of genetic information and, in some cases, live genebanks, have been destroyed by the insect. Much of the natural forest will regenerate without the substantial loss of genetic resources, but the destruction of the genetic tests represents an irretrievable loss (although any trees alive in trials after beetle attack may provide a "genetic screen" that points to resistant genotypes).

The interdependence among countries in their needs for tree germplasm is likely to increase because of demands for restoration planting, plantation and agroforestry use; new species and better-adapted varieties will be required. Countries with large-scale plantations of species such as *Pinus radiata* and *Pseudotsuga menziesii* that have been widely planted across (warming) temperate zones of the world, may be particularly affected if such species have low resilience to environmental change because of the material chosen for planting. Breeding programmes will need to consider plasticity and adaptation to increased drought, a substantial change from current practice. In theory, pest and disease attacks caused by climate change could also be addressed through breeding for resistance or tolerance, but Yanchuk and Allard (2009) have suggested that the time required to do so may be too long in relation to the rapid rate of change. Instead, the use of tolerant genotypes already found in nature, or of entirely new species, may be required.

2.2 Specific genetic characteristics/traits needed for adaptation to the challenges identified

A number of climate-related traits in some conifers, such as the timing of bud break in spring, leader shoot growth cessation in summer, bud set in autumn and annual ring lignification, are regulated by temperature during female reproduction; temperature-induced regulation of the level of gene expression (through methylation) in the developing embryos is apparently maintained in the developing trees as an "epigenetic memory" . Many such epigenetic responses have been documented in plants exposed to environmental stresses (Madlung and Comai, 2004), but the mechanisms involved are not fully understood.

Under changing environmental conditions, trees must first survive and then reproduce. To be useful to humans, they must also continue to produce the products and services for which they are valued. Some important traits needed for adaptation to different climatic conditions, but which are not often considered in breeding programmes include the following:

- *Drought resistance:* This is a complex trait that may include deep rooting systems, water use efficiency and deciduous habit. For many tree species, altered moisture regimes will be of greater concern than temperature changes.
- *Pest resistance:* Pest and disease resistance has received little attention in tree breeding. Climate-change mediated increases in pest and disease attacks are becoming a crucial issue in plantation forestry (see above). Conventional breeding approaches are inadequate as a response (Yanchuk and Allard, 2009).
- *Fire resistance/tolerance:* Increased fire frequency results from decreased precipitation and elevated temperatures combined with human activities such as forest clearance (Malhi *et al.*, 2009). Many tree species growing in semi-arid regions have developed mechanisms to confer a degree of resistance to periodic fires, but this may not be the case in more humid forest. Increased fire frequency will require adaptations such as thicker bark.
- *Cyclone resistance/salt tolerance:* The combined effects of a rising sea level and increased storm frequency have the potential to wreak heavy damage on coastal forests. Low-elevation islands are at particular risk. A differential ability to withstand storms and salt may be found more commonly among species than within, but the possibility of selection for suitable types within species needs to be explored.

- *Phenotypic plasticity:* As already discussed, this is an important but little understood characteristic that is vital for an adaptive response to changing climate and can vary at intraspecific level.

III. THE POTENTIAL ROLE OF FOREST GENETIC RESOURCES IN ADAPTING TO AND MITIGATING CLIMATE CHANGE

3.1 Analysis of the present use of FGR: are any of the characteristics needed already in use/available?

The very fact that tree species contain high genetic diversity in many of the traits and genes analysed provides an insurance policy or "option value" against future environmental change (Jump *et al*., 2008). This option value provides "high evolvability" that supports the persistence of natural forest stands that provide useful products (fuel, food, timber, medicine, etc.) and environmental services (biodiversity conservation, watershed protection, carbon sequestration, etc.) to humans. The same variation supports breeding programmes and allows the selection of appropriate genotypes for planting to adapt to and mitigate climate change.

Provenance trials that have been established at multiple locations using germplasm sourced from a variety of ecological conditions demonstrate that variation in adaptive traits is often present within tree species. However, many provenance trials were established before the need to respond to anthropogenic environmental change was considered to be an important research issue, and so the traits measured in trials have often not been the most important ones from a climate change perspective. Nevertheless, the performance of provenances in old multilocational trials provide an insight into behaviour under climate change scenarios and allow sources of (likely) adapted material to be identified while new trials specifically established to assess climate change responses are being established (see Box 1).

There has, however, been a general decline in the establishment of provenance trials in recent years for a variety of reasons, including increased difficulty in international germplasm transfer (see above; Koskela *et al*., 2009), their cost to maintain and measure, greater emphasis on social issues in the forestry sector and more attention to new technologies such as molecular marker analysis of genetic variation. While the latter can provide particular insights, for example in the new discipline of "climate change genomics" (Neale and Ingvarsson, 2008; Reusch and Wood, 2007), molecular analysis should be seen as complementary to field trial analysis and not as an alternative to it. Genomic studies are beginning to focus on the search for candidate genes that may be important in drought tolerance (Hoffmann and Willi, 2008). Association genetic studies in natural stands, where allelic patterns at candidate genes are correlated to phenotypic traits and ecological conditions, are also becoming more common in trees, making it possible to identify genes and variation linked to adaptation (Grivet *et al*., 2011).

3.2 Gaps: knowledge, collections, characterization

As noted above, there is little documented knowledge about adaptive traits or life history characteristics of the majority of tree species globally, particularly in the tropics where species diversity is very high. Although many boreal and temperate tree species are relatively well represented in genebanks, the majority of tropical species are absent. Partly, this reflects the recalcitrant or intermediate properties of the seed of many tropical species, which means that they cannot be stored for any length of time in seed genebanks. Even with boreal and temperate trees, however, capturing the range of genetic variability in species in seed collections has generally received only a low priority.

For all categories of FGR, therefore, there is a general lack of representative seed collections that could form the basis for designing climate change responses. It follows that trials to study adaptive traits important under climate change have also only received limited attention, with significant work done on only a few tree species, mostly those of importance for plantation forestry but not necessarily priority species for other growers (but see Box 1). Even in commercially important species where extensive provenance tests have been undertaken, range margins and atypical populations that may be crucial for climate change responses are rarely well represented. There is, therefore, a general lack of information on which to base proper tree–site matching during translocation. Understanding of the molecular architecture of adaptation is also in its infancy, even for so-called model trees; the application of molecular breeding to combat climate change is, therefore, also not well advanced.

Fundamental to predicting the future geographic "domains" in which particular tree species will (if given the opportunity) grow well depends on understanding current species distributions, information on which is also often lacking (e.g. www.lifemapper.org), and the ecological niche model that is adopted (Peterson *et al*., 2008). Projections of future growth domains are in any case more difficult for perennials than for annual crops, as the long lifespans of trees mean that they can realize products and services (such as carbon storage) over considerable periods of time, possibly centuries from now when climatic conditions will depend on the effectiveness of current mitigation measures (IPCC 2007). This makes tree–site matching for the future very difficult.

3.3 Efforts needed to identify characteristics relevant to adaptation to climate change

Although field and nursery trials have fallen out of favour in recent years, such tests are vital for understanding climate change responses and need to receive new attention. More such trials are needed on a wider range of species important to commercial foresters and small-scale planters, in which emphasis is placed on sampling from all parts of the ecological range of the species under study, not just those populations where survival, growth and biomass yield are best (Aitken *et al*., 2008). It is in "marginal" populations that the most interesting adaptations may be found. During evaluation, more attention needs to be given to the traits that are involved in responses to environmental change.

In addition, genomic studies, in which the quantitative trait loci believed to control responses are studied at the gene level (Namroud *et al*., 2008; Neale and Ingvarsson, 2008; Reusch and Wood, 2007), could be applied. In the case of drought tolerance, which may be a particularly important feature in responding to new climatic conditions, candidate genes include those involved in the synthesis of abscisic acid, transcriptional regulators of drought-inducible pathways, and late embryogenesis abundant proteins; shifts at such loci have been linked to responses to global warming (Hoffmann and Willi, 2008). DNA-based techniques for genomic research are developing very rapidly and need to be extended from temperate model species to a wider range of boreal, temperate and tropical trees, using modern approaches to study relationships between phenotype and genotype, though methodological problems remain to be overcome (Bessega *et al*., 2009; Pauwels *et al*., 2008; Pemberton, 2008).

Neutral molecular markers have been employed to describe patterns of genetic diversity within many tree species and contribute to an understanding of responses to past climate change events through describing genetic disjunctions and refugia (Petit *et al*., 2003, 2008). This information is very helpful for understanding past and current gene flow and population structure and is highly relevant for designing *in situ* conservation networks and prioritizing populations to archive *ex situ*. Generally, however, neutral genetic markers do not improve our understanding of adaptive traits, except perhaps in species with low population sizes (such as rare or endemic species) where demographic bottlenecks are likely to have affected neutral and adaptive genetic diversity similarly (Le Corre and Kremer, 2003).

As well as studies on trees, more research is needed on the impact of climate change on pollinators in forest and agroforestry systems, especially when tree species have specialized relationships with particular animal vectors (Bazzaz, 1998). Declining tree–pollinator interactions that may occur as a result of climate change (NRC, 2007; FAO, 2008) would limit gene flow in tree stands, reducing the effective size of populations and therefore adaptive capacity. The extent of climate change impacts on tree pollinators is, however, not well understood.

Finally, foresters and scientists need to learn from the success and failure of current planting initiatives in responding to climate change. By monitoring die back, mortality and other features in existing stands, much can be learnt when related to the origin of planting material and the silvicultural management that has been applied. Some plantation forests should be left to "suffer" altered environmental conditions in order to observe responses, even when these forests can no longer be considered productive and so would otherwise be replaced.

IV. CONCLUSIONS

Unlike major agricultural crops, the genetic resources of many important tree species have been little studied. Genetic evaluation of a few commercially important species that have been widely planted has mainly aimed to understand the inheritance of productivity-related traits rather than adaptive traits that could be important under climate change, although a few model species are the subjects of genomic research to understand the gene expression of important characteristics. For most trees, understanding the genetic basis of adaptation is still in its infancy and as a result predictions of responses to changing climates are largely based on theory. Furthermore, breeding programmes are generally based on maximizing productivity rather than increasing resilience, for example, through using more genetically diverse varieties and mixtures. Table 1 presents significant knowledge gaps and the action priorities that are needed to address these.

Seed zones and regions of provenance as they exist today, mainly in OECD countries, to define adaptation zones, will likely be of limited value under climate change and will need to be redesigned for climates of the future. The assisted migration of germplasm from existing ranges to sites expected to experience analogous environmental conditions in future years is a possibility for high value species, particularly in the case of managed, plantation and agroforestry ecosystems. Crucial, however, is a greater understanding of trends in climate that will allow proper tree–site matching during translocation (Sáenz-Romero *et al.*, 2010). Assisted migration may not only involve the movement of tree germplasm, but also of associated micro-organisms (such as nitrogen-fixing bacteria essential for the growth of leguminous trees) and important animal pollinators. In the case of natural forests, seed or pollen could be broadcast in areas where current populations are expected to become maladapted under future conditions, and other management actions such as reducing harvesting intensity may be appropriate to respond to change (Guariguata *et al.*, 2008). Genetic resource conservation must be dynamic, as it is the evolutionary potential rather than the genes themselves that require conservation, if climate change responses are to be adequate.

5.1 Access and use conditions (policies)

New approaches and flexible solutions are needed in order to allow more effective transfer of germplasm across national borders and in some cases within countries, possibly through greater inclusion of tree genetic resources within multilateral agreements such as the International Treaty on Plant Genetic Resources for Food and Agriculture and by harmonization of phytosanitary requirements (Koskela *et al.*, 2009).

Policies and regulations will also need to be developed or modified in the following three areas if future generations are to benefit from the potential of today's forest genetic resources:

- Regulations will need to be developed in coming years to meet the requirements of the Nagoya Protocol. It will be important to ensure that these regulations have the intended effect of actively promoting increased research on, access to and exchange of forest genetic resources, while at the same time guaranteeing the fair and equitable sharing of benefits arising from their utilization, bearing in mind that increased access will in the end foster benefits for all.
- National policies defining seed zones will need to be modified to allow the assisted migration of genetic material within countries and across country boundaries in order to respond to the speed of climate change.
- Market mechanisms are needed to reward the use of appropriate germplasm and conservation activities by growers, especially smallholder farmers, who are increasingly important as harbourers of tree biodiversity in the tropics.

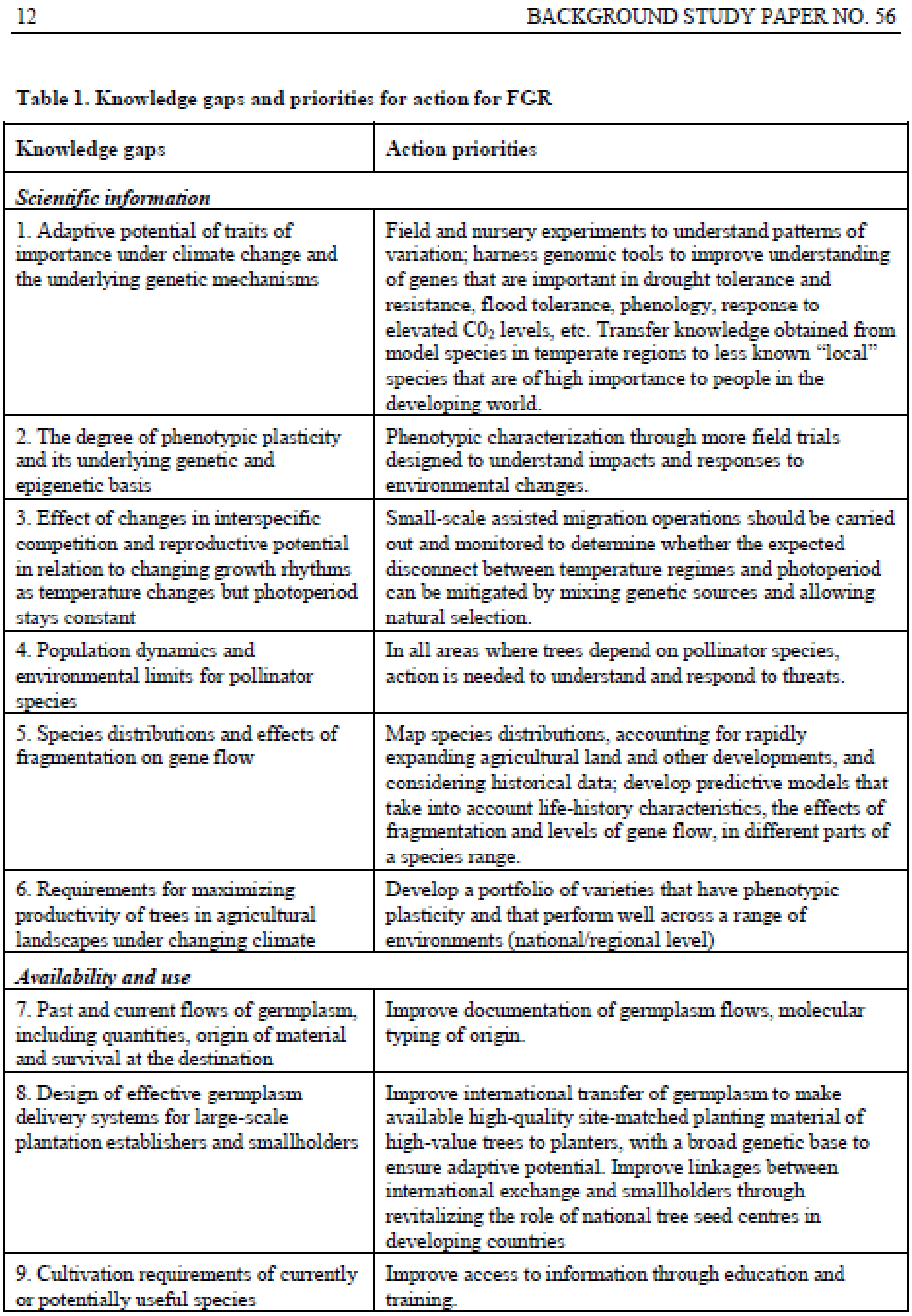

Table 1. Knowledge gaps and priorities for action for FGR

Knowledge gaps	**Action priorities**
Scientific information	
1. Adaptive potential of traits of importance under climate change and the underlying genetic mechanisms	Field and nursery experiments to understand patterns of variation; harness genomic tools to improve understanding of genes that are important in drought tolerance and resistance, flood tolerance, phenology, response to elevated CO_2 levels, etc. Transfer knowledge obtained from model species in temperate regions to less known "local" species that are of high importance to people in the developing world.
2. The degree of phenotypic plasticity and its underlying genetic and epigenetic basis	Phenotypic characterization through more field trials designed to understand impacts and responses to environmental changes.
3. Effect of changes in interspecific competition and reproductive potential in relation to changing growth rhythms as temperature changes but photoperiod stays constant	Small-scale assisted migration operations should be carried out and monitored to determine whether the expected disconnect between temperature regimes and photoperiod can be mitigated by mixing genetic sources and allowing natural selection.
4. Population dynamics and environmental limits for pollinator species	In all areas where trees depend on pollinator species, action is needed to understand and respond to threats.
5. Species distributions and effects of fragmentation on gene flow	Map species distributions, accounting for rapidly expanding agricultural land and other developments, and considering historical data; develop predictive models that take into account life-history characteristics, the effects of fragmentation and levels of gene flow, in different parts of a species range.
6. Requirements for maximizing productivity of trees in agricultural landscapes under changing climate	Develop a portfolio of varieties that have phenotypic plasticity and that perform well across a range of environments (national/regional level)
Availability and use	
7. Past and current flows of germplasm, including quantities, origin of material and survival at the destination	Improve documentation of germplasm flows, molecular typing of origin.
8. Design of effective germplasm delivery systems for large-scale plantation establishers and smallholders	Improve international transfer of germplasm to make available high-quality site-matched planting material of high-value trees to planters, with a broad genetic base to ensure adaptive potential. Improve linkages between international exchange and smallholders through revitalizing the role of national tree seed centres in developing countries
9. Cultivation requirements of currently or potentially useful species	Improve access to information through education and training.

Conservation	
10. Regions where high genetic diversity and significant threats coincide	Implement risk assessments and threat analyses to identify coincidence. Prioritize conservation of populations on the basis of importance to people, high diversity and significant threat.
11. Most effective mix of *in situ, circa situ* and *ex situ* approaches to ensure conservation and maintain evolutionary processes	Increase population representation and genetic diversity of important and threatened species in conservation areas, in farmland and in seed collections.
12. Seed storage behaviour and germination requirements for many important species	New approaches for "genebanking" are needed for many tropical species through seed physiology research, cryopreservation, pollen storage, etc. Active conservation measures are needed for species that are important for human well-being and are seriously threatened.
13. Costs and benefits of FGR conservation	Application of economic valuation approaches developed for other sectors to FGR, with an emphasis on high-value species for foresters and small-scale farmers.

Box 4. Glossary

Adaptation: The process of genetic change in structure and/or function that makes an organism or a population better suited to survive in an environment (FAO 2003; Koski *et al*., 1997).

Assisted migration: Otherwise known as facilitated translocation, a response under climate change in which populations are moved to compensate for environmental alterations to new sites expected to experience analogous conditions to the ones they originated in (Aitken *et al*., 2008).

Common garden experiments: field experiments in which seed sources from different locations are brought together for assessment under common environmental conditions.

Epigenetics: The study of heritable changes in gene expression and function that cannot be explained by changes in DNA sequence. These changes are based on a set of molecular processes that can activate, reduce or completely disable the activity of particular genes. The different classes of processes are not independent from each other but often regulate gene activity in a complex, interactive fashion (Berger, 2007; Bird, 2007; Bossdorf *et al*., 2008; Grant-Downton and Dickinson, 2005; Richards, 2006).

Leading edge: In a model of colonization under changing climate, the leading edge is the front of the distribution expanding into new, suitable territory. Expansion may be controlled by rare long-distance dispersal events followed by exponential population growth (Hampe and Petit, 2005).

Phenotypic plasticity: the ability of an organism to change its phenotype in response to changes in the environment without genetic change (Gienapp *et al*., 2008; Price *et al*., 2003).

Provenance: The geographical and/or genetic origin of an individual (FAO, FLD, IPGRI, 2004).

Receding edge: In a model of colonization under changing climate, the receding edge is the range margin which is eroding and where populations are likely to experience demographic bottlenecks. Populations located at eroding range margins may migrate with climate change or remain trapped in suitable environments while the general range of the species is moving (Hampe and Petit, 2005).

Resilience: resilience is one possible ecosystem response to a perturbation or disturbance. A resilient ecosystem resists damage and recovers quickly from disturbances such as fires, flooding, windstorms, insect population explosions, and human activities such as deforestation and the introduction of exotic plants or animals. However, disturbances of sufficient magnitude or duration may force an ecosystem to reach a threshold beyond which a different regime of processes and structures predominates . The "demographic" and "microclimatic" inertia (caused by longevity and the control of own climate, respectively) of trees may promote a level of resilience.

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ANNEX 1

EXAMPLE OF NATIONAL GUIDELINES FOR MANAGEMENT OF FOREST GENETIC RESOURCES UNDER CLIMATE CHANGE FROM FRANCE'S COMMISSION ON FOREST GENETIC RESOURCES

Commission on Forest Genetic Resources

DGPAAT/ SOUS-DIRECTION DE LA FORÊT ET DU BOIS

Preservation and use of the diversity of forest genetic resources to strengthen the adaptability of forests to climate change

Genetic resources cover an area of biodiversity of actual or potential value. In forests, genetic diversity of trees is also a key factor which fosters general biodiversity of the ecosystem and interacts with its function. The diversity within species is not always easy to observe but it exists between and within populations of trees. Driven by the laws of genetics, it is dynamic, through seed and pollen flows between stands and by selection, be it natural or artificial. In the context of climate change, sustainable long term preservation of this legacy is both supportive and dependent upon the local management of forest.

We deal here with the management of genetic diversity within each species, while acknowledging that mixed species silvicultural treatments are, of course, fully justified for sustainable management in the context of climate change.

We make some important general recommendations, without systematically detailing each type of forest management. In many cases, several options are open and there is no unique solution.

In parallel to these recommendations devoted to standard forest management, specific programmes for conservation and experimental transfer of genetic resources will be led by researchers, in particular on CRGF 's initiative

Commission Ressources Génétiques Forestières,/Commission on Forest Genetic Resources (*)
(*) This commission, whose membership is made up of scientists, public and private forest managers, and a representative of the "forest" network of France Nature Environnement, advises the Ministry of Agriculture, Food & Fisheries, implements a strategy for the evaluation and the conservation of genetic diversity in forest tree species in France.
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1 – The climatic context: a continuous change with sharp annual and regional variations

The experts of the Intergovernmental Panel on Climate Change (IPCC) predict a significant change in the climate over the next century, with a sharp rise in average temperature, changes in rainfall and more frequent extreme events (heat waves, droughts, floods, storms, etc.). These changes, while certain, will vary from one region to another. Many uncertainties remain as to the amplitude of annual variations (e.g. will the increase in average temperature be accompanied by the disappearance of frost risk ?) as well as global ecological changes induced by climate change (parasites, mycorrhizae, pollinators, seed dispersers, new invasive species etc.).

Climate change is a long- term process. During the course of the next century, forests will need to cope with a series of environmental conditions which are difficult to foresee and will no doubt be completely novel as regards their physical (temperature, drought) and biological dimensions. It is over the same timescale that today's decisions will produce effects.

2 – Genetic context: an adaptive potential to be fully used...

If current forest ecosystems are to remain in good health, much will depend on the capacity of existing trees to survive and reproduce and on adaptive changes in the forthcoming regeneration phases. The adaptive potential of a forest is its capacity to evolve genetically from one generation to the next. The drivers of genetic evolution can be natural, artificial, or both.

It is generally difficult to predict existing trees' capacity to respond to the changes they will experience in coming years (notwithstanding the uncertainty as to future climatic and ecological scenarios). On the other hand, what we do know is that forest trees are usually characterised by wide genetic diversity within individual stands: such diversity is the essential "fuel" for the proper functioning of natural selection, the mechanism which leads to adaptation. Diversity within stands varies between species (generally more limited for species whose areas are fragmented), and also for the same species from the centre to the margin of its distribution area. However, historical examples of forest material transfer have shown that genetic diversity is sufficient to encompass major adaptive changes in no more than one or two generations.

Convinced that major ecological changes will occur, but unable to describe accurately the environment of the future, we need to take maximum advantage of the adaptive potential. Consequently, we must follow two objectives:

- **the maintenance of genetic diversity over the long term by using appropriate forestry practices, and**
- **the fostering of evolutionary processes to keep stands adapted to their changing environment as closely as possible in what is a "race for change".**

QUALITY NOTIONS IN GENETIC RESOURCES

The "best quality" = a subjective criterion based on multiple parameters (economic, ecological, etc.) in relation to the goals assigned to the forest at a given time.

Adaptation = quality of population survival, growth and reproduction in the prevailing environment.

Adaptability = capacity of a population to change in a changing environment, including the plasticity (variation in morphology or physiology as a response to environmental change) of existing trees and genetic evolutions from generation to generation.

Local regions of provenance offer guarantees of good adaptation to local conditions. Their adaptability will not necessarily be sufficient : this will depend on their genetic diversity and on the intensity of environmental change.

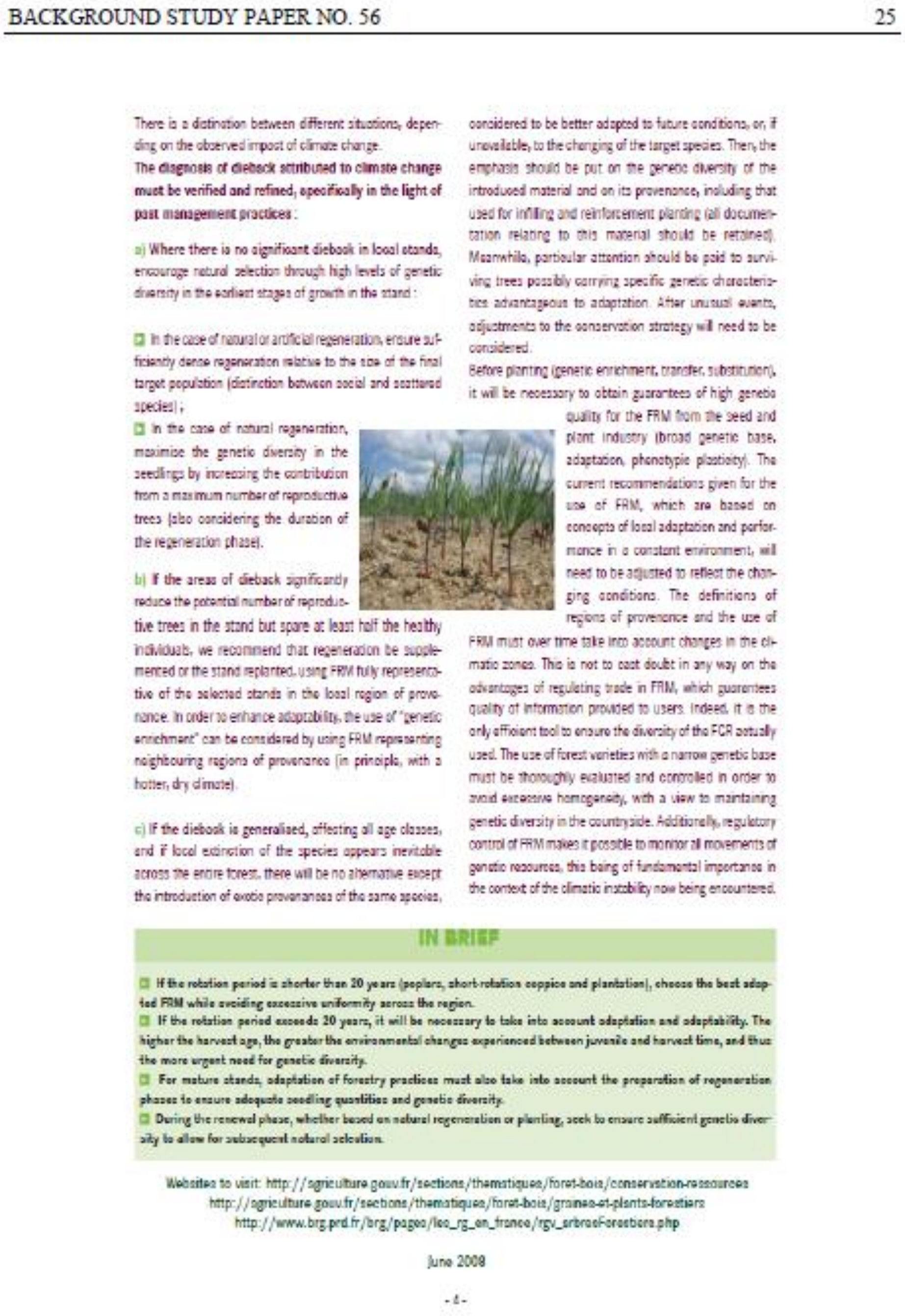
3 – Recommendations: graduated responses matching dieback intensity in forest ranges or regions

There is today a need for gradual response to raising issues, and for avoiding ill-founded measures of adaptation. While remaining active and vigilant, two pitfalls must be avoided:

- ☐ the substitution of provenances or species may be necessary in some cases, but hasty moves towards complete replacement and reckless elimination of genotypes which might survive in new conditions would not meet the objective of fostering the evolution of our genetic resources in the long term.
- ☐ the immoderate use of a single Forest Reproductive Material (FRM) supposed to be the panacea, which might endanger the preservation of genetic diversity in our resources.

Forestry practices may influence genetic diversity and evolution processes in the context of climate change. Natural selection between seedling or sapling is an important evolutionary process. Choosing natural re-generation allows the most effective advantage to be taken from the genetic diversity available within the stand. Planting can be beneficial using FRM from recommended sources and varieties selected for their adaptive characteristics or plasticity. In this case, a higher initial density of the species will enhance the opportunity for further natural selection.

Renewal by:	Natural regeneration	Planting of material from the local region of provenance	Planting of introduced material (in an area where the species is already present)
Advantages	- good adaptation - good sampling of locally available genetic diversity - allows natural selection to operate - good integration into the ecosystem, reinforcing its general resistance (co-adaptation)	- good adaptation - material usually from selected stands chosen for their quality - fairly good integration into the ecosystem, ensuring satisfactory general resistance	- remedies a lack of local genetic diversity - contributes to new adaptations
Disadvantages	- risk of a limited number of effectively reproducing trees - risk of a small number of seedlings - risk that local genetic diversity is too limited and ultimately unable to adapt to the scale of changes	- risk of poor sampling of the genetic diversity during seed harvest - leaves less room for natural selection - risk that regional genetic diversity is too limited and ultimately unable to adapt to the scale of changes	- risk of maladaptation - risk that overall genetic diversity will decline in case of massive introduction of material with a narrow genetic basis - risk of inducing "genetic suffocation" of a local resource under threat - risk of further disturbance to an already weakened ecosystem
Recommended management practices	- maximise the effective number of reproductive trees - ensure sufficient seedling density at least in the very early stage, or consider additional planting	- mix selected stands within the region of provenance where technically feasible - increase the initial planting density	- introduce material originating from a neighbouring region, in principle one with a drier climate - introduce material with a broad genetic base



There is a distinction between different situations, depending on the observed impact of climate change.

The diagnosis of dieback attributed to climate change must be verified and refined, specifically in the light of past management practices :

a) **Where there is no significant dieback in local stands,** encourage natural selection through high levels of genetic diversity in the earliest stages of growth in the stand :

- In the case of natural or artificial regeneration, ensure sufficiently dense regeneration relative to the size of the final target population (distinction between social and scattered species) ;
- In the case of natural regeneration, maximise the genetic diversity in the seedlings by increasing the contribution from a maximum number of reproductive trees (also considering the duration of the regeneration phase).

b) **If the areas of dieback** significantly reduce the potential number of reproductive trees in the stand but spare at least half the healthy individuals, we recommend that regeneration be supplemented or the stand replanted, using FRM fully representative of the selected stands in the local region of provenance. In order to enhance adaptability, the use of "genetic enrichment" can be considered by using FRM representing neighbouring regions of provenance (in principle, with a hotter, dry climate).

c) **If the dieback is generalised,** affecting all age classes, and if local extinction of the species appears inevitable across the entire forest, there will be no alternative except the introduction of exotic provenances of the same species, considered to be better adapted to future conditions, or, if unavailable, to the changing of the target species. Then, the emphasis should be put on the genetic diversity of the introduced material and on its provenance, including that used for infilling and reinforcement planting (all documentation relating to this material should be retained). Meanwhile, particular attention should be paid to surviving trees possibly carrying specific genetic characteristics advantageous to adaptation. After unusual events, adjustments to the conservation strategy will need to be considered.

Before planting (genetic enrichment, transfer, substitution), it will be necessary to obtain guarantees of high genetic quality for the FRM from the seed and plant industry (broad genetic base, adaptation, phenotypic plasticity). The current recommendations given for the use of FRM, which are based on concepts of local adaptation and performance in a constant environment, will need to be adjusted to reflect the changing conditions. The definitions of regions of provenance and the use of FRM must over time take into account changes in the climatic zones. This is not to cast doubt in any way on the advantages of regulating trade in FRM, which guarantees quality of information provided to users. Indeed, it is the only efficient tool to ensure the diversity of the FCR actually used. The use of forest varieties with a narrow genetic base must be thoroughly evaluated and controlled in order to avoid excessive homogeneity, with a view to maintaining genetic diversity in the countryside. Additionally, regulatory control of FRM makes it possible to monitor all movements of genetic resources, this being of fundamental importance in the context of the climatic instability now being encountered.

IN BRIEF

- **If the rotation period is shorter than 20 years (poplars, short-rotation coppice and plantation), choose the best adapted FRM while avoiding excessive uniformity across the region.**
- **If the rotation period exceeds 20 years, it will be necessary to take into account adaptation and adaptability. The higher the harvest age, the greater the environmental changes experienced between juvenile and harvest time, and thus the more urgent need for genetic diversity.**
- **For mature stands, adaptation of forestry practices must also take into account the preparation of regeneration phases to ensure adequate seedling quantities and genetic diversity.**
- **During the renewal phase, whether based on natural regeneration or planting, seek to ensure sufficient genetic diversity to allow for subsequent natural selection.**

Websites to visit: http://agriculture.gouv.fr/sections/thematiques/foret-bois/conservation-ressources
http://agriculture.gouv.fr/sections/thematiques/foret-bois/graines-et-plants-forestiers
http://www.brg.prd.fr/brg/pages/les_rg_en_france/rgv_arbresForestiers.php

June 2008

Plant Pathology (2011) 60, 133–149

Doi: 10.1111/j.1365-3059.2010.02406.x

Plant Pathology

REVIEW

Climate change and forest diseases

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As climate changes, the effects of forest diseases on forest ecosystems will change. We review knowledge of relationships between climate variables and several forest diseases, as well as current evidence of how climate, host and pathogen interactions are responding or might respond to climate change. Many forests can be managed to both adapt to climate change and minimize the undesirable effects of expected increases in tree mortality. We discuss four types of forest and disease management tactics – monitoring, forecasting, planning and mitigation – and provide case studies of yellow-cedar decline and sudden aspen decline to illustrate how forest diseases might be managed in the face of climate change. The uncertainties inherent to climate change effects can be diminished by conducting research, assessing risks, and linking results to forest policy, planning and decision making.

Keywords: forest management, forest pathogens, plant disease management, plant pathogens, sudden aspen decline, yellow-cedar decline

Introduction

Forests provide critical refuges for terrestrial biodiversity, are a central component of the earth's biogeochemical systems, and are a source of ecosystem services essential for human wellbeing (Shvidenko *et al.*, 2005). Forests also have the potential to mitigate global climate change by serving as net carbon sinks (IPCC (Intergovernmental Panel on Climate Change), 2007). Global forest area has been reduced by 40% over the last three centuries, primarily as a result of human activities, particularly the conversion of forested land to agricultural usage (Shvidenko *et al.*, 2005). Today, less than one-third of the earth's land area is covered by forests (FAO, 2001). Disturbance agents such as pathogens, insects and fire can decrease the ability of forests to provide goods and services, especially when the natural disturbance patterns or regimes of these agents are altered by human activities (Lewis & Lindgren, 2000; Bentz *et al.*, 2010).

Climate has always shaped the world's forests (Bhatti *et al.*, 2006), but today the world's climate has become warmer and will change further and at an unprecedented rate (Pachauri & Reisinger, 2007). For example, for the next two decades a warming of about 0·2°C per decade is projected for a range of emissions scenarios (Nakicenovic & Swart, 2000; Pachauri & Reisinger, 2007). Recent extensive tree death events in North America have been associated with climate change (Kurz *et al.*, 2008; van Mantgem *et al.*, 2009). Climate change has the potential to initiate multiple, interacting processes that affect forests (Williamson *et al.*, 2009), some positive and others negative. For example, higher atmospheric CO_2 concentrations can result in increased growth rates and water use efficiency of trees (Rogers & Dahlman, 1993), or there may be a reduced effect of carbon fertilization on tree productivity over time and in older trees (Boisvenue & Running, 2006). Elevated CO_2 was shown to increase host resistance to two forest diseases in the southern USA (Runion *et al.*, 2010). Because responses to CO_2 enrichment may differ among species and locations, a wide range of responses to increased atmospheric CO_2 should be expected worldwide.

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The purpose of this paper is to improve understanding and management of forest tree diseases under a changing climate. We do this by reviewing knowledge of relationships between climate variables and several forest pathogens and by examining current evidence demonstrating climate change, host and pathogen interactions. We also recommend and discuss forest health and forest management strategies that should be integrated to better contend with forest diseases and climate change.

The literature on climate change and forest and tree diseases has recently been synthesized (for example: Boland *et al.*, 2004; Desprez-Loustau *et al.*, 2007; Sturrock, 2007; La Porta *et al.*, 2008; Moore & Allard, 2008; Dukes *et al.*, 2009; Kliejunas *et al.*, 2009; Tubby & Webber, 2010) and some general predictions can be made:

- Because most plant diseases are strongly influenced by environmental conditions, climate change will affect the pathogen, the host and the interaction between them, resulting in changes in disease impact.
- Because abiotic factors such as temperature and moisture affect host susceptibility to pathogens and pathogen growth, reproduction and infection, changes in interactions between biotic diseases and abiotic stressors may represent the most substantial drivers of disease outbreaks.
- The distribution of hosts and diseases will change. Increases in temperature and changes in precipitation may allow the ranges of some species to expand, perhaps whilst contracting elsewhere, but models frequently predict a reduction in potential geographic distribution of tree species (e.g. Rehfeldt *et al.*, 2009) or diseases (Venette, 2009) as a result of climate change. This question has also stimulated debate with regard to infectious diseases of humans (Epstein, 2010). Pathogens may play key roles in this range reduction in forest trees.
- Pathogens that typically affect water-stressed hosts are likely to have an increased impact on forests in regions where precipitation is reduced.
- The roles of pathogens as disturbance agents will probably increase, as their ability to adapt to new climatic conditions will be greater than that of their long-lived hosts.
- Most pathogens will be able to migrate to locations where climate is suitable for their survival and reproduction at a faster rate than tree species.
- Climate change will affect the life cycles and biological synchronicity of many forest trees and pathogens, resulting in changes in the distribution and phenology of events such as budbreak in tree hosts, spore release by pathogens, and activities of insects that serve as vectors of pathogens; this may significantly alter disease incidence and severity.

Definitions

A plant disease is defined as "any malfunctioning of host cells and tissues that results from continuous irritation by a pathogenic agent or environmental factor and leads to the development of symptoms" (Agrios, 2005). Three interrelated elements result in disease: a susceptible host plant, a virulent pathogen and a favourable environment or climate and are often visualized as the 'disease triangle'.

Forest pathogens include fungi, oomycetes, bacteria, phytoplasmas, parasitic higher plants, viruses and nematodes. Native forest pathogens, which are integral components of many forest ecosystems (Hansen & Goheen, 2000), influence species richness and abundance, and forest succession, structure and composition at the stand and landscape levels (Winder & Shamoun, 2006). They also strongly affect animal populations, nutrient and water cycling, and overall ecosystem function. Native forest pathogens sometimes conflict with management objectives and the pathogens can damage valued forest resources.

Non-native or introduced forest pathogens are also widespread globally and strongly influence forest structure and composition (Dukes *et al.*, 2009). These pathogens have the potential to kill many trees, sometimes almost all individuals of a given species in a stand or landscape, because novel hosts have not coevolved with the pathogens and have limited resistance (Hansen, 2008). A similar dynamic may be observed when non-native hosts are infected by native pathogens.

Noninfectious or abiotic forest diseases are caused by persistent, nonliving factors that are directly deleterious to tree health (for example, drought, nutrient deficiency and pollution) (Boyce, 1961).

Forest decline diseases are complex and involve interacting factors (Manion, 1991; Manion & Lachance, 1992). *Predisposing factors* are long-term, static or slowly changing factors, such as soil moisture regime (a site factor), stand density (a stand factor) and precipitation (a climate factor). *Inciting factors* are short-term factors, such as defoliating insects or drought, which cause acute stress. Trees affected by inciting factors alone may recover quickly, but recovery is much slower if the trees also are affected by predisposing factors. *Contributing factors* are usually secondary pathogens or insects that kill trees already affected by predisposing and inciting factors.

Climate can be narrowly defined as the average weather, or, more rigorously, as a statistical description in terms of the mean and variability of relevant quantities (e.g. temperature, precipitation and wind), over a period of, typically, 30 years (Pachauri & Reisinger, 2007). Climate change "refers to a change in the state of the *climate* that can be identified (e.g. by using statistical tests) by changes in the mean and/or variability of its properties, and that persists for an extended period, typically decades or longer" (Pachauri & Reisinger, 2007). Climate change should be differentiated from short-term and normal decadal climate cycles, such as the El Niño-Southern Oscillation and the Pacific Decadal Oscillation.

If host susceptibility or pathogen virulence and/or aggressiveness is increased by climatic conditions, then a disease outbreak or epidemic may result (Agrios, 2005).

An epidemic is defined as a change of disease intensity in populations over time and space (Campbell & Madden, 1990), but the term is usually used to describe a widespread and severe outbreak. Plant disease epidemics may become more frequent as climate changes. Epidemics of insects and pathogens that are mobile or easily dispersed, and can kill their hosts relatively quickly, are examples of pests particularly likely to increase in frequency (Ayres & Lombardero, 2000). Many forest pathogens can take decades to spread and then to kill their hosts, yet their long-term, cumulative effects can be serious. Rates of spread of these agents and rates of tree mortality may be significantly altered by climate change.

Case studies

Climate influences the dynamics of host–pathogen interactions, so it is likely that climate change will have strong effects on the distribution (Pearson & Dawson, 2003) and behaviour of plant species and pathogens. In this section we review knowledge of relationships between climate variables and several forest diseases, as well as current evidence of how hosts, pathogens and pathosystems are responding or might respond to climate change. Currently, there are several models available to project future distribution of forest trees using climate variables (e.g. Hamann & Wang, 2006; Rehfeldt *et al.*, 2006), but relatively few specifically designed for making such projections for forest pathogens. CLIMEX, a dynamic simulation model developed in Australia (Sutherst *et al.*, 1999) for predicting the potential geographical distribution of a given species, and widely used for weeds (e.g. Goolsby, 2004), has been used to investigate the potential distribution of several pathogens (e.g. Brasier & Scott, 1994; Scherm & Yang, 1999; Venette & Cohen, 2006). Also, in Portugal, under the PHRAME (Plant Health Risk and Monitoring Evaluation) project, there has been progress made on prediction modelling for expression of pine wilt disease (Evans, 2007). For Swiss needle cast, Manter *et al.* (2005) developed a temperature-based disease prediction model in combination with geographical information systems-linked climate databases to estimate disease levels for areas in the Oregon Coast Range of the USA.

We have divided diseases and their causal pathogens or agents into three groups: diseases caused by pathogens directly affected by climate; diseases caused by pathogens indirectly affected by climate; and decline diseases. There is wide consensus that future temperatures will be warmer in much of the world; there is less certainty over future precipitation trends (IPCC (Intergovernmental Panel on Climate Change), 2007). Thus, in Table 1, we present predicted trends for the impacts of these forest diseases under two climate-change scenarios, the first with warmer and drier conditions, the second with warmer and wetter conditions. The effects of climate change on forest diseases and forest ecosystems will depend on the pathosystem and its location (Runion, 2003; Sturrock, 2007) and predicted changes in impact and accompanying uncertainty levels for sample diseases will vary under the two scenarios.

Pathogens directly affected by climate

This group of pathogens can cause disease in a healthy, vigorous host, if the pathogen's environmental requirements are met. Their life cycles are directly affected by temperature and moisture. For example, many pathogens causing needle diseases are sensitive to precipitation and humidity and their rates of reproduction, spread, and infection are greater when conditions are moist (Harvell *et al.*, 2002). In these cases, changes in temperature and moisture more directly affect the pathogen regardless of their effects on the host.

Phytophthora root rot

Among the various species of *Phytophthora* infecting woody plants the soilborne *Phytophthora cinnamomi* is one of the most destructive. This pathogen is present in most temperate and subtropical areas of the world causing disease in more than 1000 host species. Infection by *P. cinnamomi* and some other related species results in root rot and cankering, and often plant death. Temperature, moisture and pH all influence pathogen growth and reproduction. Floods and droughts are generally accepted as triggers of epidemics. Changes in climatic conditions in the last 60 years, i.e. increased mean winter temperatures, seasonal precipitation shift from summer into winter and a tendency to heavy rain are favouring infection by several species of *Phytophthora* in Central Europe. A proliferation of phytophthora root rots may be expected, increasing the instability and vulnerability of forest ecosystems dominated by beech and other susceptible tree species, including oak, alder, maple, fir and pine species (Jung, 2009).

For *P. cinnamomi*, Bergot *et al.* (2004) predict that increasing temperatures will lead to a potential range expansion of *P. cinnamomi* along the western coast of Europe of one to a few hundred kilometres eastward from the Atlantic coast within one century. For root rot caused by *P. cinnamomi*, CLIMEX models predict more widespread disease in the UK and much of coastal Europe; and globally, a marked increase of the disease in temperate zones of the northern and southern hemispheres, with a reduction across the tropics and subtropics (Brasier & Scott, 1994; Brasier, 1996).

Sudden oak death; ramorum blight

Phytophthora ramorum is an important invasive pathogen in both North America and Europe. In wildlands in the USA the disease is known to occur only in central coastal California and southwest Oregon, where infected *Notholithocarpus densiflorus* and *Quercus agrifolia* can die relatively soon after the onset of symptoms (crown dieback, stem bark lesions). In Europe in the late 1990s the pathogen was primarily found on ornamental plants in nurseries and gardens. However, in 2003 *P. ramorum*

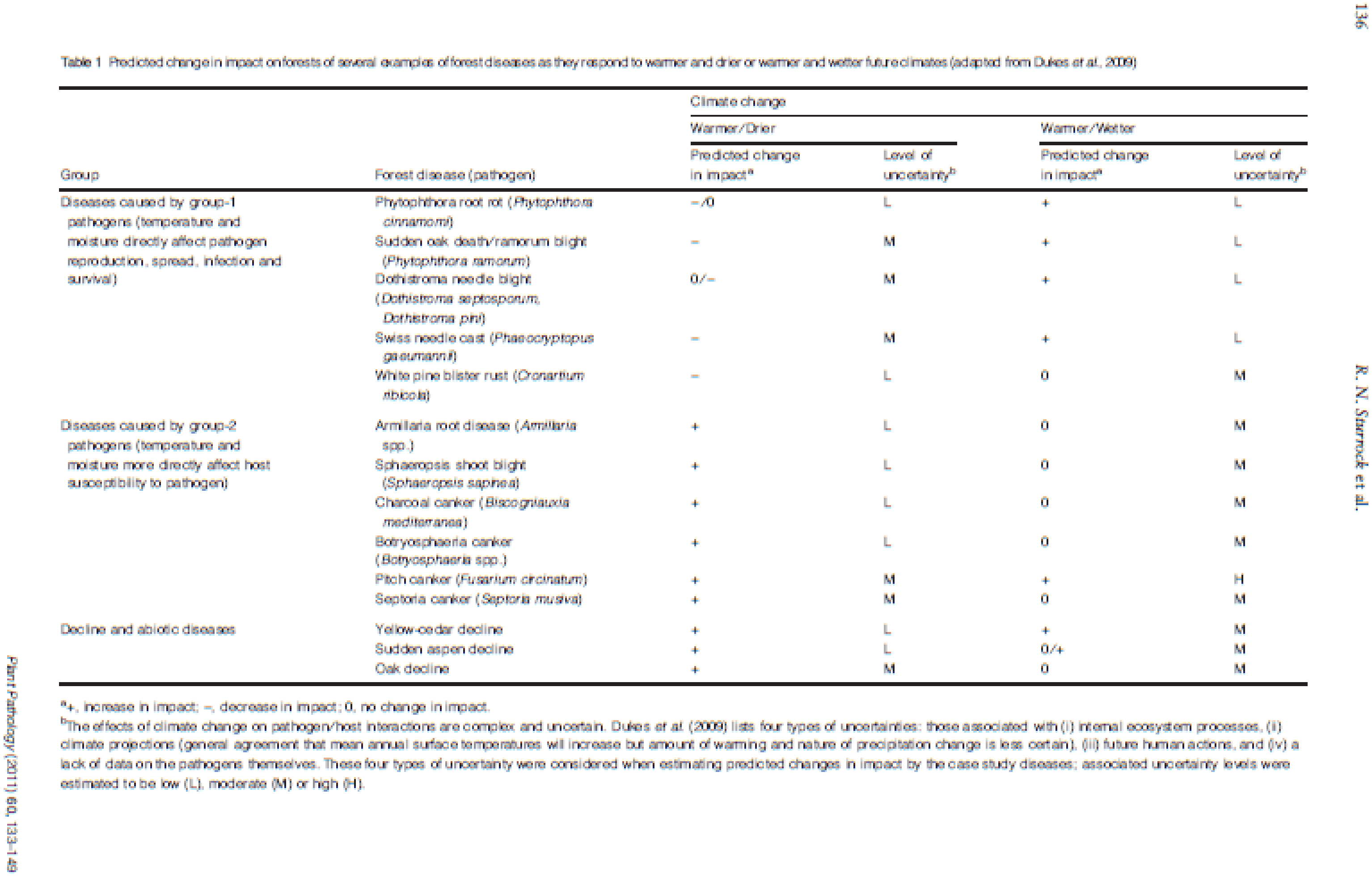

Table 1 Predicted change in impact on forests of several examples of forest diseases as they respond to warmer and drier or warmer and wetter future climates (adapted from Dukes *et al*., 2009)

Group	Forest disease (pathogen)	Climate change			
		Warmer/Drier		Warmer/Wetter	
		Predicted change in impact[a]	Level of uncertainty[b]	Predicted change in impact[a]	Level of uncertainty[b]
Diseases caused by group-1 pathogens (temperature and moisture directly affect pathogen reproduction, spread, infection and survival)	Phytophthora root rot (*Phytophthora cinnamomi*)	–/0	L	+	L
	Sudden oak death/ramorum blight (*Phytophthora ramorum*)	–	M	+	L
	Dothistroma needle blight (*Dothistroma septosporum, Dothistroma pini*)	0/–	M	+	L
	Swiss needle cast (*Phaeocryptopus gaeumannii*)	–	M	+	L
	White pine blister rust (*Cronartium ribicola*)	–	L	0	M
Diseases caused by group-2 pathogens (temperature and moisture more directly affect host susceptibility to pathogen)	Armillaria root disease (*Armillaria* spp.)	+	L	0	M
	Sphaeropsis shoot blight (*Sphaeropsis sapinea*)	+	L	0	M
	Charcoal canker (*Biscogniauxia mediterranea*)	+	L	0	M
	Botryosphaeria canker (*Botryosphaeria* spp.)	+	L	0	M
	Pitch canker (*Fusarium circinatum*)	+	M	+	H
	Septoria canker (*Septoria musiva*)	+	M	0	M
Decline and abiotic diseases	Yellow-cedar decline	+	L	+	M
	Sudden aspen decline	+	L	0/+	M
	Oak decline	+	M	0	M

[a] +, increase in impact; –, decrease in impact; 0, no change in impact.

[b] The effects of climate change on pathogen/host interactions are complex and uncertain. Dukes *et al.* (2009) lists four types of uncertainties: those associated with (i) internal ecosystem processes, (ii) climate projections (general agreement that mean annual surface temperatures will increase but amount of warming and nature of precipitation change is less certain), (iii) future human actions, and (iv) a lack of data on the pathogens themselves. These four types of uncertainty were considered when estimating predicted changes in impact by the case study diseases; associated uncertainty levels were estimated to be low (L), moderate (M) or high (H).

was found infecting mature *Quercus falcata* in the UK and *Quercus rubra* in the Netherlands. In subsequent years, over 20 different species of broadleaved trees (mainly mature *Betula*) were found to be infected with *P. ramorum* in the south of England (Webber, 2008). Since autumn 2009 there have been dramatic outbreaks of the disease in the UK, affecting stands of *Larix kaempferi* (Webber *et al.*, 2010) (Fig. 1) and several new host species (e.g. *Tsuga heterophylla*) (Brasier *et al.*, 2010). In the USA and Europe, eradication and containment strategies are being used. Regulations on movement of nursery stock and forest materials have been imposed in more than 50 countries (Kliejunas, 2010).

The life cycle of *P. ramorum*, an organism with optimal growth between 18 and 22°C, is similar to that of other aerial *Phytophthora* species. Sporangia produced on the surfaces of infected leaves and twigs of foliar hosts can be splash-dispersed to neighbouring hosts or conveyed longer distances by windblown rain (Davidson *et al.*, 2005). Moisture is essential for survival and sporulation, and the duration, frequency, and timing of rain events during the winter and spring play a key role in inoculum production. In *N. densiflorus* forests of central coastal California, winter rains are critical to persistence of the pathogen, whereas in coastal evergreen forests rain must fall in March, April and May. Increases in precipitation will probably produce optimal conditions for the pathogen in some areas, resulting in an increase in rates of infection. Scenarios of climate change produced by CLIMEX projected that the area favourable or very favourable for *P. ramorum* will decrease substantially in the eastern USA, but will increase in the west-coast states of Washington, Oregon and California (Venette & Cohen, 2006; Venette, 2009).

Dothistroma needle blight

Dothistroma needle blight – also referred to as red band needle blight – affects primarily pines (*Pinus* spp.), but also species of spruce (*Picea*), larch (*Larix*) and Douglas fir (*Pseudotsuga menziesii*) (Watt *et al.*, 2009). The disease is caused by the needle pathogens *Dothistroma septosporum* and *Dothistroma pini* (Barnes *et al.*, 2004). The disease causes premature defoliation and reduction in rates of growth, resulting in economic and aesthetic losses and, in some situations, mortality. Although the disease has a global distribution (Gibson, 1974; Bradshaw, 2004), until recently it was primarily considered a problem in the southern hemisphere, where it was introduced in commercial plantations of non-native *Pinus radiata*. Trees in Africa, Chile and New Zealand have suffered major damage from this needle blight since the 1960s.

Figure 1 *Phytophthora ramorum* affecting a stand of Japanese larch (*Larix kaempferi*) in Plym Woods, east of Plymouth, UK.

The geographic range and intensity of dothistroma needle blight, particularly in the northern hemisphere, has increased dramatically since the late 1990s (Brown *et al.*, 2003; Woods, 2003; Bradshaw, 2004). In France, the impact of the disease was minimal during the late 1960s to 1980s, but has rapidly increased since, particularly on plantations of *Pinus nigra* ssp. *laricio* (Villebonne & Maugard, 1999). In Britain, an increase in the disease since 2000 has resulted in a moratorium on planting of *P. nigra* ssp. *laricio* and *Pinus contorta* var. *latifolia* in public forests. A rapid expansion of dothistroma needle blight was initially observed on *P. nigra* ssp. *laricio*, with intense infection and mortality on the extensive plantations in eastern England. Since 2006, when the disease was reported on *P. contorta* var. *latifolia* in Scotland, the distribution and intensity of the disease has increased appreciably, with mortality of approximately 90% occurring in some areas in trees aged 50 years or older. Although the disease has been observed since the early 1800s in British Columbia, Canada (Welsh *et al.*, 2009), its range and intensity have increased considerably since 2000, particularly on *P. contorta* var. *latifolia* (Woods *et al.*, 2005).

The increase in distribution and intensity of dothistroma needle blight is attributed to multiple synergistic factors. In British Columbia and the UK, the spread of the disease appears to have been facilitated by large plantations of highly susceptible species. Until recently, British Columbia's forest management policies promoted the establishment of *P. contorta* var. *latifolia*, even in areas where it was not naturally the dominant species (Woods, 2003). In the UK, *P. nigra* ssp. *laricio* was widely planted for timber as a key species in a climate-change adaptation strategy (Broadmeadow, 2002). However, climate in particular appears to be driving the disease. Climate models developed by Watt *et al.* (2009) indicated that dothistroma needle blight can survive in diverse environments, including sub-Arctic, temperate, Mediterranean, continental, subtropical and dry tropical. Rates of infection depend on temperature, including overnight minimum temperature; the period of needle wetness; and the quantity of spores present. Ten or more consecutive hours of needle wetness are usually required for infection by *D. septosporum* (Gadgil, 1974; Bulman, 1993). The suitable temperature range for infection is 5–25°C, with an optimum of 16–20°C (Bulman, 1993). Rainfall is particularly critical for infection; amount of summer rainfall and rates of infection in the following year are positively correlated (Bulman, 2006). In British Columbia and the UK (Woods *et al.*, 2005; Archibald & Brown, 2007; Brown & Webber, 2008), an increase in disease intensity has coincided with an increase in spring and summer rainfall and increases in daily minimum temperatures during late summer since the 1990s. The positive correlation between daily minimum temperature and intensity of the disease may decrease if summer rainfall decreases.

Swiss needle cast

Swiss needle cast of Douglas fir is caused by *Phaeocryptopus gaeumannii* and symptoms include chlorosis, reduced needle retention, and reduced tree growth. Boyce (1940) reported that the native pathogen was widespread but had little impact throughout the *P. menziesii* region of western North America. However, a severe epidemic began in the coastal fog belt of Oregon in the early 1990s and has persisted since (Hansen *et al.*, 2000). In the Pacific Northwest, high levels of Swiss needle cast usually occur at low elevations (for example, in close proximity to the Pacific Ocean or Puget Sound), often in areas with summer fog and high rainfall and on sites formerly occupied and better suited to *Tsuga* and *Picea* spp. or to hardwoods (Hansen *et al.*, 2000). Occurrence of this disease in the Pacific Northwest is also positively correlated with degree-day accumulation during winter and leaf wetness hours during spring to autumn (Manter *et al.*, 2005). Winter temperatures and spring precipitation have increased by 0·2–0·4°C and 0·7–1·5 cm, respectively, per decade since 1970 in the Oregon Coast Range, suggesting that regional climate changes may be influencing the distribution and severity of the disease in the Oregon Coast Range (Stone *et al.*, 2008). Further increases in winter temperature of approximately 0·4°C per decade through to 2050 are projected for the Pacific Northwest, suggesting that the severity and distribution of Swiss needle cast also are likely to increase (Stone *et al.*, 2008).

A positive correlation between spring precipitation and relative abundance of *Phaeocryptopus gaeumannii* was found in southern British Columbia (Hood, 1982). In New Zealand, where *P. menziesii* is not native, the climate variable with the strongest positive correlation with severity of disease was winter mean temperature, which explained about 80% of the variation in infection and damage (Stone *et al.*, 2007).

White pine blister rust

Cronartium ribicola, a fungus native to Asia and causing blister rust of white pines (*Pinus* spp.), was introduced into Europe in the mid-1850s and to North America in the early 1900s. Infection by *C. ribicola* results in branch dieback, reproductive failure and tree mortality (Fig. 2). In North America, white pine blister rust has caused more damage and costs more to control than any other conifer disease (Bega, 1978). In many regions of Canada, mortality of *Pinus monticola* and *Pinus strobus* has been so extensive that the species no longer are considered commercially viable. In the western USA, the number of *P. monticola* grown for reforestation has been reduced by 95% because forest managers consider it too risky to plant (Kinloch, 2003). Synergistic effects of *C. ribicola*, drought, increasing temperatures and outbreaks of mountain pine beetle (*Dendroctonus ponderosae*) are thought to drive extensive mortality in high-elevation *Pinus albicaulis* populations (Logan & Powell, 2001; Kegley *et al.*, 2004; Gibson *et al.*, 2008).

Figure 2 White pine blister rust, caused by *Cronartium ribicola* on *Pinus lambertiana* (sugar pine) at Happy Camp, California, USA.

The environmental conditions associated with *C. ribicola* infection are well documented (Spaulding, 1922; Mielke, 1943; Van Arsdel, 1954; Bega, 1960). Infections of pine typically occur in 'wave' years, when weather conditions are ideal for the fungus. White pine blister rust is considered a cool weather disease (basidiospore germination and infection occurs from about 0 to 20°C), with spread driven largely by moisture, air temperature and air circulation (Van Arsdel, 1965). For example, *C. ribicola* basidiospore germination and pine needle infection requires 48 h with conditions of 100% relative humidity and temperatures not exceeding 20°C (Van Arsdel *et al.*, 1956). In the USA, portions of some north-central states and southern California are too warm for infection.

Changes in temperature and the frequency of 100% air humidity events will influence the epidemiology of *C. ribicola*. Since infection requires a cool, moisture-saturated environment, conditions suitable for *C. ribicola* to cause infection will decrease with fewer wet periods in spring or early summer. The probability of years when weather conditions especially favourable for new infections result in significant intensification and spread (wave years) will diminish as the climate becomes warmer and drier, resulting in less rust infection (Kinloch, 2003). Locations in which these changes are projected include the southern Sierra Nevada in California.

Cylindrocladium leaf blight

The fungus *Cylindrocladium quinqueseptatum* causes a severe leaf blight of many tree species in tropical and subtropical forests, primarily in Australia and countries in Southeast Asia, including Laos, Thailand and Vietnam. Severe epidemics are associated with warm temperatures and long periods of leaf wetness. Modelling suggested that small increases in temperature and precipitation can substantially increase the area in which there is a high probability of severe epidemics (Booth *et al.*, 2000). Based on weather records of the latter 20th century, the only area of China considered climatically suitable for severe epidemics is Hainan, an island off the southern coast. However, consistent with climate change projections, temperature and precipitation recently have increased in parts of China, especially the south. Accordingly, the disease has become a substantial problem in those areas (F. Zhang, Fujian Agriculture and Forestry University, Fuzhou, China, personal communication).

Pathogens indirectly affected by climate

Pathogens indirectly affected by climate tend to infect hosts that are stressed by (i) environmental factors, (ii) pathogens directly affected by climate, or (iii) insects. Such pathogens can sometimes infect a healthy host and remain latent until the host is stressed. Whilst the ability of these pathogens to sporulate, spread and infect new hosts is affected by temperature and moisture, factors that stress their hosts are often critical to their successful invasion of host tissues. For example, an increased incidence of summer drought will increase the probability that trees will be infected by pathogens whose activity is facilitated by host stresses, such as root pathogens, wound colonizers and latent colonizers of sapwood (Brasier & Scott, 1994; Lonsdale & Gibbs, 2002; Desprez-Loustau *et al.*, 2006).

Armillaria root disease

Armillaria species cause root disease in natural and managed forests worldwide (Kile *et al.*, 1991), infecting conifers and occasionally hardwoods, and also occasionally woody shrubs and herbaceous plants. Infection results in wood decay, growth reduction and mortality. *Armillaria* species can grow over a range of temperatures, from 10 to 31°C, although the optimal temperature for many species is at 20–22°C (Rishbeth, 1978; Keca, 2005 as cited in La Porta *et al.*, 2008). Some *Armillaria* species are primary pathogens and infect healthy trees in forests, whereas other species act as secondary agents, infecting after host immunity has been impaired by drought, temperature extremes, other pathogens, insects or reductions in site quality (Wargo & Harrington, 1991; Goheen & Otrosina, 1998). *Armillaria* spp. can also increase the probability that bark beetles or other insects will colonize trees. Armillaria root disease caused by *A. solidipes* (= *A. ostoyae*) is responsible for losses of 2–3 million m^3 timber per year in Canada's Pacific Northwest (Morrison & Mallet, 1996). Tree failures caused by decay are substantial hazards in recreational and urban areas. In general, losses attributed to armillaria root disease are greatest in relatively dry Mediterranean or continental climates (Kile *et al.*, 1991). The incidence of this root disease is likely to increase as temperatures increase and precipitation decreases (Shaw & Kile, 1991; US Office of Technology Assessment, 1993; La Porta *et al.*, 2008; Klopfenstein *et al.*, 2009). Klopfenstein *et al.* (2009) demonstrated that the area in which climate supports persistence of *P. menziesii*, a major host for *A. solidipes* in the interior northwestern USA, is likely to decrease by 2060, and suggested that the stressed *P. menziesii* will also be more susceptible to armillaria root disease.

Pine wilt

Pine wilt disease, caused by the pine wilt nematode, *Bursaphelenchus xylophilus*, originated in North America but is now found in parts of Europe (e.g. Portugal) and East Asia (e.g. Japan, China and Vietnam). It has long been known that, where mean July temperature is less than 20°C, the disease is rare, even though the pathogen may be present (Rutherford & Webster, 1987). Under elevated summer temperatures and seasonal moisture stress, the pine wilt nematode may cause rapid wilting and mortality (Evans *et al.*, 2008). The nematode was introduced to China via Japan in the early 1980s (Zhao, 2008) and has since caused mortality on over 80 000 ha of Chinese forests. Disease occurrence and severity in China are positively correlated with annual mean temperature and winter and spring precipitation, but negatively correlated with June precipitation (Xi & Niu, 2008; Zhao, 2008). Currently, climate restricts the area suitable for pine wilt disease to less than half of China, southeast of a line from Beijing to Yunnan Province. Warmer temperatures and increased precipitation, especially if combined with seasonal or occasional moisture stress, may increase the probability of the disease occurring in some northern and western regions of China (Zhao, 2008).

Under the PHRAME project (Evans, 2007) in Portugal, there has been progress made on prediction modelling for expression of pine wilt disease. This has been achieved by linking together models of tree suitability parameters and tree physiological responses relative to ecological and climatic conditions. This complementary modelling approach has yielded valuable predictive tools for improved future risk assessment of pine wilt disease for Portugal and probably for other parts of Europe (Evans, 2007).

Canker pathogens

Although numerous canker pathogens are capable of infecting vigorous trees, canker-causing fungi are more likely to reach epidemic levels and cause substantial damage to trees weakened by heat and drought stress (Schoeneweiss, 1975, 1981). Most canker diseases are caused by facultative parasites, such as species of *Biscogniauxia* (*Hypoxylon*), *Botryosphaeria*, *Diplodia*, *Septoria* (Desprez-Loustau *et al.*, 2006) and *Valsa*.

Biscogniauxia mediterranea causes charcoal canker in *Quercus suber* and *Quercus cerris* woodlands in the Mediterranean and has recently been found on oaks with cankers in Slovenia (Jurc & Ogris, 2006). Disease symptoms in Slovenia first appeared after severe drought and unusually high temperatures. Total rainfall before the onset of symptoms in summer 2003 was significantly below the 30-year average, whilst average monthly temperatures for the same months were 5·8, 3·6 and 5·6°C higher than the 30-year average. This fungus is expected to continue moving north as temperatures increase (Vannini & Valentini, 1994; Desprez-Loustau *et al.*, 2006; Vannini *et al.*, 2009).

Botryosphaeria dothidea causes serious damage only to weak, stressed or off-site trees (Ma *et al.*, 2001). Drought stress and winter injury have been associated with increased rates of infection and canker expansion of *B. dothidea* on apple trees (*Malus*) in the eastern USA (Brown & Hendrix, 1981). Severity of diplodia shoot blight, caused by *Diplodia sapinea*, has consistently been associated with water stress (Bachi & Peterson, 1985; Blodgett *et al.*, 1997a,b; Paoletti *et al.*, 2001). Similarly, cankers caused by *Septoria musiva* on inoculated, water-stressed trees were significantly larger than those on non-stressed trees (Maxwell *et al.*, 1997).

Cytospora canker of *Alnus incana* subsp. *tenuifolia*, caused by *Valsa melanodiscus*, is currently epidemic in the southern Rocky Mountains, Alaska, and other areas of western North America (Trummer, 2006; Worrall, 2009). In Colorado and adjoining areas, over 60% of standing stems are dead or diseased. Recent evidence suggests that warm temperatures in midsummer, even for a few weeks, are associated with explosive canker growth and host mortality (Worrall *et al.*, 2010a).

Decline diseases

Forest declines are diseases caused by a complex of predisposing, inciting and contributing factors. As these difficulties accumulate the tree gradually becomes less able to produce, store and mobilize carbohydrates. It typically develops symptoms of ‘dieback’, and unless the situation improves significantly the tree eventually dies. Three forest decline diseases are considered: The first – oak decline – is described below whilst descriptions for yellow-cedar decline and sudden aspen decline are included later in management case studies.

Oak decline

Decline of *Quercus* spp. worldwide is caused by interactions among environmental stressors (e.g. drought, pollution, low minimum winter temperatures, and flooding) (Brasier & Scott, 1994), insects and pathogens (e.g. *Armillaria* and *Phytophthora* spp.). In the USA and throughout Europe, episodic, extensive decline and death of oaks has been recorded since around 1900 (Wargo *et al.*, 1983; La Porta *et al.*, 2008). Additional drivers of oak decline in Mediterranean regions of Europe include changes in land use (Brasier, 1996). Studies of oak decline in Mexico (Alvarado-Rosales *et al.*, 2007) concluded that low temperatures and water deficits cause stress and, in some cases, result in death of oaks. Furthermore, the fungus *Biscogniauxia atropunctata* is associated with some stressed trees; in other cases, *P. cinnamomi* was identified as a primary pathogen (Manion & Lachance, 1992; Thomas *et al.*, 2002).

Climate and forest tree death

Whether climate ‘alone’ causes tree mortality is difficult to evaluate, yet the number of reports of forest dieback, decline and mortality attributed to climatic drivers is increasing. Because the role of climate cannot be demonstrated as definitively as that of pathogens, the scientific community often must rely on circumstantial evidence. Evaluating whether climate change drives tree mortality is even more difficult. For instance, tree mortality in response to drought and heat has recently been associated with climate change, but episodic droughts have long been implicated in mortality independent of climate change. Thus, in the literature it is frequently unclear whether effects of climate are direct or synergistic. For example, mortality rates increased in 87% of 76 plots, and on average doubled, in unmanaged old-growth forests in western North American sampled over an average of 23 years (van Mantgem *et al.*, 2009). An increase in mortality occurred among trees of all sizes; warm temperatures and consequent moisture deficits were considered likely causes. A recent assessment of drought- and heat-induced mortality concluded that some of the world’s forested ecosystems may already be affected by climate change, and that further increases in mortality should be expected even in environments that are rarely water-limited (Allen *et al.*, 2010).

In China, substantial tree mortality thought to be a result of climate change has been reported, but the mechanisms and biological details are unclear. In many areas of China, increases in temperature and precipitation over the past 50 years (Yang, 2008) may have increased the incidence of some forest diseases. In recent decades, the distribution of forests has changed substantially. In the Qi Lian Shan Mountain area of northeastern Qinghai Province and western Gansu Province of western China, forest area was reduced by 16·5% and the lower elevation limit of the forest increased from 1900 to 2300 m between 1950 and 1992, reportedly as a result of combined effects of climate change and local human development (Wang *et al.*, 2002). A northward shift between 1966 and 2003 in the distribution of species including *Larix gmelinii*, *Picea jazoensis*, *Abies nephrolepis* and *L. potaninii* was documented in Heilongjiang Province of northern China (Zhu *et al.*, 2007). Budbreak has occurred earlier in response to warmer spring temperatures in some areas, but has been later in other areas in response to cooler temperatures. Forest productivity increased between 1981 and 2000 because of the increased length of the growing season. Inland ecosystems have been particularly sensitive to climate change

(Zhu *et al.*, 2007). Severe droughts have led to mortality on a regional scale (Wang *et al.*, 2007).

Managing forest diseases as climate changes

Given the numerous examples of interactions between forest disease and climate change, the ecological, economic and social value of forests, and the role that forests may play in mitigating global climate change, it is valuable to conduct a comprehensive assessment of management options for forest diseases. Although trees in much of the world's forests will have to adapt to climate change without human intervention (Spittlehouse, 2009), many forested areas can be managed to minimize the undesirable effects of projected increases in tree mortality driven by biotic and abiotic phenomena. Implementation of management approaches that enhance tree species richness across forested landscapes can help minimize adverse consequences of pathogen activity when there is uncertainty about effects of climate on forest ecosystems.

Assuming that a forest unit is managed to meet a given objective, such as timber, habitat for specific animals, watershed protection or recreational use, and furthermore, that models project that within the next 70 years, the climate will no longer support many of the tree species currently present, then a gradient of potential management responses exists between two unrealistic extremes. One extreme, if confidence in the models is extremely high, is to promote the rapid transition of the species composition of the site. The other extreme is to make no changes in management, assuming that the approach can be changed if and when species distributions change. Projections about the magnitude, location and timing of climate change are highly uncertain at all spatial extents and resolutions. In some regions there is even uncertainty over the direction of changes in precipitation (IPCC, 2007) which strongly influences rates of disease incidence and severity. Indeed, the potential for forests to mitigate climate-change effects should be considered carefully, as shown by recent research suggesting that afforested sites, particularly in temperate and boreal forests, may actually contribute to local surface warming from the positive radiative forcing effect of albedo (Betts, 2000; Thompson *et al.*, 2009).

Regardless of these uncertainties, impacts of climate change on forest health must be mitigated. This will require proactive thinking and a modified suite of forest management approaches, because status quo management strategies will not protect forest values in a changing climate. Climate change is already disrupting practices and policies for managing commercial and non-commercial forests, such as forest classification systems, projections of growth and yield and subsequent models of supply for timber and other forest products, plans and projections for managing habitat for different species of animals, and cycling of carbon, nutrients and water (Graham *et al.*, 1990). That restoration may no longer be a universally useful concept or goal for forest management, because climate is not static, must also be acknowledged. The health of forests should be evaluated in terms of how future climate may influence the overall ecology of forest vegetation and pathogens, not how forests can be maintained or returned to some current or past condition. As damage increases in a forest type, managers will need a triage or similar prioritization system to decide which tree species have a long-term future and are worthy of management, and on which sites the forest type or species may be lost and therefore should not be promoted. Increased disease activity caused by climate change will probably exacerbate the extent and impact of these disruptions and it is not appropriate to set aside forests as refugia for biodiversity or other goals without a full evaluation of the impacts of future climatic conditions.

Essential components for managing forest diseases as climate changes

We recommend four categories of management tactics: monitoring, forecasting, planning and use of mitigating strategies. Implementation of these tactics will vary, depending on the 'state of the science' to support the activities, where forests and their stewards are on the globe, what financial, human and other resources exist, and what resource-management objectives are intended. Regardless, action must begin, with the most critical first step being identification of locations suitable for the deployment of as wide a range of forest tree species that are as ecologically resilient and stress-tolerant as possible.

Monitoring

Monitoring the spatial occurrence of forest diseases relative to both the ranges of host trees and annual weather patterns will inform adaptive management. The reliability of monitoring data will be maximized if systematic surveys of tree health, mortality and growth, whether remote or ground-based, are conducted by skilled personnel, ideally at stand, watershed and landscape levels, at regular intervals. Forest inventory plots also can be used to detect trends in growth and mortality for individual species and incidence of diseases or other disturbance agents. The ability of these activities to effectively inform the long-term management of forests might be increased by coordinating with monitoring for other disturbance agents, such as insects or fire, and by monitoring across jurisdictional boundaries.

Forecasting

The profound changes in environmental conditions expected from global climate change mean that forest professionals cannot rely on historical observations and experiences to forecast and plan for the future, but instead must develop and use a variety of modelling tools (Beukema *et al.*, 2007). Models of diverse phenomena, from climate to vegetation to disturbance agents, can guide management of forests under a changing climate, especially when they are well integrated. Bioclimatic envelope models, for example, which integrate spatially explicit historic and contemporary data from weather stations, general circulation models and other sources, can be used to correlate current tree and pathogen species distributions with climate variables or to project future distributions on the basis of understanding of species' physiological responses to environmental variables (Pearson & Dawson, 2003). Modelling pathogens' climate envelopes alongside host reactions to climate can thus enhance the ability to predict disease outcomes.

Despite their power as predictive tools, models have at least three continuing problems: model inputs may have a high degree of uncertainty (e.g. disease distribution); nonlinear relationships between climatic variables and epidemiological responses are common, which means there may be insufficient data for clear projections; and the potential for genetic adaptation by both plants and pathogens is often ignored in models (Scherm, 2004). Efforts to improve modelling of climate change and forest pests (diseases and insects), such as those outlined in a workshop report by Beukema *et al.* (2007), are underway. Whilst models cannot provide certainty, they can provide qualitative insights on the magnitude and direction of changes, give focus to monitoring activities, and aid in the evaluation of management strategies (Woods *et al.*, 2010).

Planning

Jurisdictions that already have forest health strategies must ensure that they are maintained and adequately funded. Also, they should review and revise pertinent legislation and policies to ensure that forest health problems can be responded to quickly and effectively (Woods *et al.*, 2010). The success of management intended to minimize the potential undesirable effects of climate change on forest pests on large spatial scales depends, in part, on the synergistic effects of other major disturbances, such as wildfire (Lertzman & Fall, 1998; Peterson & Parker, 1998). Climate change-induced increases in tree mortality from pathogens and insects may increase the occurrence and severity of fires (Bergeron & Leduc, 1998; Kliejunas *et al.*, 2009).

Hazard- and risk-rating systems are integral components of forest management plans and can be applied in the absence of disease epidemics, and have proven useful for projecting effects of climate change on forest pests (Woods *et al.*, 2010). Pest risk analysis processes have been established in the European Union. Nevertheless, methods are being reviewed and improved (Baker *et al.*, 2009). Rating systems for most pathogens either have not been developed or do not account for climate change.

Strategies for mitigating effects of climate change

Ecological resilience is the capacity of an ecosystem to absorb disturbance without shifting into a qualitatively different state (Campbell *et al.*, 2009). Adaptive capacity, by contrast, is a property of individuals, populations or species. The establishment and maintenance of forests with diverse species and age classes can help maintain resilience to mortality and reduction in growth rates of trees in response to diseases and climate change.

Facilitated or assisted migration of trees may be an effective and cost-effective strategy to increase the probability of persistence of populations or species (Woods *et al.*, 2010). Facilitated migration is the deliberate movement by humans of genotypes and species into areas where the projected climate is believed to be associated with high probabilities of persistence. In some cases, genotypes and species currently present in those areas are believed to be unlikely to persist as climate changes. Facilitated migration may be emphasized for species with narrow resource requirements or poor dispersal ability (Warren *et al.*, 2001). However, facilitated migration can have unintended consequences. For example, new pathogens may be introduced along with the target species. The introduced trees may have little immunity against diseases in the areas into which they are moved. Also, it is highly uncertain which pathogens will become more evident as climate changes. In British Columbia, for example, pines such as *P. contorta* var. *latifolia* that originated in wet ecosystems, where foliar diseases are relatively common, were more resistant to dothistroma needle blight diseases, and had higher levels of defensive, secondary metabolites, than pines from comparatively arid ecosystems (Wallis *et al.*, 2008, 2010).

Breeding programmes for forest trees can promote genetic diversity, disease resistance and tolerance to environmental stresses. A tree's resistance to pathogens depends on stochastic genetic variation, evolved immunity, plasticity and environmental conditions (Yanchuk *et al.*, 1988; Liu & Ekramoddoullah, 2003; Cruickshank *et al.*, 2010). Fungicides may be an effective method of controlling forest diseases in forest nurseries and in natural forests, especially in the short term, despite negative public perception.

Management case studies

Yellow-cedar decline

Since the early 1900s, there has been extensive mortality of *Chamaecyparis nootkatensis* (yellow cedar), a culturally and economically important species, over more than 250 000 ha of forests in southeast Alaska (Hennon *et al.*, 2006) (Fig. 3) and nearby British Columbia (Hennon *et al.*, 2005). Yellow-cedar decline is characterized by slow decline in tree condition over several years. These forests are composed of standing long-dead and recently dead and dying *C. nootkatensis* and other tree species. Insects (*Phloeosinus* beetles) and pathogens (*Armillaria* spp. and other fungi) are contributing factors in yellow-cedar decline, but are less aggressive against unstressed trees. Predisposing factors include landscape, site and stand conditions (Hennon *et al.*, 2008) that increase the probability that the fine roots of *C. nootkatensis* will freeze during cold weather events in late winter and early spring (Schaberg *et al.*, 2008).

Long-term climate and short-term weather events affect the probability that the roots of *C. nootkatensis*

Figure 3 Yellow-cedar decline on Chichagof Island in Alaska, USA.

Figure 4 Sudden aspen decline on the Dolores Ranger District, San Juan National Forest, Colorado, USA.

will freeze. The cool, moist climate that developed in the late Holocene created bogs and forested wetlands in which the species became abundant. However, yellow cedar developed shallow roots to acquire nitrogen in wet soils (D'Amore & Hennon, 2006; D'Amore *et al.*, 2009). Open forest canopies in bogs create microclimatic extremes; in late winter and early spring these include rapid warming as an inciting factor that triggers cedar dehardening (Schaberg *et al.*, 2005) and penetration of cold temperatures into soils (D'Amore & Hennon, 2006; Hennon *et al.*, 2010). *Chamaecyparis nootkatensis* are tolerant of cold temperatures in autumn and early winter (Schaberg *et al.*, 2005). However, roots deharden quickly in late winter and early spring, when soil temperatures below −5°C are lethal (Schaberg *et al.*, 2008). These lethal temperatures are common in shallow soil horizons, but do not occur when snow is present to buffer soil temperature (Hennon *et al.*, 2010). The onset of yellow-cedar decline in about 1880–1900 (Hennon *et al.*, 1990) corresponded with the end of the Little Ice Age. Weather-station data indicated a trend towards warmer winters but persistent early spring freezing events throughout the 1900s (Beier *et al.*, 2008). *Chamaecyparis nootkatensis* trees are healthy where snow persists past the last cold period in spring, or where they are deep-rooted on relatively well-drained soils.

Drivers of yellow-cedar decline can be reduced to two factors for risk modelling: soil drainage and snow accumulation. Planting or thinning is often needed to ensure the initial regeneration and competitive ability of *C. nootkatensis* (Hennon *et al.*, 2009). These activities are directed at higher elevations or on well-drained soils where snow or deeper rooting, respectively, protects *C. nootkatensis* roots from cold temperatures. In declining forests, salvaged wood from dead cedars is economically valuable (Hennon *et al.*, 2007) because the heartwood retains its integrity for up to 100 years after death (Kelsey *et al.*, 2005).

Sudden aspen decline

Sudden aspen decline is a recently described disease of *Populus tremuloides*. It is characterized by rapid, synchronous branch dieback and tree mortality on a landscape scale (Fig. 4), rather than on a stand scale, without the involvement of aggressive, primary pathogens and insects (Worrall *et al.*, 2008, 2010b). Typically, there is no increase in aspen regeneration as overstory cover decreases, and in smaller size classes there is a decrease in recruitment. This lack of vegetative regeneration is associated with root mortality, which in turn is correlated with crown loss. Sudden aspen decline extends from Colorado into southern Wyoming, and similar damage began around 2000 in northern Arizona and in the early 1990s in southern Utah, USA (Ohms, 2003; Bartos, 2008; Fairweather *et al.*, 2008). Declining aspen in the parklands and southern boreal forests of Alberta and Saskatchewan, Canada (Hogg *et al.*, 2004, 2008) may be part of this same phenomenon.

In Colorado, sudden aspen decline was first noticed in 2004. By 2008, it covered about 17% of the area dominated by aspen in the state, about 220 000 ha. In 2009 the expansion appeared to stop, although severity continued to increase in many affected stands. A severe drought and record high temperatures, centered in 2002, was suspected as the cause. This drought was also the driver of unprecedented levels of mortality in *Pinus edulis* associated with an outbreak of the bark beetle *Ips confusus* (Breshears *et al.*, 2005).

Spatial analysis of a moisture index provided evidence that drought was an important inciting factor. Sites with aspen mortality detected by aerial survey in 2008 had greater moisture deficits in the 2002 hydrologic year

(October 2001 to September 2002) than did sites with healthy aspen (Worrall *et al.*, 2010b). Rehfeldt *et al.* (2009) showed that the mortality was consistent with projections of the effect of climate change on aspen. Annual values of an index of climate favourability for aspen were lowest in 2002. Locations where sudden aspen decline is occurring are at the edge of aspen's climate envelope. The lower elevation at which climate supports aspen in the southern Rocky Mountains is expected to increase by 250 m by 2030 and 750 m by 2090. Projections suggest that 82% of sites with sudden aspen decline will be outside aspen's climate profile by 2060. In some areas, root systems may be able to regenerate if aboveground biomass is cut or burned. Aspen less than about 40 years old appears to have greater tolerance to drought and high temperatures than older aspen (Worrall *et al.*, 2010b). Growth of aspen also might be encouraged at higher elevations, where conifers are expanding yet climate is expected to be suitable for aspen at least until 2100.

Summary and conclusions

Forests serve important ecological functions and also contribute to the economic, aesthetic and spiritual health of humans. Climate has always shaped the Earth's forests, but human activities over the past 200–300 years have led to unprecedented changes in the world's climate. Climate change will interact with forest disturbances, such as pathogens, insects and fire, to increasingly impact the geographic distribution, growth and sustainability of the world's forest tree species. Outbreaks of forest diseases caused by native and introduced forest pathogens are predicted to become more frequent and intense as drought and other abiotic stressors are amplified under climate change. However, uncertainty pervades predictions about the future impacts of these diseases, in part because the effects of climate change on host–pathogen interactions are complex. For example, under a climate-change scenario of warmer and drier future conditions, we predict that diseases caused by pathogens directly affected by climate (e.g. dothistroma needle blight) will have a reduced or unchanged impact on their hosts, but an increased impact under a scenario of warmer and wetter conditions. For diseases caused by pathogens indirectly affected by climate (e.g. armillaria root disease) and for decline diseases, in general, we predict an increased impact on hosts under a climate-change scenario of warmer and drier future conditions and a reduced or unchanged impact under warmer and wetter future conditions.

The cumulative mortality of forest trees, including tree death potentially attributable solely to climatic drivers, is a serious problem facing forest professionals and policy makers. Whilst trees in much of the earth's forests will have to adapt to climate change without human intervention, many forested areas can be managed to minimize the undesirable effects of projected increases in tree mortality. This will require proactive and 'new' thinking and a modified suite of forest management approaches. We recommend four categories of tactics for managing forest diseases under a changing climate: monitoring, forecasting, planning and use of mitigating strategies. Aspects of these tactics have been considered or implemented in the evolving management of yellow-cedar decline and aspen decline in the USA. To have the best possible chance of success in the face of global climate change, each of the four management tactics we have recommended will require, to varying degrees: the development of techniques and tools; informed discussion of research needs and integration of results when the research is done; prioritization of research needs using risk analyses; and the development of clear and solid links to forest policy.

Acknowledgements

Thanks to Kerry Britton and Ellen Goheen, USDA Forest Service; and Erica Fleishman, UC Santa Barbara, and two anonymous reviewers for helpful comments. Support for forest-disease and climate-change research from the USDA Forest Service, Western Wildland Threat Assessment Center and the Pacific Southwest Research Station is also appreciated.

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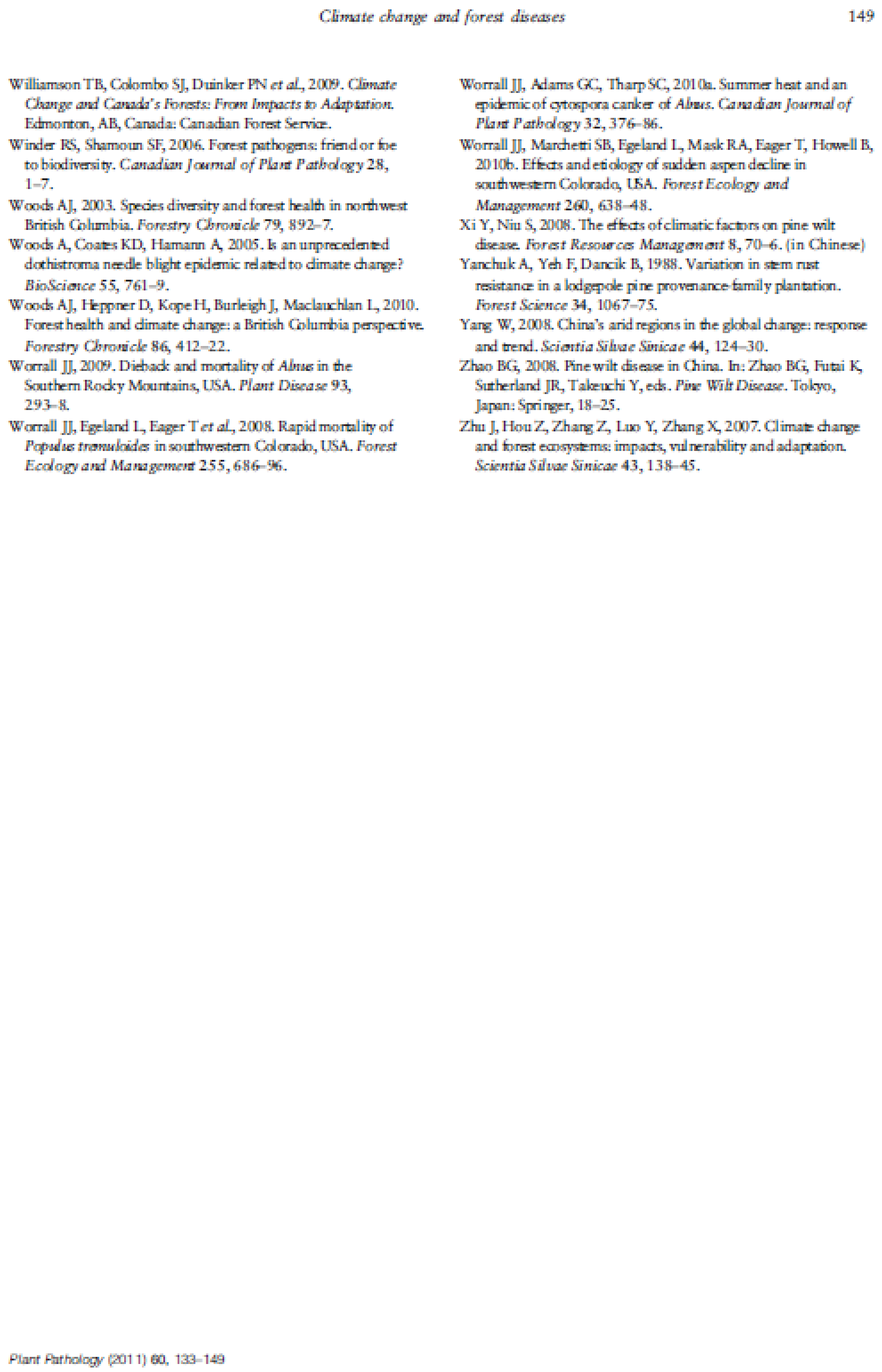

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Forestry An International Journal of Forest Research

Institute of Chartered Foresters
IUFRO INTERNATIONAL UNION OF FOREST RESEARCH ORGANIZATIONS

Forestry 2016; **89**, 245–252, doi:10.1093/forestry/cpw018
Advance Access publication 22 March 2016

Forest health in a changing world: effects of globalization and climate change on forest insect and pathogen impacts

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Received 19 February 2016

Forests and trees throughout the world are increasingly affected by factors related to global change. Expanding international trade has facilitated invasions of numerous insects and pathogens into new regions. Many of these invasions have caused substantial forest damage, economic impacts and losses of ecosystem goods and services provided by trees. Climate change is already affecting the geographic distribution of host trees and their associated insects and pathogens, with anticipated increases in pest impacts by both native and invasive pests. Although climate change will benefit many forest insects, changes in thermal conditions may disrupt evolved life history traits and cause phenological mismatches. Individually, the threats posed to forest ecosystems by invasive pests and climate change are serious. Although interactions between these two drivers and their outcomes are poorly understood and hence difficult to predict, it is clear that the cumulative impacts on forest ecosystems will be exacerbated. Here we introduce and synthesize the information in this special issue of *Forestry* with articles that illustrate the impacts of invasions of insects and pathogens, climate change, forest management and their interactions, as well as methods to predict, assess and mitigate these impacts. Most of these contributions were presented at the XXIV IUFRO World Congress in 2014.

Keywords: biological invasions, climate change, forest resistance, modelling, risk, diagnostics

Introduction

There is growing recognition among the scientific community and policy makers that sustainable forest management is affected by multiple factors associated with global change. Exponential population growth has resulted in the addition of ~1 billion people between 1999 and 2012, leading to a global population of over 7 billion people that must be sustained by Earth's resources. Forests are of vital importance to humanity as they provide a wide range of essential ecosystem services (e.g. fuelwood, fibre, carbon sequestration etc., see Thompson *et al.*, 2011) but the ongoing loss of forest cover means the increasing demand must be met from an ever shrinking resource (Brockerhoff *et al.*, 2013). Concomitant with population growth has been the expansion of global trade networks and an increase in the volume of traded goods (e.g. Hulme, 2009). This has led to a considerable increase in the establishment of populations of non-native species in virtually all parts of the world (e.g. Roques *et al.*, 2009; Aukema *et al.*, 2010; Wingfield *et al.*, 2015). While many of these species appear to be relatively benign, some have major deleterious impacts on trees in natural and managed ecosystems, as well as urban environments. For example, the invasive emerald ash borer has been devastating ash trees in North America (Poland and McCullough, 2006) and *Phytophthora ramorum* is causing dieback and mortality of a wide range of tree species in Europe and North America (Grünwald *et al.*, 2012).

Climate change can exacerbate invasions of forest pests as well as impacts of native pests. For example, climate change can facilitate the range expansion of both native and exotic pests (insects and pathogens), or affect tree resistance to pests (Jactel *et al.*, 2012a), and there is increasing evidence that this is a widespread phenomenon (Battisti *et al.*, 2005; Marini *et al.*, 2012; Anderegg *et al.*, 2015). Using the planetary boundaries approach of Steffen *et al.* (2015), Trumbore *et al.* (2015) identified that the main stressors of the world's forests today are invasive species and diseases as well as climate change, along with deforestation and the increasing demand for forest resources. An additional contributor to forest health problems is the ongoing intensification and

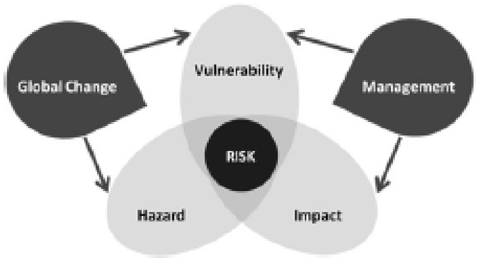

Figure 1 Risk depends on the combination of (1) the likelihood of hazard (e.g. frequency of wind, fire, pathogen, pest) which is the cause of damage, (2) the vulnerability of the system (e.g. forest stand) to the hazard thus resulting in damage and (3) the socio-economic impact of the damage (e.g. productivity loss) which depends on the value at stake (e.g. standing volume). Both global change and forest management can affect risk: global change mainly through change in hazard occurence (e.g. spread of invasive species, higher frequency of storms) and forest vulnerability (e.g. water stress reducing resistance to pest) and forest management mainly through forest vulnerability (e.g. thinning improving tree vigour and thus resistance to pest) and impact of damage (e.g. short rotation forestry reducing standing volume).

mechanization of forest management which has increased the vulnerability of forests to disturbance from biological invasions, climate change and other stressors (Seidl *et al.*, 2011). However, there is increasing recognition that forest management can be adapted to increase the resistance and resilience of forests to disturbance (Jactel *et al.*, 2012b; DeRose and Long, 2014; Bahamondez and Thompson, 2016, this issue). The effects of global change and forest management on the risks to forests are influenced by the interaction of these drivers on the likelihood of hazard occurrence, the vulnerability of the system and the socio-economic impact of the damage as illustrated in the conceptual diagram presented in Figure 1.

The present contribution has two functions: it serves to review the topic and as an introduction to the special issue of *Forestry* which comprises articles that were presented at the International Union of Forest Research Organizations (IUFRO) XXIV World Congress in Salt Lake City, USA, from 6 to 11 October 2014. The theme of this special issue is 'Forest Health in a Changing World' and each article addresses various issues related to impacts of global change on forests and forest ecosystems. The articles have been contributed by researchers based in North and South America, Australasia, Europe and South Africa and were presented at various sessions sponsored by IUFRO's Division 7 – Forest Health. The articles address impacts, risks, management, and tools to mitigate increased damage caused by pests through introduction into new areas or changes in climatic suitability. Taken as a whole, this collection of articles illustrates the complex issues that are associated with understanding, preventing and managing the impacts associated with spread of invasive pests or outbreaks of native forest pests.

Impacts of invading pests and benefits of prevention and eradication

Biological invasions cause a wide range of environmental and economic impacts (e.g. Mack *et al.*, 2000; Lockwood *et al.*, 2013). In the case of forest insects and pathogens, impacts include damage to trees that causes nuisance, growth loss or even tree death, loss of amenity value from forests or urban trees, impacts on biodiversity, reduced provision of ecosystem services and numerous other direct and indirect impacts and costs (e.g. Liebhold *et al.*, 1995; Aukema *et al.*, 2011; Boyd *et al.*, 2013; Lockwood *et al.*, 2013).

One of the most damaging recent invaders is the emerald ash borer (*Agrilus planipennis*) which was accidentally introduced to North America and western Russia, probably with wood packaging material. While it is only a minor pest in its native range in northeast Asia, in the introduced areas its impacts are very serious as it kills virtually all native species of ash (*Fraxinus*) in North America and Europe (Poland and McCullough, 2006; Baranchikov *et al.*, 2008). The effects of this invasion undoubtedly have important implications for the biodiversity of the affected areas, especially the organisms associated with ash trees. Some effort has been directed at determining the economic impacts of emerald ash borer. A simulation study modelling the impacts of emerald ash borer over the 10-year period from 2009 to 2019 predicted the combined cost of tree treatments, removal, and replacement at $10.7 billion USD (Kovacs *et al.*, 2010). A study of damage caused by non-native forest insects in the US estimated annualized damages from emerald ash borer at $38 million USD federal government expenditures, $850 million local government expenditures, $350 million household expenditures, $380 million residential property value loss and $60 million forest landowner timber loss (Aukema *et al.*, 2011). In Europe, the economic impact of the pinewood nematode (*Bursaphelenchus xylophilus*) has been estimated to reach 22 billion Euros by 2030 (Soliman *et al.*, 2012).

Gypsy moth (*Lymantria dispar*) is another well-known invasive tree and forest pest. This defoliator, mainly of broadleaved trees, especially oaks, has been present in eastern North America since its accidental release in Massachusetts in the late 1860s (Liebhold *et al.*, 1995). To this day, large sums are spent annually to minimize defoliation and tree death and to reduce its rate of spread into uninvaded areas. Annualized damages from gypsy moth exceed $200 million USD, mainly for government and household expenditures as well as residential property value loss (Aukema *et al.*, 2011). These figures demonstrate how costly the damages from invasive species can be. However, some damages such as the loss of ecosystem services provided by forests (e.g. flood mitigation, water purification, recreational and cultural values) (Boyd *et al.*, 2013) are difficult to quantify in financial terms (Holmes *et al.*, 2009). A more insidious impact of gypsy moth is its role in the reduction of oak dominance in affected regions (Morin and Liebhold, 2016, this issue). The authors used national forest inventory data to show how gypsy moth has contributed to the removal of young oaks from the ecosystem, which has implications for successional pathways, ecosystem function and the fate of these forest types.

Clearly, it would be beneficial to prevent the establishment and spread of such high-impact invaders and thereby avoid the occurrence of damages in the long term. The detection of the Asian longhorn beetle (*Anoplophora glabripennis*) in northern Italy in 2009 prompted an economic analysis comparing the costs of beetle eradication and the benefits of preventing damages such as the loss of trees and their amenity value (Faccoli and Gatto 2016, this issue). They concluded that the eradication, if successful, clearly provides net benefits. Similar conclusions were drawn by Brockerhoff *et al.* (2010) who compared the costs and benefits of eradications of forest insects in New Zealand. However, eradication programmes are often controversial, require substantial resources, and success is not guaranteed. Therefore, the implementation of measures to minimize the arrival of potential invaders should be even more beneficial than responding to incursions (Leung *et al*., 2002). In fact, a cost-benefit analysis of a phytosanitary policy, using ISPM 15 (International Standards for Phytosanitary Measures No. 15, Regulation of Wood Packaging Material in International Trade) as a case study, determined that the policy provides substantial net benefits (Leung *et al*., 2014) despite the fact that ISPM 15 does not prevent all arrivals of pests moved by this pathway. Finally, another important factor relates to the structure and composition of forests which can affect their resistance to invasive species and other disturbance agents (see below).

Climate change effects on insect outbreaks

Climate change has direct and indirect effects on insects, thereby influencing forest structure and composition at broad scales (Figure 2). Indirectly, changing temperature and precipitation regimes will influence the spatial distribution of host trees and their suitability to herbivorous insects, for example, because host defenses are compromised and phenological markers, such as bud break, are disrupted resulting in a phenological mismatch (Baltensweiler, 1993; Anderegg *et al*., 2015). Community associates that influence insect population success, including pathogens, fungi, natural enemies and competitors, will also be influenced by climatic changes, thereby having both positive and negative indirect effects on outbreaks of forest insects and pathogens (Sturrock *et al*., 2011; Addison *et al*., 2015; Kalinkat *et al*., 2015; Kolb *et al*., 2016). Although the importance of an integrated understanding of indirect climatic effects on community associates and host trees is recognized, most research has been targeted at direct effects of temperature on insect population dynamics. Temperature directly affects many insect life-history traits that influence population success including diapause, cold hardening, and development time (Bentz and Jönsson, 2015). Bentz *et al*. (2016, this issue) show how warming temperatures can decrease generation time and increase overwintering survival for the mountain pine beetle (*Dendroctonus ponderosae*), an important native forest insect in North America (Figure 3). Their model simulations also show, however, that evolved life history traits can be disrupted in some thermal habitats as climate continues to change, resulting instead in reduced population growth.

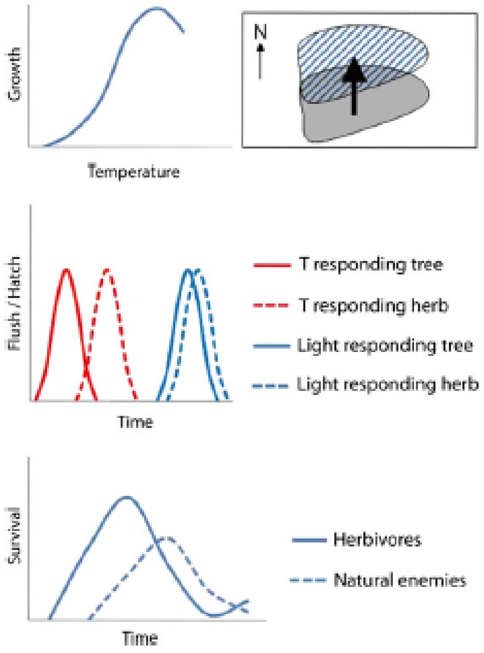

Figure 2 Direct and indirect effects of climate warming on the populations of forest pests. (A) The increase of temperature (*T*) promotes population growth and insect performance especially in temperate and boreal ecosystems, prompting range expansion at high latitude and elevation. (B) Matching between host flush and egg hatch is a crucial point for the survival of many spring herbivores; an increase of temperature may disrupt the mechanism in those species of trees and herbivores that respond to temperature with a different reaction norm (red lines), while others that are more depending on the photoperiod do not show changes (blue lines). (C) The regulation of herbivore populations by natural enemies can be affected by a different response of these organisms to warmer temperature (A. Battisti, personal communication).

Generally speaking, shorter generation times of forest insect species can result in increased tree mortality, and generation time is influenced by several thermally dependent life history traits. For example, many forest insect species in temperate regions have a facultative winter diapause that is induced by cold temperatures. Increasing temperatures can cause a reduction in generation time when diapause is averted, as has been shown for several guilds of Eurasian and North American forest insect species (Marchisio *et al*., 1994; Battisti *et al*., 2000; Lange *et al*., 2006; Jönsson *et al*., 2007; Faccoli, 2009; Bentz and Jönsson, 2015; McKee and Aukema, 2015). In addition to temperature cues, diapause in some species, such as *Ips typographus*, is also influenced by photoperiod. Geographic variability in diapause induction along latitudinal clines thereby limits the number of generations that can be produced in areas with short summer day lengths (Faccoli, 2009). Although averting diapause can be beneficial to population growth of many forest insects, warm temperatures can also desynchronize life-cycle timing resulting in the presence of cold-intolerant life-stages in winter, thereby causing increased insect mortality and reduced population growth (Faccoli, 2002; Wermelinger *et al*., 2011; Bentz *et al*., 2016, this issue). Desynchronization of evolved insect traits with host tree phenology was also shown to occur. The larch bud moth (*Zeiraphera diniana*) relies on a crucial timing of egg hatch with host tree bud break, and warm spring temperatures disrupt the timing, resulting in reduced population growth (Baltensweiler, 1993). Invasive species with limited phenotypic plasticity in new habitats could be vulnerable to both desynchronization of seasonality and with host tree phenology.

In addition to reductions in generation time, increasing minimum temperatures associated with climate change can release populations from the constraint of periodic extreme cold and contribute to range expansion northward and upward in elevation (Weed *et al*., 2013, 2015). Increased likelihood of extreme

Figure 3 Bark beetle-caused tree mortality in western North America exceeded 11 million ha in a recent 13 year period. In the western US, *Dendroctonus ponderosae* was responsible for >50% of all tree mortality. As shown here in the US northern Rocky Mountains, *Pinus* spp mortality (red trees) due to *D. ponderosae* was spatially extensive and temporally synchronized. B. Bentz photographer.

warm winter events, however, could limit northward expansion of native and invasive species when winter acclimation is disrupted and metabolic reserves are depleted (Sobek-Swant *et al.* 2012). Although cold temperatures in some habitats could continue to limit population success, winter-breeding species or species that are not constrained by diapause and instead use plastic life history traits are predicted to do best in a changing climate (Sinclair *et al.*, 2003). For example, the pine processionary moth (*Thaumetopoea pityocampa*), and the bark beetles *Tomicus destruens*, *D. frontalis* and *D. ponderosae* are documented to have taken advantage of thermal increases at multiple times of the year and become more active at higher elevations, or reaching new hosts and new areas further north than previously reported (Battisti *et al.*, 2005; Faccoli, 2007; Weed *et al.*, 2013).

Warm and dry conditions in recent years associated with climate change have manifested in increased population activity of multiple forest insect species globally. In addition to the influence of temperature documented in this special issue (Bentz *et al.*, 2016, this issue), drought is one of the most important climatic drivers of host tree susceptibility to forest insects as reduced water availability compromises tree defences and vigour (Jactel *et al.*, 2012a). Globally, recent outbreaks of several bark beetle and defoliator species have been attributed to drought (Marchisio *et al.*, 1994; Marini *et al.*, 2012; Kolb *et al.*, 2016). Moreover, because environmental conditions are a critical component of disease processes, in addition to host tree stress, increases in deleterious effects due to forest pathogens and their interactions with insects are also likely (Sturrock *et al.*, 2011; Kolb *et al.*, 2016). Continued research aimed at quantifying the influence of warm and dry conditions on forest insect and pathogen success will be necessary to predict future disturbance events and associated risks of damage.

Effects of forest management and composition on forest resistance to disturbance

To quantify disturbance and the state of forest ecosystems, in order to determine when control or mitigation measures are necessary, it is useful to develop relevant indicators or metrics of degradation. Bahamondez and Thompson (2016, this issue) suggest the use of forest productivity as an indicator that can quantify impacts in a manner that is readily interpreted by forest managers and policy makers. The use of forest productivity has the advantage that such data are typically available for many forests where foresters have monitored tree growth. Bahamondez and Thompson (2016, this issue) have developed calculations that use forest inventory and stocking data to identify a point below which a stand can be considered degraded. This process has utility for multiple disturbance types and can identify areas where stand management objectives are compromised by forest damage.

The increasing damage from invasive and native forest insects and pathogens has led to growing demand for pest control measures in natural, planted and urban forests. Traditionally, managing forest pests often involved the use of insecticides and fungicides. However, pesticide use may induce potential selection for resistance, cause negative effects on non-target species or lack effectiveness (Speight and Wainhouse, 1989; Pimentel, 1995). Thus, various alternative methods have been developed to reduce pest population levels below the economic threshold, including mechanical approaches (e.g. sanitation cutting), biological control based on natural enemies (e.g. release of parasitoids) and the use of pheromones and other semiochemicals (e.g. mass trapping) (Wainhouse, 2005). All of these pest management techniques are more or less environmentally friendly but they remain difficult to implement, for a variety of reasons. The height of trees, difficult

access to forest land, and the need to repeat treatments may make these alternative methods costly. Therefore, it is advantageous to prevent or minimize pest problems and invasions before they occur, rather than responding to and suppressing outbreaks once damage is happening. Prevention is basically a pest management strategy that relies on the ability of the forest ecosystem to defend itself. It is based on the assumption that the use of good silvicultural practices would increase the resistance of individual trees and forest stands to pests. Indeed, reviews of the scientific literature have shown that every single silvicultural operation can have a significant effect, positive or negative, on forest stand vulnerability to pest insects (Fettig *et al*., 2007; Jactel *et al*., 2009).

In the case of planted forests, the first management decision is the selection of planting material. Ideally, the tree species and variety is adapted to the site conditions. The use of exotic tree species requires additional consideration as such trees are more likely to recruit native insect herbivores when native congeneric tree species are present in the area of introduction (Branco *et al*., 2015). Of even greater importance is the species composition of forest stands. Two comprehensive reviews of the international scientific literature have shown that mixed forests are more resistant to forest insect damage than monocultures (Jactel and Brockerhoff, 2007; Castagneyrol *et al*., 2014). Another study showed that this trend also applies to impacts of invasive species (Guyot *et al*., 2015). Several mechanisms are thought to explain these results. The presence of non-host species in mixed forests is expected to raise physical or chemical barriers that limit host tree finding and colonization by insect herbivores. Mixed forests may also provide natural enemies with complementary habitat or feeding resources, thus enhancing biological control. How natural biocontrol can be affected by both direct and indirect effects of forest management is explored by Klapwijk *et al*. (2016, this issue). Classical biological control is generally considered a promising method to achieve self-sustaining long-term control of invasive pests by restoring more sustainable pest population dynamics. Nahrung *et al*. (2016, this issue) report some of the challenges associated with biological control as exemplified with their experience controlling *Sirex* in Australia. The woodwasp was discovered attacking *Pinus taeda* and *P. radiata* in Queensland in 2009 and biological control efforts were initiated shortly thereafter and inundative release of nematodes has been conducted for four consecutive years. It was observed that parasitism rates of *Sirex* by the nematode were low (Nahrung *et al*., 2016, this issue); however, variability of biological control efficacy in this system is not unusual, likely due to the complexity of the interactions between the host, insect, fungi and nematode (Slippers *et al*., 2015).

Site preparation treatments, including soil preparation, stump treatment and weed management may reduce the amount of breeding substrate available for important pests such as bark beetles and weevils (Jactel *et al*., 2009). Fertilization may be either beneficial or detrimental, depending on the type of fertilizer (nitrogen *vs* phosphorus) and on the category of pest (primary *vs* secondary) (Jactel *et al*., 2009). Management of the understorey vegetation may reduce the competition for light and water thus improving individual tree vigour and resistance. On the other hand, preserving diverse understorey vegetation may benefit parasitoids through the presence of nectariferous plants (Hougardy and Grégoire, 2000). Because thinning operations improve individual tree vigour this may reduce tree susceptibility to a number of secondary pests (such as secondary bark beetles), whereas it can favour primary pests such as several insect defoliators (Jactel *et al*., 2009). Sanitary thinning, which aims at removing weakened and dying trees, is often recommended to avoid breeding of insects which could later attack living trees, such as the European spruce bark beetle (*I. typographus*) that can attain high population densities on weakened trees (Stadelmann *et al*., 2013).

Logging operations with heavy machinery may result in bark injuries which can in turn trigger pest infections. Logging residues or stumps can also serve as breeding substrates for weevils and many bark beetles in conifer forests. Also, it has been suggested that single-tree or group selection cuttings would increase stand structural diversity, leading to improved individual tree vigour and thus resistance to pest insects (Brang *et al*., 2014). Besides affecting tree and stand vulnerability, forest management may have a more general effect on the risk of biotic damage as the economic value of growing stock is also dependent upon the type of silvicultural systems that are employed (Figure 1). For example, short rotation forestry may be less prone to risk than longer-rotation plantation forestry simply because very young trees used for bioenergy are of a lower value than mature trees used for timber (Jactel *et al*., 2012b).

Technological advances in diagnostics for managing forest health and biological invasions

A critical requirement for forest health and biosecurity/phytosanitary research and management is to ascertain the identity of organisms of interest. Traditionally, this has been accomplished through pest morphology and the highly specialized taxonomic expertise of entomologists and mycologists. The development of molecular tools for identification of species and genotypes has transformed this field. These molecular tools have developed to the point that they can now be used to study populations of organisms in economically important contexts, such as the invasion pathway (Adamowicz, 2015). The utility of molecular data was demonstrated by Bérubé and Nicolas (2015) who screened asymptomatic plants that were imported into Canada and found that two of 267 fungal operational taxonomic units (OTUs) were classified, with the potential to have moderate impacts on Canadian forests. A further 37 OTUs were classified as having the potential for low risk. This study illustrates how DNA can be utilized to detect latent pathogens in association with the international trade in live plants (also known as the 'plants for planting' pathway).

The risks associated with this pathway are not limited to the movement of seedlings and larger plants but also concerns the movement of seed. The presence of the *Eucalyptus* stem canker pathogen *Teratosphaeria zuluensis* was detected within seed and seed capsule material collected from eucalypts in a stand where the pathogen was known to be present (Jimu *et al*., 2016, this issue). This study revealed the possibility of pathogen movement with infested seed material and the potential risk of this pathway, as well as the utility of DNA-based methods for detecting pathogens. DNA analysis was also used by Buys *et al*. (2016, this issue), to develop a system by which species of Myrtaceae in New Zealand can be rapidly identified in the event of an incursion by the myrtle rust pathogen (*Puccinia psidii*). This pathogen is not present in New Zealand; however, it has become established in Australia where it is causing considerable damage. The risk of a subsequent invasion of New Zealand is high, given the large amount of trade, movement of people and air currents between the countries, all of which could facilitate the transport of pathogen spores. If *P. psidii* were to arrive in New Zealand, the tool developed by Buys *et al.* (2016, this issue) could be utilized as part of an incursion response, to confirm the identity of host and non-host species among the Myrtaceae, a family of which hundreds of species are present in New Zealand.

The availability of cost effective and rapid DNA-based diagnostic tests has furnished regulatory agencies and researchers with tools to improve the detection of invasive organisms, such as loop-mediated isothermal amplification (LAMP) that is less time consuming than traditional PCR (Villari *et al.*, 2013). It is important to note that these tools rely heavily on collections of expertly identified insects and fungi that are held in institutions throughout the world. It is critical that these collections are maintained and that the training of the next generation of taxonomists continue in order to ensure that molecular diagnostics are accurate and reliable. Molecular tools are widely accessible, relatively inexpensive and can be readily implemented by quarantine agencies thereby providing knowledge that can be used to reduce the probability of the establishment of exotic pests.

Conclusions

The impacts of invasive species are multifaceted and complex as illustrated by the articles in this special issue. Coupled with uncertainty related to climate change and its influence on insect and pathogen populations, the challenges for policy makers and regulators to manage impacts of invasive and native pests will become increasingly difficult. Regulators rely heavily on the results of robust scientific enquiry, and understanding these complex interacting forces is an important research focus. The articles in this special issue demonstrate the utility of various computer modelling strategies to estimate future impacts of forest pests, and also investigate new forest management practices and tools to detect and prevent the spread of invasive pests or the outbreaks of native pests. The provision of ecosystem goods and services by productive and natural forest ecosystems, as well as trees in urban environments, will continue to be threatened as a result of issues related to globalization. The impacts of invasive pests on natural and managed forest ecosystems are evident and phytosanitary measures such as ISPM 15 have been implemented to reduce the probability of inadvertent movement of pests through trade. The role of climate change in native and invasive pest population outbreaks has also been documented. Although it is clear these two complex drivers interact, there is uncertainty about the shape and nature of their interactions. Knowledge provided through process-based computer simulations, and the development of forest ecosystems that are inherently resistant and resilient, however, will allow us to anticipate future problems and consider these issues in proactive forest management plans.

Author contributions

All authors contributed equally to the writing of this manuscript.

Acknowledgements

The authors thank the organisers of the XXIV IUFRO World Congress for the opportunity to present the papers in this special issue during the congress. We also thank Gary Kerr, Editor-in-Chief of *Forestry*, and Lulu Stader for supporting this special issue. The editorial advice of Anssi Ahtikoski and Berthold Heinze is greatly appreciated. Figure 2 was kindly provided by Andrea Battisti. Jon Sweeney, Simon Shamoun and Andrew Liebhold provided useful comments on an earlier version of the manuscript.

Conflict of interest statement

None declared.

Funding

The contribution of T.D.R. was funded by the Canadian Forest Service. Contributions by B.J.B. were supported by the United States Department of Agriculture Forest Service. Contributions by E.G.B. were supported by Ministry of Business Innovation and Employment core funding to Scion (contract C04X1104) via the Better Border Biosecurity Collaboration (www.b3nz.org).

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ADAPTIVE FOREST MANAGEMENT IN INDIA IN THE CONTEXT OF CLIMATE CHANGE: ISSUES AND CHALLENGES

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1. Introduction:

Global warming and climate variability that cause immense concern today are the consequences of human-induced rise in Green House Gas (GHGs) concentrations in the atmosphere particularly after the onset of industrial revolution. According to fifth assessment report of the Intergovernmental Panel on Climate Change (IPCC, 2014), there had been an increase in atmospheric temperature of about 0.89°C and 0.72°C respectively over a period of more than 100 years and 50 years till 2012 and the predicted global temperature change at the end of the century is likely to be in the range between 1.5 and 4.5°C over the baseline period of 1986-2005 (IPCC, 2013). The report also states that globally there will be changes in rainfall pattern and increase in the frequency and intensity of extreme weather events associated with rise in atmospheric temperature. It is now realized that the impacts of climate change are no longer a distant conjured up problem. Rather it manifests as the most important environmental and developmental challenge globally and is an issue of great concern to all countries and regions irrespective of their size or level of development. Climate change is being experienced in various forms particularly as rising temperature, erratic weather events, variable rainfall, frequent droughts, sea level rise and inundation of low lying areas, cyclones and similar other coastal and marine catastrophes (Auffhammer *et al*., 2011 and Lobell *et al*., 2012). Though several countries have taken cognizance of the effects of climate change and have adopted measures to reduce its impacts, there is a long way to go with regard to the efficacy of fruition of these initiatives in view of the impending crisis looming over the planet.

The forests in India are facing increasingly difficult challenges. The most obvious challenge is to meet the growing demand for forest products, while safeguarding the ability of forests to provide a range of environmental services including among others, conservation of biodiversity, regulate hydrological cycle, amelioration of climate and protection of soil and water resources. Considering the overall pressure on the forests in general and also that of climate change in particular, it is imperative to adopt management strategies for improving the management effectiveness and resilience of forest ecosystems for its continued and improved deliverance of ecosystem goods and services. Adaptive management of forest resources become relevant in this context.

This paper highlights the importance of adaptive forest management in the context of climate change and recommendations for managing India's forests as a bulwark against climate change.

2. Impacts of Climate Change on Forest:

Human existence is inextricably linked with the goods and services provided by forests. Being a developing country located in the warmer tropics, India is considered highly vulnerable to climate change. Betts *et al*. (2008) pointed out that tropical forests are vulnerable to climate change and its impacts could be so severe as to threaten their structure, functionality and services. This is probably because the developing countries have limited capacity to deal with the issues related to climate change. Although, the impacts of climate variability are wide and far reaching on all facets of the physical and biological world, its impacts on forest ecosystems are particularly relevant and crucial as forests is one of the prime source of carbon sink and an important agent for mitigating the problem.

The climate change impacts on forest ecosystem are found to manifest both on species level and ecosystem level. Species are becoming rare/endangered together with their range shifts and changes in life cycle pattern, genetic trait, growth pattern, etc. In critical forest ecosystems like rain forests, mangroves, etc., loss of biodiversity, changing boundaries of ecosystems and other biotic and abiotic responses/stresses are being increasingly noticed. Forecasts of future impacts due to climate change predict large-scale range reduction and extinction of most species (Moritz and Agudo, 2013). Variation in precipitation and temperature are reported to be one of the key factors of climate change that is likely to have significant impacts on biodiversity (Krishnan *et al*., 2012).

Several studies have been conducted (mostly in developed countries) regarding the impacts of climate change on natural resources and forest ecosystem (Lemmen *et al.,* 2008; Lemprière *et al.,* 2008; Williamson *et al*., 2009 and Johnston *et al*., 2010). However, such studies and literature specific to Indian context are fragmentary and few except a few studies like that of Ravindranath *et al*. (2006) and Gopalakrishnan *et al*. (2011) who predicted vegetation changes and vulnerability status of the forested ecosystems in the context of climate change (IGNFA, 2016). Climate change impact on alpine forests of Uttarakhand (*Betula utilis*) revealed clear shift of tree line over the period from 1970-2006 (Singh *et al*. 2012).

According to the latest India State of the Forest Report (FSI, 2017), there has been net increase in land area of 6778 km^2 under forest cover, however on the other hand, several studies show that the quality and quantity of the forests is not rosy everywhere as there has been reports of biome shifts under scenarios of future climate change (Rasquinha and Sankaran, 2016). The climate modelling and likely impacts of climate change on forests according to India's Second National Communication to UNFCC, states that 30.6% and 45.9% forested grids under study out of the total are to become vulnerable respectively by the end of 2035 and 2085 as per AIB SRES IPCC scenario (MoEF, 2012).

3. Adaptive Forest Management:

Intense pressure on forests both due to climatic and anthropogenic factors have led us to make serious rethinking on what needs to done in the changing scenario especially on devising suitable management measures on improving the resilience of forests and dependent communities so as to circumvent or minimize the impacts of forest degradation, resource depletion and to ensure maximum sustainable utilization of the available resources. The increasing threat from climate change impacts on the productive capacity of tropical forests need to be addressed with the principles of adaptive forest management. In spite of various managerial initiatives, the advancement in this line is restricted largely due to poor resource information, reduced institutional capacity utilization and lack of foreseeing and innovative planning and policies. Adaptive forest management is relatively a new field and only very limited studies have been addressed this so far (Ray *et al*., 2015 and Yousefpour *et al*., 2017), however this at the core of the forest management research today (Yousefpour *et al*., 2012). From tropical countries, not much information is available with regard to implementation of adaptive forest management in response to climate change (Guariguata *et al*., 2012). In India, accurate projections of climate change impact on forest ecosystems at a scale which could be useful for developmental planning, livelihood and conservation strategies are largely lacking (Devi *et al*., 2018).

As Stern (2009) defines adaptation as *development in a more hostile climate*. Adaptation to climate change involves monitoring and anticipating change and undertaking actions to avoid the negative consequences and take advantage of potential benefits of those changes. For individual countries, reduction in GHGs emissions will demand major changes in energy policy as well as action to augment the process of carbon sink like forest cover increase. Effective management measures to combat the changes arising out of climate variability includes various policies and attitudes of the government towards understanding and devising strategies, more research oriented towards modelling & prediction, case studies of reference conditions with which the impacts are more pronounced in ecological and socio-economic aspects and party to consensus for global agreements to protect the atmosphere. Decision making in adapting forest management involves several crucial aspects. The three pillars of the suggested framework for adaptive forest management are the baseline understanding and knowledge of the decision makers, identification and selection of appropriate management options for both current and future changes in anticipation and analysis and implementation of the correct decision strategy (Yousefpour *et al*., 2017). According to World Bank (2010), more climate-resilient development is needed. Potential adaptive management and planning must be the solution for a way forward to curb the serious implications of climate variability and related issues. Mitigation response will not reduce adverse effects of GHGs that is already in the atmosphere, but would significantly reduce the rate of growth in global warming. Therefore, along with fast mitigation responses, we require adaptation to climate change. Forest management planning provides an excellent solution for considering climate change impacts and adaptations.

It is high time to start developing adaptive management strategies now as far as the climate change related issues in India are concerned. These include vulnerability assessment of forests to climate change, revising expectations of forest use, determining research and educational needs, development of forest policies to facilitate adaptive management, and determining when to implement responses. Government agencies should take the lead in creating an environment to foster adaptive management in forestry and in developing the necessary information required to respond.

Adaptive management should be practiced at various levels though more often local actors may have to play a major role as they are the ones that bear the brunt of the problem. This process involves two steps, the first being correct perception to the climate change and associated risks and the second being appropriate steps to be taken to minimize the adverse effects of climate change. Assessment of adaptive capacity of forests and its components, its dependent communities and their economy will not only help us to identify and address sources of vulnerability areas, but also useful in helping us to develop policies to enhance the adaptive management capacity of various forestry stakeholders and to assist them in identifying realistic adaptation options.

4. Major Issues and Challenges Ahead:

The choice of adaptation measures require complete understanding of the micro-level changes happening in the system and particularly discretion of the local managers to select the most appropriate measure suitable for their condition (IUFRO, 2009). Some of the key adaptation measures suitable to manage the climate related issues on forest ecosystems in India are as follows:

4.1 Vulnerability Identification:

India's forests are the lifeline of its rural population. Pressure from unsustainable development, declining availability of forest products, inadequate access to climate friendly energy sources and absence of viable economic and social alternatives drive the rural poor and tribal communities to intense dependence on forests that often transcend the thresholds of sustainable yield. It is very important to identify the critical ecosystems/areas/species that are likely to get impacted by climate change as well as factors/processes like forest fire, grazing, insect and pests, etc., that may become more deleterious under the influence of climate change and to adopt suitable management measures for the conservation, management and sustainable utilization of the same.

4.2 Improved Forest Productivity and Ecological Services:

India's forest productivity is significantly below the global average. Rapid land-use changes occurring around the forests have, at several places, resulted in fragmentation and disjoints in habitat connectivity. This is impeding the genetic flow and crippling ecosystem functionality. Besides, deterioration in site quality and second rotation decline in forest plantations have started impacting the long term performance of forest production sector. Improvement of plantation forestry by adopting silvicultural practices and by employing improved planting materials raised through tree improvement programmes/clonal technology and micro-propagation techniques may be carried out for enhancing forest productivity. A major research need is to explore and identify climate resilient plantation species and perform their new provenance trials. Identification of the tangible and intangible services provided by the forest is very important to suitably manage the forest so that the same can continue to be ensured to its dependents in the wake of the climate change problems. Also, this will ensure to reduce the overexploitation of forests by bringing improvement in the livelihoods of forest dependent communities.

4.3 Reclamation and Rehabilitation of Degraded Lands by Afforestation:

As per an estimate, around 41 percent of India's forests have been already degraded and dense forests are slowly losing their crown density. More than 70 percent of the forests have problems in regeneration and 55 percent prone to fire. As much as 78 percent of the forest area is subjected to heavy grazing and other unregulated use (NFC, 2006; FAO, 2009). Climate change and proliferation of invasive species compound this situation. The forest land under degradation is to be reclaimed and rehabilitated under green cover to ensure its sustainable utility for future. As per ISFR 2017, 10.58% of the total geographical area of the country is open and scrub jungle, which needs suitable management measures like plantation, afforestation, assisted natural regeneration, eco-restoration, etc., to make them more productive. Strong initiatives with surplus funding needs to be ensured under various plans/from alternate sources like, Green India Mission, Clean Development Mechanism, REDD-plus, etc., and the government machineries of forest management can better play a vital role in this.

4.4 Capacity Building of the Personnel:

Capacity building related challenges include insufficient financial investment; inadequate knowledge base and technology; absence of incentive structure and extension support to farmers for agro/farm forestry, etc. The capacities of field staff working at the cutting edge of the forest management require significant up-scaling to effectively manage the impacts of climate change. It is also necessary to strengthen the forest knowledge management system, use of technology, which will help in informed decision making.

4.5 Institutional Factors:

Current policies and practices adopted by Forest Department have its origins in the colonial era and premised largely on production forestry. This is amply reflected in the content of Working Plans too. In view of the far reaching and rapid changes occurring with regard to natural resource management, adequate and appropriate changes need to be there in forest management also. In other words, amendment to forest policy and legislation is a prerequisite for employing adaptive forest management.

4.6. Knowledge Factors:

Though there is general understanding and realization on the impending impacts of climate change, there are very few specific studies on this aspect. Even when such studies are available they may not be in a user-friendly and retrievable format for the field managers for taking informed decisions. Sufficient research especially to know the resource base and its implication in the wake of climate change scenario with clear cut objective and goals need to be planned and accomplished.

4.7. Reinvigorating Livelihoods:

Resilience of forest dependent communities is a critical aspect of the adaptive forest management. This is particularly relevant in India where still a very large population reliant on forest resources for livelihoods. Unless understood and addressed the impacts of climate change could very well adversely affect the very fabric of local livelihoods and induce poverty and thus deepen the already existing vulnerability of the local communities and thereby the dependency on forestry resources.

5. Conclusion:

Forests in India are already at stake due to multitude of disturbances and climate change impacts are relatively new addition to it and that likely to cause severe uncertainty in future forest ecosystem services and productivity. It is important to note that informed forest management planning in the physical and biological aspects of the forest and socio-economic aspects of the forest dependent communities for the current level of issues and future issues in anticipation as well as development of resilient forest to climate change can only yield better results in combating the problem. Decision making in adapting forest management involves several crucial aspects. The three pillars of the suggested framework for adaptive forest management are the baseline understanding and knowledge of the decision makers, identification and selection of appropriate management options for both current and future changes in anticipation and analysis and implementation of the correct decision strategy. Adaptive forest management is considered to be a relatively new subject in Indian context. Our forest managers and forest management policy makers are yet to conceive the very basic idea of the principle of adaptive forest management. Moreover, the reflection of the same in national and state level forest policies require a great level of effort in terms of information, manpower and monetary resources such as grass root level understanding of the intricacies of both the magnitude and dimension of the problem, taking the appropriate decision at the correct point of time by anticipating the future changes, capacity building of the personnel involved in decision making, developing information of the resources, which include everything related to forest and forest produce and its monitoring and evaluation, identifying the vulnerability sectors, giving timely warning of the extreme events, etc. Better adaptive forest management plan and implementation of the same by the informed decision makers at the correct point of time may ensure the future sustainability of the forests and their goods and services to the people.

SUMMARY

Climate change has become a reality and its impacts on all spheres of life especially resilience of the forest and its products and services are far reaching. Studies conducted elsewhere have pointed out categorically that range shifts of disturbance agents both across latitude and altitude are the early warning signals that mark the onset of considerably more severe changes in future. Apart from mitigation measures, effective adaptive management strategies together with improved adaptation capacity of the forests will conjure up the aftermaths sustainably over a quite long period of time. The increasing threat from climate change impacts on the productive capacity of tropical forests need to be addressed with the principles of adaptive forest management. In spite of various managerial initiatives, the advancement in this line is restricted largely due to poor resource information, reduced institutional capacity utilization and lack of foreseeing and innovative planning and policies. Adaptive forest management is relatively a new field and only very limited study have been addressed this so far. From tropical countries, not much information is available with regard to implementation of adaptive forest management in response to climate change. In India, accurate projections of climate change impact on forest ecosystems at a scale which could be useful for developmental planning, livelihood and conservation strategies are largely lacking. Decision making in adapting forest management involves several crucial aspects. The three pillars of the suggested framework for adaptive forest management are the baseline understanding and knowledge of the decision makers, identification and selection of appropriate management options for both current and future changes in anticipation and analysis and implementation of the correct decision strategy. This paper highlights the importance of adaptive forest management in the context of climate change and recommendations for managing India's forests as a bulwark against climate change.

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Issues and Challenges in Adaptive Forest Management

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Commanding seven per cent of world's biodiversity, India is one of the 17 mega diversity countries. It supports 16 major forest types, varying from alpine pastures in the Himalayas to temperate, sub-tropical and tropical forests, mangroves of the coastal regions, having a vast variety of flora and fauna. The country's forest cover is 70.82 million ha, constituting 21.54 per cent of its geographical land area. In the history of human civilization, build-up of green house gases (GHGs) in the atmosphere has been phenomenal in the last century due to the very rapid pace of human development, including industrialization. The cumulative effect in form of warming of earth and its associated fall outs will have far reaching impacts on the entire humanity.

CO_2 is among the chief constituents of the GHGs. Over the past 150 years, deforestation has contributed to an estimated 30 percent of the atmospheric build-up of CO_2 and is responsible for about 20 percent of green house gases. The redeeming feature of the forests is that as a whole, they absorb more carbon than they emit as of now. FAO estimated that the world's forests and forest soils store more than 652 giga tons of carbon – many times more than the amount found floating free in the atmosphere. It has been estimated that carbon stock of India's forests as on 2017 is 7,083 million tons. Therefore, forest has immense potential to capture atmospheric carbon and it functions as store house or carbon reservoir.

However, the problem is that this critical carbon-regulating service of forests could be lost entirely, if the earth heats up 2.5 degrees Celsius or more relative to pre-industrial levels, which is expected to occur if emissions are not substantially reduced. Further, higher temperatures, along with the prolonged droughts, more intense pest invasions, and other environmental stresses that could accompany climate change, would lead to considerable forest destruction and degradation.

Study of climate change modeling for the period 2020-2050 and its impact on forest types of India has been undertaken by Indian Institute of Science in the four eco sensitive regions of the country viz., the Himalayas, the Western Ghats, the Coastal region and the North-Eastern States, accounting for more than half of the country's forests. The study predicts that only one fourth of the forest grids (69 out of the total 285 studied) falling in these four regions will be vulnerable to changes in the mid period, namely by 2035 and vegetation in those grids would change type. CO^2 concentration by that period is estimated to be around 490 ppm. While the Himalayas would be more vulnerable, the Western Ghats and the Coasts are moderately vulnerable, the North Eastern states would be impacted the least. However, in the long term, it is expected that there would be large scale shifting of forest biomes throughout India. The highest impact is expected on the teak and sal forests of central and eastern regions and the temperate Himalayas.

Some broader and general predictions on the shift of vegetation from the current forms to entirely altered vegetation mix in various forest types across the regions of India are available. Broadly, the tropical dry forest, dry and moist savannas are projected to change to tropical dry forest and tropical moist forest. Xeric scrubland, to a smaller extent, is set to decrease in area and xeric woodland is expected to increase in the drier regions. In the colder regions, Boreal and temperate conifer coverage will decrease, while temperate deciduous and temperate evergreen coverage increases.

The key issue that the forest planners and managers will face is the direction in which they have to focus their management attention. Achievement of the societal goal of sustainable forest management that aims to maintain and enhance the economic, social and environmental value of all types of forests for the benefit of present and future generations will continue to be the nation's forest sectors' primary agenda. This will call for continuous effort in minimizing the impacts of global climate change on forest ecosystems. Foresters need to focus on the climate change mitigation as a first step to minimize its impacts on forests. Hard woods particularly serve as carbon blocks, helping to lock up carbon on a permanent basis. India, having over 100 million hectares of wasteland and degraded forests, mitigation through the forest sector and afforestation seems like an attractive solution. Use of such woods is seen as an option to substitute more emission-intensive, maximum carbon foot print resources. The priority before the forest managers would be to plan and implement afforestation, reforestation and assisting natural regeneration of the forests besides building tree assets on private lands with a view to create additional carbon sink. In this regard, research on enhancing the capacity of the forest ecosystems for carbon sequestration needs to be taken up on priority. However, using forests as carbon sinks has been a contentious issue. The fear is that it legitimizes the continued destruction of old-growth and pristine forests which are rich ecosystem and have an established biodiversity base that naturally maintains the environment.

Integrating the climate change concerns into the forest management will be the key driver in our adaptive forest management strategy. Adaptive forest management is "a forest management approach that expressly tackles the uncertainty and dynamism of complex systems". Given the prevailing uncertainty regarding ecosystem structure, function, and inter-specific interactions in a climate change scenario, precaution demands an ecosystem approach rather than single-species approach to management. This approach includes the recognition that adaptation occurs through a process of 'plan-do-review-act'. In practice, adaptive management also recognizes seven key components that should be considered for quality natural resource management practice viz., 1) Determination of scale, 2) Collection and use of knowledge, 3) Information management, 4) Monitoring and evaluation, 5) Risk management, 6) Community engagement, and 7) Opportunities for collaboration.

Adaptive forest management will be essential to address arising challenges and reduce forest vulnerability. Adaptation measures might include, for example, selection of pest-resistant or drought-tolerant varieties, use of stocks from a range of provenances, under planting of genotypes of species adapted to expected new climate conditions, or assisted natural regeneration of functional species. The measures need to be adapted to forest condition and the specific site. Forestry research will have to address these challenges.

The most important challenge to the forest managers will be to track the precise movement of vegetation in a given forest area with reference to short term and long term time frames. As the level of GHGs is likely to gradually move up, the predicted changes with the passage of time are bound to be dynamic in nature. Such shifts in vegetation including trees would have influence on the associated lesser flora and the dependent faunal species. As these changes will occur in a more subtle manner in the larger landscapes bearing a specific forest type, the projected shift in vegetation may lead to large-scale forest dieback and loss of biodiversity, especially in the transition zones between forest types. The current temporal prescriptions in form of Working Plans for managed forests and the Management Plans for the protected areas are made for a brief tenure ranging from five to ten years with no credible weightage given to climate change forecasts. In the absence of reliable and accurate assessment of anticipated change events consequent to global warming in the spatial scale for specific forest management units like a forest division or a protected area, it would be rather difficult to suggest the most appropriate management prescriptions for the area. In this context, forest working plans, management plans and practices need to be adapted to modifications caused by climate change, both gradual and abrupt. This need sound backing from research inputs. It is heartening to note that the draft National Forest Policy 2018 lays focus on factoring in climate change concerns in all the forests/ wildlife areas working/management plans.

POLICYFORUM

LAND USE

Managing Forests and Fire in Changing Climates

Policy focused on fire suppression only delays the inevitable.

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With projected climate change, we expect to face much more forest fire in the coming decades. Policymakers are challenged not to categorize all fires as destructive to ecosystems simply because they have long flame lengths and kill most of the trees within the fire boundary. Ecological context matters: In some ecosystems, high-severity regimes are appropriate, but climate change may modify these fire regimes and ecosystems as well. Some undesirable impacts may be avoided or reduced through global strategies, as well as distinct strategies based on a forest's historical fire regime.

Fire regimes are commonly characterized by burn frequency and severity within a given area. Severity is often estimated as the proportion of overstory trees killed by fire. In general, as frequency increases, fuels have less time to accumulate, reducing intensity and subsequent tree mortality. However, a great deal of variation occurs even within fire regime types (*1*). The spatial scale and patch-size distribution of different severity classes are key in assessing whether fire regimes have changed over time and whether changes maintain or compromise forest ecosystems.

Globally, fire frequency and severity vary among forest types. Essentially all fires have high-severity effects, where most of the trees are killed, at some spatial scale and patch size. The critical issue is whether tree mortality patch sizes (and their temporal and spatial frequency) allow recovery of the same or similar vegetation types. If high-severity patch sizes are too large, microclimates and regeneration mechanisms (e.g., seed abundance and dispersal) can limit tree reestablishment (see the figure). Large high-severity patches may produce vegetation type changes, especially in forests adapted to frequent, low- to moderate-severity fire regimes or in forests that lack in situ propagule sources. Introduced species, such as nonnative grasses, also may alter forest fire regimes and lead to changes in vegetation type (*2*).

Changing fire severity is at the heart of ecological debates about historically high-frequency, low- to moderate-severity fire regimes, such as ponderosa pine (*Pinus ponderosa*) and semiarid mixed-conifer forests. A central concern is whether high-severity patches in wildfires are too large, which results in undesirable ecosystem changes (see the figure). Rising temperatures, related drought stresses, and increased fuel loads are driving high-severity patches to extraordinary sizes in some areas (*3*).

In contrast, forests adapted to low-frequency, high-severity regimes such as Rocky

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Historical forest fire regimes. (Top) Mixed-conifer forest in northern California with fuels accumulated from a century of fire suppression (left), mature surviving and regenerating trees in an area that had been mechanically thinned to reduce fuels and residues either removed or burned (center, 10 years after the 2002 Cone Fire), and an adjacent untreated area lacking live seed trees, now dominated by shrubs (right, 10 years after the Cone Fire). **(Bottom)** Lodgepole pine forests in Greater Yellowstone (left) regenerated abundantly from the canopy seedbank after the stand-replacing 1988 Yellowstone Fires (center, 15 years postfire), but regeneration was greatly reduced in forests of comparable age and serotiny after the 2000 Glade Fire, which was followed by summer drought 1 year after the burn (right, 10 years postfire). Forests are within 4 km of each other at each site.

CREDIT (TOP) MALCOLM NORTH; (BOTTOM) MONICA TURNER

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Mountain lodgepole pine (*Pinus contorta* var. *latifolia*) have evolved to regenerate after large, high-severity events. Seed banks stored in tree crowns survive even the highest-severity fires and are released shortly after the fire ends. If seeds germinate in open conditions conducive to relatively high growth rates, a new forest can become established in a few decades (see the figure). Other species can regenerate a new crown from one burned by fire because of dormant buds.

Future Fire Under Changing Climates

With projected climate warming (*4*), forests around the globe will likely undergo major landscape-scale vegetation changes in coming decades. In some areas, plant productivity may decline to a point where fire will become less frequent (*5*). In more productive areas, fire regimes may shift from being mostly climate-controlled (top-down) to mostly fuel-controlled (bottom-up) (*6*). In both cases, slow vegetation change may be abruptly accelerated by a change in fire regime driven by novel climatic conditions.

Increased frequency and size of large, severe forest fires are expected in Australia, the Mediterranean Basin, Canada, Russia, and the United States (*3*, *7*, *8*). In the western United States, increased frequency and size of fires is associated with increased temperatures, earlier spring snow melt, and longer fire seasons (*9*)—mechanisms that are applicable to other regions of the world.

Trends and projections of climate and fire responses suggest that new strategies to mitigate and adapt to increased fire are needed to sustain forest landscapes. Identifying and implementing appropriate responses will not be easy because the complexity of local-to-regional dynamics makes uniform, simple, or unchanging policy and management strategies ineffective (*10*). It is especially difficult to motivate social response to environmental transitions that unfold slowly and are thus difficult to detect before it is too late (*11*).

We suggest strategies for forests of all fire regimes: *Landowners should follow "Firewise" guidelines (www.firewise.org/) for houses and other infrastructure.* Increased development in fire-prone landscapes has increased suppression costs, exacerbated risk to human safety and infrastructure, and reduced management options. People living in these forests must be prepared rather than relying solely on fire departments. Some places may be so hazardous that building should be prevented, discouraged, or removed (e.g., by regulation or insurance and/or tax incentives).

Fire managers should avoid trying to uniformly blacken wildfire landscapes through burnout and mop-up operations, especially in burn interiors. As wildfire sizes have grown in recent decades, direct attack has been replaced with indirect attack, where fire lines are placed some distance from the active fire front, and then the area between is intentionally burned, often with high-severity fire, to reduce fuel and create a wider fire barrier. Unburned or partially burned patches are critical refugia that aid postfire recovery in forests of all fire regimes and should be conserved whenever possible.

Land managers could anticipate changes using models of species distribution and ecological processes and should consider using assisted migration (12). Dominant forest species may be unable to recover from fires with large high-severity patches. Replacement ecosystems of shrublands or grasslands may provide some ecological benefits, but they offer very different habitats for wildlife and have reduced carbon storage relative to native forests.

We also suggest several distinct strategies based on a forest's historical fire regime. *Mitigation in forests with historically high-frequency, low- to moderate-severity fire regimes:* (i) Restore resilient forest structure similar to historical patterns that survived during past high-fire periods (and those anticipated in the future) (see the figure). Fuel reduction and restoration treatments can increase resiliency by reducing density-dependent tree mortality (*4*) and excessive insect and/or disease problems and can increase spatial heterogeneity.

(ii) Fund forest restoration. We know how to treat forests to reduce fire hazards, with generally positive or neutral ecological effects, although impacts to wildlife with large home ranges have not been fully assessed (*13*). Public acceptance of these treatments is increasing (*14*); the barrier is cost. Treatment rates are far below what is needed for landscape resilience (*15*). Because the federal government has no jurisdiction in development policies in the privately owned urban-wildland interface, state and local jurisdictions could pay for fire suppression in the interface. This would enable a significant increase in critical forest restoration funding and would probably reduce building in the interface.

Adaptation in forests with historically low-frequency, high-severity fire regimes: (i) Expect changes in forest type and age across the landscape (see the figure). Some forest types will be relatively resilient to more frequent fires, notably resprouting or seed-banking species. However, even these forests will likely exhibit substantial changes in landscape structure, such as shifts to a preponderance of young stands (*16*).

(ii) Some forests will change to nonforest vegetation after fire. Spruce-fir (*Picea-Abies*) and interior Douglas fir (*Pseudotsuga menziesii*) forests may exhibit large changes in structure and species composition because they lack persistent seed banks or sprouting capability. Some areas may even shift to a nonforest state, especially if trees cannot reestablish in a warmer, drier climate. Such changes will not necessarily be catastrophic (e.g., a shift to nonforest could potentially increase water yield) and could be expected to reduce intensity of subsequent fires. However, shifting from forest to nonforest would affect most ecosystem services. There are no clear guidelines for increasing the resilience of these forest types—unlike for forests adapted to high-frequency, low- to moderate-severity fire regimes—other than minimizing additional stresses from excessive grazing, recreation, and salvage logging.

The annual cost of fire suppression is increasing and unsustainable; costs exceeded \$2 billion in the United States in 2012. Fire policy that focuses on suppression only delays the inevitable, promising more dangerous and destructive future forest fires. In contrast, land management agencies could identify large firesheds (20,000 to 50,000 ha) where, under specified weather conditions, managed wildfire and large prescribed fire are allowed to burn, sometimes after strategic mechanical fuel treatments (*15*). Acknowledging diversity in fire ecology among forest types and preparing forests and people for larger and more frequent fires could help reduce detrimental consequences.

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Ecological Applications, 17(8), 2007, pp. 2145–2151

CLIMATE CHANGE AND FORESTS OF THE FUTURE: MANAGING IN THE FACE OF UNCERTAINTY

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Abstract. We offer a conceptual framework for managing forested ecosystems under an assumption that future environments will be different from present but that we cannot be certain about the specifics of change. We encourage flexible approaches that promote reversible and incremental steps, and that favor ongoing learning and capacity to modify direction as situations change. We suggest that no single solution fits all future challenges, especially in the context of changing climates, and that the best strategy is to mix different approaches for different situations. Resources managers will be challenged to integrate adaptation strategies (actions that help ecosystems accommodate changes adaptively) and mitigation strategies (actions that enable ecosystems to reduce anthropogenic influences on global climate) into overall plans. Adaptive strategies include *resistance* options (forestall impacts and protect highly valued resources), *resilience* options (improve the capacity of ecosystems to return to desired conditions after disturbance), and *response* options (facilitate transition of ecosystems from current to new conditions). Mitigation strategies include options to sequester carbon and reduce overall greenhouse gas emissions. Priority-setting approaches (e.g., triage), appropriate for rapidly changing conditions and for situations where needs are greater than available capacity to respond, will become increasingly important in the future.

Key words: carbon sequestration; climate change; desired conditions; ecosystem management; facilitated conservation; forest management; historical variability; resilience; resistance; wildfire.

INTRODUCTION

During the last several decades, forest managers have relied on paradigms of ecological sustainability, historical variability, and ecological integrity to set goals and inform management decisions (Lackey 1995, Landres et al. 1999). These concepts commonly use historical forest conditions, usually defined as those that occurred before Euro-Americans dominated North American landscapes, as a means of gaining information about how healthy forests should be structured. There is no doubt that historical data have immense value in improving our understanding of ecosystem responses to environmental changes and setting management goals (e.g., Swetnam et al. 1999). However, many forest managers also use the range of historical ecosystem conditions as a management target, assuming that by restoring and maintaining historical conditions they are maximizing chances of maintaining ecosystems (their goods, services, amenity values, and biodiversity) sustainably into the future. This approach is often taken even as ongoing climate changes push global and regional climates beyond the bounds of the last several centuries to millenia (Intergovernmental Panel on Climate Change 2007). As importantly, novel anthropogenic stressors such as pollution, habitat fragmentation, land-use changes, invasive plants, animals, and pathogens, and altered fire regimes interact with climate change at local to global scales. The earth has entered an era of rapid environmental changes that has resulted in conditions without precedent in the past no matter how distantly we look. Attempts to maintain or restore past conditions require increasingly greater inputs of energy from managers and could create forests that are ill adapted to current conditions and more susceptible to undesirable changes. Accepting that the future will be different from both the past and the present forces us to manage forests in new ways. Further, although quantitative models can estimate a range of potential directions and magnitudes of environmental changes and forest responses in the future, models rarely can predict the future with the level of accuracy and precision needed by resource managers (Pilkey and Pilkey-Jarvis 2007). We might feel confident of broad-scale future environmental changes (such as global mean temperature increases), but we cannot routinely predict even the direction of change at local and regional scales (such as increasing or decreasing precipitation). A healthy skepticism leads us to use models to help organize our thinking, game different scenarios, and gain qualitative insight on the

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Manuscript received 11 October 2006; revised 14 May 2007; accepted 15 May 2007. Corresponding Editor: D. McKenzie.
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range of magnitudes and direction of possible future changes without committing to them as forecasts.

Facing an unknowable and uncertain future, however, does not mean "anything goes" for natural resource management. Managing in the face of uncertainty will require a portfolio of approaches, including short-term and long-term strategies, that focus on enhancing ecosystem resistance and resilience as well as assisting forested ecosystems to adapt to the inevitable changes as climates and environments continue to shift. Historical ecology becomes ever more important for informing us about environmental dynamics and ecosystem response to change. We offer here a conceptual framework for developing forest management strategies in a context of change.

FOREST AND ECOSYSTEM MANAGEMENT IN THE FACE OF CHANGE

The premise of an uncertain but certainly variable future is effectively best addressed with approaches that embrace strategic flexibility, characterized by risk-taking (including decisions of no action), capacity to reassess conditions frequently, and willingness to change course as conditions change (Hobbs et al. 2006). Learning from experience and iteratively incorporating lessons into future plans (adaptive management in its broadest sense) is the necessary lens through which natural resource management must be conducted (Spittlehouse and Stewart 2003, Stephens and Ruth 2005). Decisions that emphasize ecological process, rather than structure and composition, become critical (Harris et al. 2006). An example is increased use of managed wildfire in remote places (Collins and Stephens 2007). Similarly, institutional flexibility will be more effective than rigid or highly structured decision making.

A central dictum under uncertain futures is that no single approach will fit all situations (Spittlehouse and Stewart 2003, Hobbs et al. 2006). A toolbox approach, from which various treatments and practices can be selected and combined to fit unique situations, will be most useful. Some applications will involve traditional management approaches, but used in new locations, seasons, or contexts. Other options may require experimenting with new practices. A toolbox approach recognizes that strategies may vary based on the spatial and temporal scales of decision-making. Planning at regional scales will often involve acceptance of different levels of uncertainty and risk than appropriate at local scales (Saxon et al. 2005).

The framework of options presented below includes both adaptation strategies, that is, actions that help forested ecosystems accommodate changes, and mitigation strategies, actions that reduce the causes of stress, such as reducing anthropogenic climate change by sequestering CO_2 and reducing greenhouse gases (Papadopol 2000, Millar et al. 2006). Integrative approaches that combine adaptation and mitigation practices in complementary ways are favored. A first consideration in building an integrative strategy is to evaluate the types of uncertainty. These could include, for example, knowledge about present environmental and ecological conditions, models and information sources about the future, institutional resources (staff, time, funds available), planning horizon (short- vs. long-term), and public and societal support (Lindner et al. 2000, Wheaton 2001). A further decision is whether, or to what degree, to adopt deterministic or indeterministic approaches. The former accepts certain kinds of information about the future as reliable enough upon which to base decisions. By contrast, indeterministic approaches base planning on an assumption that information about the future is not adequately known, and plan instead directly for uncertainty. Deterministic approaches "put all the eggs in one basket" and risk potential failures if an assumed future does not unfold, whereas indeterministic approaches employ "bet hedging" strategies that attempt to minimize risks by taking multiple courses of action. Below we offer management options and examples for populating a manager's climate-change toolbox.

ADAPTATION OPTIONS

Create resistance to change

One set of adaptive options is to manage forest ecosystems and resources so that they are better able to resist the influence of climate change or to forestall undesired effects of change (Parker et al. 2000). Whereas this may seem a denial of future change, it is a defensible approach to uncertainty. From high-value plantations near harvest to high-priority endangered species with limited available habitat, maintaining the status quo for a short time may be the only or best option. Resistance practices seek to improve forest defenses against direct and indirect effects of rapid environmental changes. In western North America these will commonly include reducing undesirable or extreme effects of fires, insects, and diseases (Agee and Skinner 2005). Treatments might include complete fuel breaks around highest risk or highest value areas (such as wildland–urban interfaces, forests with high amenity or commodity values, or at-risk species); intensive removal of invasives; or interventions such as those used in high-value agricultural situations (resistance breeding, novel pheromone applications, or herbicide treatments). Abrupt invasions, changes in population dynamics, and long-distance movements of native and nonnative species are expected in response to changing climates (Keeley 2006). Climate changes may also catalyze conversion of native insects or disease species into invasive species in new environments, such as with mountain pine beetle (*Dendroctonus ponderosae*) east of the Continental Divide in Canada (Carroll et al. 2006). Taking early defensive actions at key migration points to remove and block invasions is important to increase resistance.

Resisting climatic and other environmental changes to forests often may require intensive intervention, accelerating efforts and investments over time, and a recognition that eventually these efforts may fail as conditions change cumulatively. Creating resistance to directional change is akin to "paddling upstream," and eventually conditions may change so much that resistance is no longer possible. For instance, site capacities may shift from favoring one species to another. Forests that have been treated to resist climate-related changes may cross thresholds and be lost catastrophically (Harris et al. 2006). For this reason, resistance options are best applied in the short-term and to forests of high value. Forests with low sensitivity to climate may be those most likely to accommodate resistance treatments, and high-sensitivity forests may require the most intensive efforts to maintain.

Promote resilience to change

Resilient forests are those that not only accommodate gradual changes related to climate but tend to return toward a prior condition after disturbance either naturally or with management assistance. Promoting resilience is the most commonly suggested adaptive option discussed in a climate-change context (Dale et al. 2001, Price and Neville 2003, Spittlehouse and Stewart 2003), but like resistance, is not a panacea. Resilience in forest ecosystems can be increased through practices similar to those described for resisting change but applied more broadly, and specifically aimed at coping with disturbance (Dale et al. 2001, Wheaton 2001). Given that the plant establishment phases tend to be most sensitive to climate-induced changes in site potential (Betancourt et al. 2004), surplus seed-banking (Ledig and Kitzmiller 1992), and intensive management during revegetation through early years of establishment may enable retention of desired species, even if the site is no longer optimal (Dale et al. 2001, Spittlehouse and Stewart 2003).

Capacity to maintain and improve resilience may become more difficult and require more intensive intervention as changes in climate accumulate over time. These options are best exercised in projects that are short-term, have high amenity or commodity values, or under ecosystem conditions that are relatively insensitive to climate change effects.

Enable forests to respond to change

This group of adaptation options intentionally accommodates change rather than resists it, with a goal of enabling or facilitating forest ecosystems to respond adaptively as environmental changes accrue. Treatments implemented would mimic, assist, or enable ongoing natural adaptive processes such as species dispersal and migration, population mortality and colonization, changes in species' dominances and community composition, and changing disturbance regimes. The strategic goal is to encourage gradual adaptation and transition to inevitable change, and thereby to avoid rapid threshold or catastrophic conversion that may occur otherwise.

Depending on the context, management goals, and availability and adequacy of modeling information (climate and otherwise), different approaches may be chosen. Changes in fundamental ecosystem state are assumed to happen, either in some general direction (deterministic) where specific goals are planned for the future, or in unknown directions (indeterministic) where goals are developed for uncertainty. A sample of potential practices follows.

1. *Assist transitions, population adjustments, range shifts, and other natural adaptations.*—Qualitative indications of future change may be adequate to trigger actions at least in broad outline. With such information, managers might plan for transitions to new conditions and habitats, and assist the transition, e.g., as appropriate, assist species migrations along expected climatic gradients, plan for higher-elevation insect and disease outbreaks, anticipate forest mortality events and altered fire regimes, or accommodate loss of species' populations on warm range margins (Ledig and Kitzmiller 1992, Parker et al. 2000). For forest plantations, examples would include modifying harvest schedules, altering thinning prescriptions and other silvicultural treatments, replanting with different species, shifting desired species to new plantation or forest locations, and taking precautions to mitigate likely increases in stress on plantation and forest trees.

A nascent literature explores the advantages and disadvantages of "assisted migration," that is, intentional movement of propagules or juvenile and adult individuals into areas assumed to be their future habitats (Halpin 1997, McLachlan et al. 2007). Some environments have broad and regular gradients, making adaptive migration directions obvious. Others, such as patchy mountainous terrain, are heterogeneous, and migration direction is far more difficult to determine. On-the-ground monitoring of native species can provide insight into what organisms are experiencing, and indicate the directions of change and appropriate response at local scales. This can allow management strategies to mimic emerging natural adaptive responses rather than rely on quantitative projections. For instance, new species mixes (mimicking what is regenerating naturally or outperforming plantation species), altered genotype selections, modified age structures, and new management contexts (e.g., uneven vs. even-aged management, altered prescribed fire regimes) may be considered.

2. *Increase redundancy and buffers.*—Here we suggest using redundancy and creating diversity through practices that spread risks rather than concentrate them. These can be achieved, for instance, by introducing species over a range of environments rather than within historical distribution, "preferred habitat," or projected future environments. Redundant plantings across a range of environments can provide monitoring infor-

mation if survival and performance are measured and analyzed. Reexamining replicated forest plantations, such old genetic provenance or progeny tests, is a means of gathering information about adaptation to recent and ongoing changes. Opportunistic assessment, such as of horticultural plantings of native species in landscaping, gardens, roadsides, or parks, can give clues on how species respond in different locations as climate changes.

3. *Expand genetic diversity guidelines.*—Existing guidelines for genetic management of forests and restoration projects specify actions to retain local gene pools. In the past, strict transfer rules that minimized movement of germplasm and small seed zones were developed to avoid contamination of populations with ill-adapted genotypes. These rules were based on assumptions that neither environments nor climate were changing. Relaxing these guidelines may be appropriate under assumptions of changing climates (Ledig and Kitzmiller 1992, Spittlehouse and Stewart 2003, Millar and Brubaker 2006). In this case, either deterministic or indeterministic options could be chosen. In the former, germplasm would be moved in the expected adaptive direction, for instance, rather than using local seed, seed from a warmer population would be used. New transfer rules could be developed for expected future climate gradients. By contrast, if an uncertain future is assumed, expanding seed zone sizes or relaxing rules to admix germplasm from adjacent zones might be considered. Adaptive management of this nature is experimental by design, should be undertaken cautiously, and requires careful documentation of treatments, seed sources, and outplanting locations to learn from both failures and successes.

Enforcing traditional best genetic management practices that equalize germplasm contributions and enhance effective population sizes becomes especially important under uncertain futures. Genotypes known or selected for broad adaptations would also be favored. By contrast, using a single or few genotypes (e.g., a select clone or small clonal mix) is far riskier in a long-term context of uncertainty.

4. *Manage for asynchrony and use establishment phase to reset succession.*—Changing climates over paleohistorical time scales have repeatedly altered biotic communities as plants and animals responded to natural changes (Huntley and Webb 1988). To the extent that climate acts as a region- and hemispheric-wide driver of change, the resulting shifts in biota often occur as synchronous changes across the landscape (Betancourt et al. 2004). At decadal and centennial scales, for instance, recurring droughts in the west and windstorms in the east have synchronized forest composition and age- and stand structure across broad landscapes, which then become vulnerable to climate shifts. This appears to have happened in some western forests as widespread drought has induced diebacks (Breshears et al. 2005). Opportunities exist to manage early successional stages following widespread mortality by deliberately reducing landscape synchrony (Betancourt et al. 2004). Asynchrony can be achieved by promoting diverse age classes, species mixes, within-stand and across-landscape structural diversities, and genetic diversity. Early successional stages provide the most practical opportunities for resetting ecological trajectories in ways that are adaptive to present and future rather than past conditions.

5. *Establish "neo-native" forests.*—Information from historical species ranges and responses to climate change can provide unique insight about species responses, ecological tolerances, and potential new habitats. Areas that supported species in the past under similar conditions to those projected for the future might be considered sites for "neo-native" stands of the species. These may even be outside the current species range, in locations where the species would otherwise be considered exotic. For instance, Monterey pine (*Pinus radiata*), endangered throughout its small native range, has naturalized along the north coast of California distant from its present native distribution. Much of this area was paleohistorical range for the pine, extant during climate conditions that have been interpreted to be similar to expected futures in California. Using these locations for "neo-native" conservation stands, rather than removing trees as undesired invasives, is an example of how management could accommodate climate change (Millar 1998).

6. *Promote connected landscapes.*—The capacity to move (migrate) in response to changing climates has been key to adaptation and long-term survival of plants and animals in historical ecosystems. Plants migrate (shift ranges) by dying in unfavorable sites and colonizing favorable sites, including internal species' margins. The capacity to do this is aided by managing for connected landscapes, that is, landscapes that contain continuous habitat with few physical or biotic impediments to migration, and through which species can move readily (Halpin 1997, Noss 2001). Promoting connected forested landscapes with flexible management goals that can be modified as conditions change may assist species to respond naturally to changing climates (Noss 2001). Desired goals include reducing fragmentation and planning at large landscape scales to maximize habitat connectivity.

7. *Realign significantly disrupted conditions.*—For forests that have been significantly disturbed and are far outside historical ranges of variation, restoration treatments are often prescribed. Re-alignment or entrainment with current and expected future conditions rather than restoration to historical pre-disturbance conditions may be a preferred choice (Harris et al. 2006, Millar and Brubaker 2006). In this case, management seeks to bring processes of the disturbed landscape into the range of current or expected future environments (Halpin 1997). The Mono Basin case in California exemplifies this approach, where water balance models were used to determine appropriate lake levels buffered

for current and expected future climate variability (Millar and Woolfenden 1999).

8. *Anticipate surprises and threshold effects.*—Evidence is accumulating that species interactions and competitive responses under changing climates can be complex and unexpected (Suttle et al. 2007). Managers can evaluate the potential for indirect and surprise effects that may result from cumulative climate changes or changes in extreme weather events. This involves anticipating events outside the range of conditions that have occurred in recent history. For example, reductions in mountain snowpacks lead to more bare ground in spring such that even "average" rain events may run off immediately, rather than being buffered by snowpacks, and produce extreme unseasonal floods. In many parts of western North America, additional stresses of extended summer water deficits are pushing plant populations over thresholds of mortality, as occurred in the recent multi-year droughts in the Southwest (Breshears et al. 2005). Other examples already observed in some areas are year-round fire seasons and fires in atypical locations, such as subalpine and coastal environments.

9. *Experiment with refugia.*—Plant ecologists and paleoecologists recognize that some environments are more buffered against climate change and short-term disturbances than others. If such environments can be identified, they could be considered sites for long-term retention of plants or for establishment of new forests. For instance, microclimates in mountainous regions are highly heterogeneous. Furthermore, unusual and nutritionally extreme soil types (e.g., acid podsol, ultramafic, limestone) have been noted for their long persistence of species and genetic diversity, resistance to invasive species, and long-lasting community physiognomy compared to adjacent fertile soils. During historical periods of rapid climate change and widespread population extirpation, refugial populations have persisted on unusual local sites that avoided extremes of regional climate impacts or the effects of large disturbance (Huntley and Webb 1988).

MITIGATION OPTIONS

Reduce greenhouse gases

This set of options has the goal of using forested environments to ameliorate greenhouse gas emissions and sequester carbon, thereby lessening the human impact on climate. The forestry sector has a huge potential to contribute at global to regional scales (Malhi et al. 2002). Evaluating and determining best choices, however, are hampered by considerable uncertainty and difficulty in analyzing net carbon balances (Cathcart and Delaney 2006).

1. *Sequester carbon.*—Forest management strategies designed to achieve goals of removing CO_2 and storing carbon are diverse, and include avoiding deforestation, promoting afforestation and reforestation, manipulating vegetation to favor rapid growth and long-term site retention, and sequestering carbon after harvest in wood products (Harmon and Marks 2002, Kobziar and Stephens 2006, Krankina and Harmon 2006). Some approaches duplicate long-recognized best forest-management practices, where goals are to maintain healthy vigorous trees, keep sites fully occupied with minimal spatial or temporal gaps in non-forest conditions, and minimize severe disturbance by fire, insects, and disease. As noted above, however, in many cases uniform forest conditions are best avoided, as they are vulnerable to mortality from insects, disease, and fire (Stephens and Moghaddas 2005*a*, Stephens et al. 2007). Under changing climates, these conditions may need to be intensively managed to minimize risk of severe fire (Weatherspoon and Skinner 1995), and to reduce the potential for carbon losses from wildfire.

Once wood is removed from the forest or plantation, its subsequent use affects its sequestration status. Options for minimizing return of carbon to the atmosphere include storing carbon in wood products, or using it as biomass to fuel electricity production, thereby providing alternative forms of energy to replace fossil fuels. For successful choices to be made, life-cycle analysis research must assess carbon accounting from forest through utilization phases (Cathcart and Delaney 2006).

2. *Reduce emissions.*—Wildfire and extensive forest mortality as a result of insect and disease are primary sources of unintentional carbon emissions from forests in western United States (Stephens 2005), and can lead to widespread loss of centuries' worth of carbon storage. This effect will likely be exacerbated in coming decades under continued warming, with increasingly severe fire years leading to what have been modeled as widespread "brown-downs" for many western and eastern forest types (Westerling et al. 2006).

One obvious means of slowing this release of sequestered carbon is to increase forest resistance to fire, drought, and disease, usually by reducing the density of small trees. In roaded or otherwise accessible areas, such density reductions might be accomplished by mechanical thinning, prescribed fires, or both (Stephens and Moghaddas 2005*b*). In remote or rugged terrain, wildland fire use or appropriate management response suppression fire may be the only reasonable option (Collins et al. 2007). In either case, some carbon inevitably will be released in the process of increasing forest resistance to sudden release of much greater quantities of carbon. If small trees are physically removed during the density reduction, then subsequently used for energy generation or long-term sequestration, the net carbon release might be minimized.

PRIORITIZING MANAGEMENT UNDER CONDITIONS OF RAPID CHANGE

Species respond to changing climates and environments individualistically. Some species will be sensitive and vulnerable whereas others will be naturally buffered and resilient to climate-influenced disturbances. Management goals across the spectrum of forest types and ownerships also vary. As a result, proactive climate planning will include a range of approaches having different management intensities. Some species and ecosystems may require aggressive treatment to maintain viability or resilience, others may require reduction of current stressors, and others less intensive management, at least in the near future.

Evaluating priorities has always been important in resource management. However, the magnitude and rate of change and the management responses these demand, combined with finite human resources and declining budgets, dictate that priorities be evaluated swiftly and definitively. A useful systematic approach for prioritizing high-demand situations might be adopted from the medical practice of triage (Fitzgerald 2000). Deriving from the French word *triare*, to sort, triage approaches were developed from the need to prioritize care of injured soldiers in battlefield settings where time is short, needs are great, and capacity to respond is limited. Triage applied in a resource context offers a systematic process to sort management situations into categories according to urgency, sensitivity, and capacity of available resources to achieve desired goals. Cases are rapidly assessed and divided into three to five major categories that determine treatment priority. The categories range from high urgency (treat immediately), mid-urgency (treat later), to highly urgent but untreatable given current capacity (no action taken). Reassessing and re-prioritizing must be done frequently, especially when conditions are changing rapidly.

Although triage approaches are valuable under conditions of scarce resources or overwhelming choice, they are rarely adequate as long-term approaches. Other planning processes may be used for prioritizing current management plans and practices. An example is rapid assessments of forest management plans by teams of climate-expert reviewers who convene to intensively review existing management plans, assess current needs, and recommend top priorities for revision.

CONCLUSIONS

Over the last several decades, forest managers in North America have used concepts of historical range of variability, natural range of variability, and ecological sustainability to set goals and inform management decisions. An underlying premise in these approaches is that by maintaining forest conditions within the range of presettlement conditions, managers are most likely to sustainably maintain forests into the future. We argue that although we have important lessons to learn from the past, we cannot rely on past forest conditions to provide us with adequate targets for current and future management. This reality must be considered in policy, planning, and management. Climate variability, both naturally caused and anthropogenic, as well as modern land-use practices and stressors, create novel environmental conditions never before experienced by ecosystems. Under such conditions, historical ecology suggests that we manage for species persistence within large ecoregions. Such a goal relaxes expectations that current species ranges will remain constant, or that population abundances, distribution, species compositions and dominances should remain stable. Management practices such as assisting species migrations, creating porous landscapes, or increasing diversity in genetic and species planting mixes may be appropriate. Essential to managing for uncertainty is the imperative to learn-as-you-go. Although general principles will emerge, the best preparation is for managers and planners to remain informed both about emerging climate science as well as land-use changes in their region, and to use that knowledge to shape effective local solutions. A goal of this paper is to engage dialogue on this issue.

ACKNOWLEDGMENTS

We thank K. Norman Johnson and Sally Duncan (Oregon State University) and the sponsors and participants of the National Commission on Science for Sustainable Forestry “Future Range of Variability” project for discussion and support leading to development of this paper. We especially thank Tom Swetnam (University of Arizona) for pointing out ambiguous phrasing in the manuscript.

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STATUS PAPER ON CLIMATE-SMART FORESTRY: RESEARCH AND MANAGEMENT

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Forests play an important role in the economic development of a country. They provide a large variety of tangible and intangible benefits for the people at large and are prime source of livelihood for millions of poor people. Forests have close link with climatic condition of a given area. Climatic variation influence vegetation types and a changing climate over very long period had been the major reason for the present scenario of forest type distribution on earth (Oliver and Larsen, 1996). However, anthropogenic activities are causing an accelerated change in climate at present (Santer *et al.* 1996) affecting the forest vegetation, especially its structure, functions and services around the world.

While forests themselves are affected by climate change, the solution for its adverse impacts also lies in forests. Hence, over the past two decades, the mitigation potential of forests and the forest sector has been progressively included in the international climate regime. Forests, when cleared, overused, degraded or unsustainably managed, contribute to the one-sixth of global carbon emissions while a properly managed forest sequesters and store carbon thereby mitigating the effect of greenhouse gases. Forests have the potential to absorb about one-tenth of the carbon projected to be emitted globally in the first half of this century into their biomass, soils and products and in principle, to store this carbon in perpetuity. For example, it is estimated that European Union (EU) forests and the forest sector currently produce an overall climate mitigation impact that amounts to about 13 percent of the total EU emissions. This includes both the forests and harvested wood products as a carbon sink, as well as the substitution effect of forest products for materials and bio-energy (Nabuurs *et.al.* 2015). As per estimates, the annual CO_2 removals by India's forests and tree cover is enough to neutralize 11.25 per cent of India's total GHG emissions (CO_2 equivalent) at 1994 levels and therefore, India's forests and tree cover serve as a major sink of CO_2 and a major mode of carbon mitigation (MoEF&CC, 2009)

India is a large developing economy with $1/6^{th}$ of the world population and the resource requirement of such a large population, including the fossil fuel requirement is quite substantial. Hence it is inevitable to have emission of green house gases to some extent to keep pace with development. In future, fossil fuels will remain the predominant fuel for India in 2030s, with more than 70 percent of primary energy coming from fossil based fuels (TERI, 2015). India's energy sector accounts for 71 percent of total green house gas emissions in the country. In 2013, India figured in the top three countries affected by climate risk. The country with only 2.4 percent of the world's land area, is also the home to 7-8 percent of all recorded species (UN,2018) and it has given us the onerous responsibility of biodiversity conservation in a mega-diverse country.

Climate smart Forestry

Climate-smart approaches in forestry are connected with most major cross-sectoral themes of development and environment and it is expected that 'climate-smart' will become the default development approach. India has adopted a climate smart approach through its National Action

Plan on Climate Change (NAPCC) which is a directional shift in the development pathway. NAPCC identified eight missions to address climate change mitigation, adaptation and knowledge management. The focus of these missions is on "promoting understanding of climate change, adaptation and mitigation, energy efficiency, and natural resource conservation". The NAPCC provides a comprehensive policy framework to address the relevant issues to tackle climate change in India including the creation of strategic knowledge mission. It provides the framework for the various stakeholders and States to engage with the respective missions to build on, develop, expand, enable and implement the required regional and sectoral programs and strategies. This requires tremendous effort from all concerned - public sector, private sector, knowledge leaders, non-governmental organizations (NGOs), civil society and local communities, to consolidate and collaborate to enable the implementation of these Missions (Kattumuri and Ravindranath, 2016). Following NAPCC, the State level Action Plan on Climate Change (SAPCC) are being implemented by the Indian States. FAO (2018) has outlined certain key considerations for implementing a climate-smart approach to development in the forest sector and its important points are the following:

- Respond to considerable increases in global demand for wood and NWFPs in the face of climate change and other factors.
- Address specific issues related to food access and the livelihoods of forest-dependent people across the supply, value and benefit chains.
- Interact effectively with emerging technological, commercial and socially driven changes in, or associated with, the forest sector.
- Identify gaps in capacity, efficiency and system resilience in the forest sector, particularly those gaps that are likely to increase under climate stress, and develop generic or specific actions to address them.
- Identify options for strengthening the coordination of activities within the forest sector to improve, for example, the flow of goods and services, ensure efficient resource use and enhance functional resilience.
- Connect activities in the forest sector in a coherent manner with other development objectives, including hunger eradication, poverty alleviation, natural resource protection and rehabilitation, nutritional safety and health, personal and community empowerment, self-determination and vulnerability reduction.
- Ensure that responses are clearly recognizable and actionable by policy agents working effectively with practitioners and beneficiaries at all levels and are based on clear evidence of functionality and effectiveness.
- Sustainably manage forests to increase forest growth and carbon storage.
- Use forest raw materials to manufacture products as a way of storing carbon.
- Conserve forests to protect standing trees; provide ecosystem services, such as water replenishment and shelter for fauna; and sustain the livelihoods of forest-dependent indigenous peoples and local communities.
- Use forests and trees to reduce reliance on oil, coal and gas by delivering more raw materials for climate-smart products, such as bio-based fuels and timber products.

Climate smart approaches in forestry have certain distinct characteristics, particularly the significant level of socio-economic dependence of many poor and marginalized people on forests and trees. Integration of climate-smart approaches in forestry needs research on : (1) assessing the risk the climate change poses to the objectives of forest management (2) identifying the most vulnerable forest-dependent people and forest areas (3) develop management measures that would reduce their vulnerability (4) finding out source of availability of financial and technical support for undertaking adaptation measures (5) Identifying options available in the forest management unit for mitigating climate change, including cost-benefit assessment and (6) evolve management practices to achieve the specified mitigation and adaptation goals (FAO,2013)

Some of the practices suggested for adapting to the changing climate are anticipatory plantations, sanitary harvest, linking fragmented forests, planting mixed species and pest and fire management, conservation of biodiversity hotspots, managing man-animal conflict, *in situ* and *ex situ* conservation of genetic resources, adopting long term and short term adaptation policies, promoting community forestry and capacity building to develop adaptation strategies (Chaturvedi *et al.* 2010; Gupta *et al*. 2017). Management intervention might focus on strengthening adaptive capacity that enable forest ecosystem to adapt to future changes. On social front, increased resource conflict makes women and children vulnerable to changing climate. In spite of various efforts to uplift women, changing climate might put the women and weaker section of the society at a disadvantage (Nelson and Stathers, 2009).

The significance of climate variability for agricultural production indicates that the impact of variations in temperature and precipitation on Indian agriculture is an important source of information for coping with the impact of climate change on agriculture in the future (Jayaraman and Murari,2014). In this scenario, agroforestry as an alternative livelihood to the climate stressed agriculture is being seen as a viable adaptation model.

Green India Mission – opportunities for research and management

The National Mission for Green India was launched in February 2010, which is one of the eight missions under the National Action Plan on Climate Change. It was initiated to safeguard the country's biological resources and associated livelihoods against the perils of climate change recognising significant impacts of forestry on ecological sustainability, biodiversity conservation as well as food, water and livelihood security to the nation. Apart from carbon sequestration through tree planting, it envisages to achieve biodiversity enhancement, ecosystem restoration and economic security of local communities at landscape level in the context of climate change adaptation and mitigation. The mission has an objective to increase forest / tree cover in 5m ha of land and improve quality of forest cover in another 5m ha of lands. Apart from enhancing ecosystem services from 10m ha of land it also aims at improving livelihood of 3 million forest dependent households and enhances CO_2 sequestration by 50 to 60 MT in the year 2020, through a decentralized participatory approach (MoEF, 2010).

Under one of its sub mission viz. Agro-Forestry and Social Forestry (increasing biomass and creating carbon sink), the mission supports participatory mode of raising quality seedling addressing the socio economic livelihood of the rural poor. The mission supports technology for value-added products, certification and marketing of NTFP, which would support bridging the knowledge gap. As a climate smart approach the mission allows identification of vulnerable hill slopes and to take up protection and soil/water conservation measures backed up with plantation of suitable indigenous species. The mission promotes research to understand the linkage between vegetation, groundwater and surface flows, and encourage the identifying and protecting areas of hydrological importance within the various sub-missions. Some of the key research areas includes long-term research to study vegetation response to climate change; silvicultural and management response to achieve the mission objectives; pilot adaptation projects to develop adaptation options, strategies and practices; benchmarking carbon capture potential of ecosystems and economic evaluation of ecosystem goods and services; measuring degradation within density class ranges; social and economic research and studies, etc. The scientific and technical capability of forestry research institutions including Indian Council of Forestry Research and Education (ICFRE) would be significantly enhanced for ecological research and modelling of climate change impacts, mitigation and adaptation aspects. The mission supports the strengthening of the research institutes under ICFRE and the State Forest Departments, including financial support for increased strength of scientists and their support staff, better infrastructure, equipment, etc.

Many of the proposed interventions are innovative, it would require collaboration of research institutions and the implementation agencies. ICFRE collaboration with academic scientific institutions of repute, both in country and overseas, joint research programs, exchange visits; capability building etc would be strongly supported under the Mission.

The mission has setup REDD-plus cell which will have the task of creating awareness/capacity building on the REDD-plus process for all stakeholders, including the community institutions. The Cell will have multiple role in designing, formulating appropriate REDD-plus projects/strategy, propose for implementing /funding support to the designated bodies , provide technical advice on development and implementation of Monitoring Reporting & Verification (MRV) protocols and fair benefit-sharing mechanisms in the forestry sector through improved capacity and comprehensive methodology design for forest carbon inventory as per internationally and domestically agreed rules for MRV. The Mission will improve capacity of multiple stakeholders, particularly forest-dependant communities, to implement REDD Plus at decentralized levels. A majority of interventions under the Mission have potential to qualify under REDD-plus.

The mission has also endeavoured to provide innovation funds at national, state and district level Mission organizations for cross-cutting research/action research studies and initiatives by the local-level organization to try out things in consonance with the overall Mission goals and objectives. Green India Mission has landscape based approach for implementation of activities on forest and non-forest land. The criteria for identification of the landscapes include vulnerability of forests to climate change, status of forest cover, biodiversity, critical habitats, corridors, potential of area for carbon sink and socio economic criteria like poverty and ethnicity (tribal /non-tribal) etc. Green India Mission (GIM) is being implemented in some states at present namely Andhra Pradesh, Chhattisgarh, Karnataka, Kerala, Manipur, Mizoram, Odisha, Punjab and Uttrakhand. The Government has received Perspective Plans from the other States namely; Bihar, Madhya Pradesh, Jammu & Kashmir, Maharashtra, Meghalaya and Himachal Pradesh. Fresh Proposals are taken up for funding approvals subject to availability of resources and progress of previous works. The Green India Mission includes a sub-mission to enhance tree cover in 0.20 million hectare of Urban and Peri-Urban areas, including institutional lands. This includes support for urban greening on various categories of land including open spaces/green spaces like parks/wood lots, avenues and in households and Institutional lands belonging/allotted to business/industrial houses and educational institutions, etc. through afforestation (Rajya Sabha, 2017) Further, the Ministry of Environment, Forest and Climate Change (2014) implements an urban forestry scheme namely “Nagar Van-Udyan Yojana -EK KADAM HARIYALI KI OR” a programme for climate smart green cities on pilot basis to create 200 City Forests in the country.

REDD-plus

Reducing emissions from deforestation and forest degradation (REDD) and the role of conservation, sustainable management of forests and enhancement of forest carbon stocks in developing countries (REDD plus) was first negotiated under the United Nations Framework Convention on Climate Change (UNFCCC) in 2005, with the objective of mitigating climate change through reducing net emissions of greenhouse gases through enhanced forest management in developing countries. At the twenty-ninth meeting of the UNFCCC Subsidiary Body for Scientific and Technological Advice in Poznan, Poland in 2008, the avoided carbon emissions from conservation of forest carbon stocks, sustainable management of forests and the enhancement of forest carbon stocks were given the same level of priority as deforestation and forest degradation and since has been referred to as REDD-plus (IGNFA, 2013).

REDD-plus is a mechanism developed by Parties to the United Nations Framework Convention on Climate Change (UNFCCC). It will become a comprehensive climate change mitigation solution, helping to reduce up to 20 percent of global carbon emissions. REDD plus creates a financial value for the carbon stored in forests by offering incentives for developing countries to reduce emissions from forested lands and invest in low-carbon paths to sustainable development. Developing countries would receive results-based payments for results-based actions. REDD+ goes beyond simply reducing deforestation and forest degradation, and includes the role of conservation, sustainable management of forests and enhancement of forest carbon.

In addition to addressing capacity building, REDD plus will identify gaps under the present forest management system. The financial incentives generated through carbon added or carbon saved will support the livelihood of communities and contribute to overall socio-economic development. The incentives received from REDD plus are to be passed on to local communities involved in protection and management of forests to ensure sustained protection of India's forests. India's submission to UNFCC (2011) states its commitment to transfer REDD plus benefits to the local, forest dependent, forest dwelling and tribal communities who are contributing towards forest conservation and enhancement of forest carbon stocks (TERI, 2013).

India's first REDD-plus pilot project by Plan Vivo in the East Khasi Hills district (Mawphlang) in Meghalaya, has been initiated in 2010. Some other pilot projects have been concluded with the help of institutions such as TERI which carried out pilot studies in Uttarakhand, U.P., M.P., Orissa, West Bengal, Nagaland, Gujarat, and Rajasthan. ICFRE is involved in 'REDD-plus pilot project in Van Panchayats of Uttarakhand and IGNFA has also carried out a 'Pilot study on REDD-plus' in the same state. Another project on 'Partnership for Land Use Science (Forest-PLUS) funded by USAID under bilateral agreement with MoEF&CC has been implemented in four locations in H.P., Karnataka, M.P. and Sikkim in collaboration with FRI with the aim to explore methods and approaches to REDD-plus implementation

Oppurtunities under REDD Plus

Ministry of Environment, Forest & Climate Change, Government of India has drafted a National policy on REDD-plus to provide roadmap for India's REDD-plus preparedness and lays down the broad principles for developing and implementing REDD-plus programmes in the country to enable India to gain from international REDD-plus mechanism for its pro conservation policies and efforts and at the same time create financial incentives to local communities which are in the forefront of conservation of forests. The draft identifies that India has considerable advantage in view of scientific and technical capacity and institutional strength in respect of the 3 phases of REDD-plus i.e. (i) Strategy Development (Readiness), (ii)

Implementation and Results Based Demonstration Activities, (iii) Fully measured, reported and verified emissions reductions. India has strong forest conservation policies including progressive policies and arrangements for community participation and benefit sharing. India has robust remote sensing and forest area monitoring and reporting institutions and arrangements. Among the strategy to carryout REDD-plus, the scope of various proposed programmes viz. Developing a National Forest Monitoring System, Setting up of National REDD-plus Architecture and Governance, Creation of a Platform for Stakeholder engagement, National REDD-plus information system including National Forest Carbon Accounting And Monitoring System (NFCAMS), System for managing data on valuation and equitable sharing of multiple benefits of forests, Capacity Building, Developing institutions and technical capacity for modeling landuse change, deforestation rates, carbon stock changes and carbon sequestration rates requires consistent research input. ICFRE along with other scientific institutions and State Forest Departments have been identified to take up capacity building activities of various stakeholders (MoEF&CC 2014).

Forest investment programme

India and five other developing countries - Brazil, the Democratic Republic of Congo, Morocco, Nepal, and Romania have joined five contributor countries, Australia, Denmark, Norway, the United Kingdom, and the United States embarked on Forest Investment Programme (FIP) in a unique partnership to combat climate change through forest management. The FIP is one of the three specialized programmes of the Strategic Climate Fund under the Climate Investment Funds, which is being implemented jointly through the multilateral development banks in close collaboration with other development partners such as the United Nations and bilateral agencies. It is considered as first in a new generation of partnerships among developing and developed countries and other stakeholders which takes in to account of the need for a level playing field in addressing climate change situation (FIP,2017).

National Working Plan Code - 2014

The National Working Plan Code formulated by the MoEFCC, Govt. of India has recognized that climate change phenomenon seriously affects and alters the distribution, type, composition, quality and mitigation potential of forests of the country, especially in the realm of anthropogenic stressors. The Working Plan Code states that, “since forest ecosystems operate on large temporal scales, long observational studies are necessary to identify the key changes”. Therefore, grid based sampling has been designed to capture relevant information to cover the characteristic time scales to fully understand the impact of climate change on forests of India, so as to undertake appropriate managerial interventions.

In this context, the following research aspects need immediate attention:

Research needs

- Long term research to study response of vegetation to climate change.
- Formulating pilot projects for developing adaptation options.
- Study carbon capturing potential of various ecosystems and economic evaluation of goods and services of ecosystems.
- Understanding impact of climate change on forest degradation.
- Influence of climate change on flowering phenology, reproductive biology and pollination ecology.
- Changes in behaviour pattern of pollinators in response to climate change situation.

- Studies on social and economic impact of climate change, especially on forest dependent communities and weaker sections of the society.
- Changes in distribution pattern of endemic and threatened species in climate change scenario.
- Inter-relationship of climate change with forest fire and invasive alien species and their impact on forest ecosystem.
- Influence of climate change on forest health- epidemics caused by insect pests and diseases.
- Conventional breeding and biotechnological interventions to develop drought, salt, pest and disease tolerant trees.
- *In-situ* and *ex-situ* conservation of forest genetic resources, including RET species.

Capacity building

It is an accepted fact that forestry can play a pivotal role in modulating the climate change scenario. But, the forest managers and forest scientists in developing countries are not fully equipped with the technical knowhow to meet this challenge, so as to combat the impact of climate change on forests very effectively. Therefore, the skill up gradation of the forest managers and scientists in various aspects of climate change including practical mitigation and adaptation strategies is the need of the hour.

Infrastructural development

Action to combat climate change is directly linked to pooling of accurate meteorological data and its analysis. Most of the developing countries including India lack the state-of-the art facilities for collecting, collating and analyzing meteorological data. Therefore, it is essential that more meteorological observatories are established at strategic locations to collect climatological data and required computer facilities established for data analysis and interpretation.

Forest fire is the major cause of forest degradation in climate change situation. But, most of the State Forest Departments in India lack infrastructure and trained manpower to manage the fire incidence in the forests. So, it is high time we develop the infrastructure to combat fire and train the frontline forest staff in fire management.

Summary

Climate change has posed newer challenges in the management of forests and prioritising forest research to cater to the emerging scenario. Forests are resilient to the ever changing climate. The present day forests had been shaped over a million of years changing climate. But the present day accelerated climate change due to anthropogenic activity does not provide sufficient time for the forests to co-evolve. World has come to understand the danger accelerated climate change is posing to the ecosystem and various efforts had been taken to mitigate and adapt to the changing climate. India has started implementing various climate smart policies and programmes like the action plans on climate change, green india mission, policy on REDD plus etc adhering to the commitment it has provided to the international communities. The National working plan code 2014 has incorporated the climate smart forest management to address the climate change issues. Forestry research need to respond to the challenges in implementing these policies and programmes. Capacity building, developing criteria and indicators to monitor the impact of implementation of the forests, long term observation of forest health, co evolving mitigation and adaptation strategies are some of the research priorities. The success of the policies and the programmes shall depend on how fast we understand them and how practically we implement them. It has thrown up numerous opportunities for the forest managers and the researchers to gear up to meet the nation's commitment.

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Smart Forests: Research and Management.

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Smart Forests are those that are managed on sound principles of silvilcultural management tools and techniques to promote bio-diversity and ecological stability of a given landscape which are highly resistant to climate change impacts. This concept is developed and implemented to promote the best forest management practices to insulate forests from climate change impacts.

The climate change projections carried out by different agencies under different scenarios of GHG emission have shown that, the Forests will be impacted due considerably to rise in temperature and consequent changes in the rainfall pattern in India. The Forests in India are highly vulnerable for the changes in the climate in the regions that are projected to experience either excess or deficit rainfall.

High-resolution climate change scenarios for India using PRECIS , has shown that, there will be 20% increase in the West coast and North-east rainfall in future scenarios. The model also predicts increase in rainfall in all the states except Rajasthan, Punjab and Tamil Nadu.
The excess rainfall in Southern part of India will impact the Teak forests in Kerala and Tamil Nadu affecting growth regeneration and other associated ecological functions.

Similarly , it is also projected that \central India may experience deficit rainfall affecting the Sal regeneration and associated bamboo growth and regeneration.

Himalayan regions are projected to experience again rise in temperature which will make the lower elevation species to migrate upwards towards cooler regions. Some studies have indicated that, the Sal forests are expanding towards higher elevation due to change in the temperature and rainfall regimes in the North-eastern states of India.

Similarly, it is reported that the lower elevation Himalayan species like *Abies pindrow* and *Pinus walichiana* changing their ecological niche and moving upwards into higher elevation. The species *Pinus geradiana* is also found occupying higher elevations.

Shola forests are enlarging. Due to change in the rainfall pattern and temperature regimes, it is found that Shola forests of western Ghats getting expanded towards lower elevations.

In view of these projections, the Foresters have to initiate smart actions to insulate these forests from climate change impacts. Some of the measures include anticipatory planting, silvicultural interventions to promote the species mix that withstand the climate change impacts and host of such measures.

The session on the smart forests: Research and management would cover the issues that are relevant to make forests resistant to impacts and make them more adaptive through enhanced plasticity of biological response.

Strategies to Develop Smart Forests.

The term smart forests is a widely used concept to describe the resilience of a forest ecosystem capable of tolerating the extreme impacts of climate change without undergoing any structural changes while continuing to provide the ecosystem services.
The forests are projected to e highly vulnerable to extreme climate changes. The following strategies are to be adopted to develop smart forests capable of withstanding the climate change impacts.

(i) **Reduction of emission from the Forest ecosystem**. Forests emissions are considered as the source of GHG emissions due to decaying, fire and other biotic interferences which needs to be reduced with better management strategies.

(ii) **Fire control and fire resistant species planting**. Fire is a major disturbance factor that damages the forests structure and functions depending on the intensity of fire occurrence. The fire affected forests fail to maintain the normal ecological services and contribute for higher emission rates leading to global warming.

(iii) **Assisted migration of species to higher elevations**. The climate change in the temperate forests is found to promote the migration of species to higher elevations. The Forest managers can assist the migration of species in higher elevations by taking appropriate silvicultural decisions.

(iv) **Assisted anticipatory regeneration**. At landscape level , the species movement across different elevations and micro-climatic conditions, the forest managers can identify the suitable sites for the threatened species and accordingly promote the regeneration across the landscape so as to balance the population size.

(v) **Harvesting cycles of NTFP .** In Tropical forests, where the community dependency is large on the Non-timber forest products, the forest managers can develop sustainable forest management and harvesting practices that can support the communities.

(vi) **Innovative approach.** To ensure smart forest management, the innovative management approaches are to be found through long term and short term research programs to practice best management practices that enhances the multi=function capability of smart forests.

(vii) **Ecosystem service based management.** Most of the forest ecosystems are managed for single or few management objectives accomplishment, however we must develop multifunctional and multiple objectives based management to safeguard and enhance the ecosystem services.

(viii) **Smart forest inventory tools and methods.** Using the advanced technology the forest inventory including boundary fixing, monitoring crown density, canopy monitoring and individual trees management can be done to ensure the forest are best managed to provide the highest ecosystem services.

Some of the Areas of Research for Smart forest management.

1. Canopy research of High Forests. We do not have any research data or information on the canopy ecosystem interactions and associations of plant and animal community.
2. Inventory of Trees and stand structure. Information on the stand models, tree growth, regeneration and mortality of the stand can be measured and models can be developed to predict the performance of smart forests under different scenarios.
3. Ecosystem value, and ecosystem services are to be modeled and [projected for multifunction's under different scenarios.
4. Fire impact studies and fire management models are to developed and fire management maps are to be prepared.
5. Carbon flux monitoring and other gaseous exchange related studies are to be initiated.
6. Genome mapping, Genetic frequency, and other reproductive biology studies are to be initiated in the climate change context.
7. Research programs to monitor changes in the vegetation changes in context of climate change.
8. Water regime changes in different projected climate change impacted areas in both scenarios. And appropriate mitigation measures.
9. Studies on the climate change impacts on livelihood changes.

Promoting Green Cover through value addition technologies for non-traditional materials for wood based industries

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Introduction

After cement and steel, plywood and panel and wood processing industries are the third most important contributors to the housing sector. According to FIPPI, there are about 62 large and medium size plywood mills and over 2500 SSI units out of which more than 1000 of these are located in States of Haryana, Punjab, Uttaranchal, Western part of the Uttar Pradesh which operate based on the plantation wood like poplar, and eucalyptus grown by the farmers under agroforestry system. With the R&D backup received from IPIRTI and other Institutes, Wood based industries are now in a position to produce speciality value added panel products such as shuttering & marine plywood, pre-laminated particle board and MDF, Laminated Veneer Lumber, moulded skin doors, bamboo composites, finger jointed and edge laminated timber in addition to general purpose plywood, block board and flush door as per national and international standards.

However, the Plywood and Panel Industry, which is by and large an agroforestry based industry, have been totally deprived of Government support. The main problem faced by the industry is raw material availability. The gap between demand and supply is also widening.

Indian wood processing industry is currently undergoing major structural changes with a gradual switch from the production of timber products using large diameter trees to those utilizing smaller diameter from second cuts, as well as moving toward plantations and the estate sector. Product diversity has increased. Rubber wood, poplar, eucalyptus and silver oak are used as raw material in wood-based panel industry. With the technological advancement in finger jointing and edge lamination technique short length plantation timbers are finding extensive use in making joinery and furniture.

While India’s use of particle board and MDF board still remains modest by Asian standard, a recent upswing in the economy and Govt. forecasts, predicted economic growth would bring about changes in future. There is 7% growth annually in utilization of particle board and MDF and likely to rise as Indian architects and furniture manufacturers has to choose more modern materials rather than to stick to their traditional material like plywood.

MDF has emerged as price competitive alternatives to the more traditional products such as plywood, particleboard and hardboard for certain applications. Their greatest advantage is that low quality and low value raw materials (including non-wood fibres) can be turned into high value and high quality wood-panels. Because of the desirable and user-friendly physical properties and favourable machining properties, MDF has a variety of end-uses and can replace tropical hardwood timbers for furniture. In addition, it is marketed as an environmentally friendly product which relies on sustainable resources. Technologies for manufacture of panel products from Agro/forest residues like Baggase, Rice husk, Bamboo, Coir, Cotton stalk, etc., are available from reputed Institute like IPIRTI, ICFRE and other similar organizations. Bamboo mat board is becoming an alternate to plywood especially in the lower thickness range. Bamboo mat corrugated sheet has become an alternate to asbestos cement sheet for roofing.

Another composite wood technology which has recently emerged has opened up opportunities for the production of high quality stable wooden sections from relatively inferior quality wood raw material. Laminated veneer lumbar (LVL) described as glued laminated veneer similar to solid wood sections. Most of the plantation species can be converted to reasonably good quality veneer which can be further converted into LVL suitable for applications like structural components (I &WEB Griders), door and window frames, rails and stiles in flush door manufacture, bent wood furniture components and many other uses. LVL from rubber wood is being produced in the country on a limited scale.

Alternative raw materials sources

The option left for wood based industries for sustainable supply of wood raw material are 1 . Raising of the Plantation in areas outside forest with facilitate reduction in on natural forest. Hence Plantation forestry should be considered as a major option for sustained availability of Timber . in this context, wood based industry should join hands with Govt of India to encourage agro/farm forestry which will not only help in increase forest / tree cover but also helps in getting required raw material on a sustainable basis . 2. Utilization of agro / forest residues as wood substitutes . India is rich in agro / forest residues which are not put proper use. Conversion of these residues in to panel products will not only helps in value addition but also keeps environment clean. Technological intervention with regard to its economic viability and commercial adoption is need of hour .

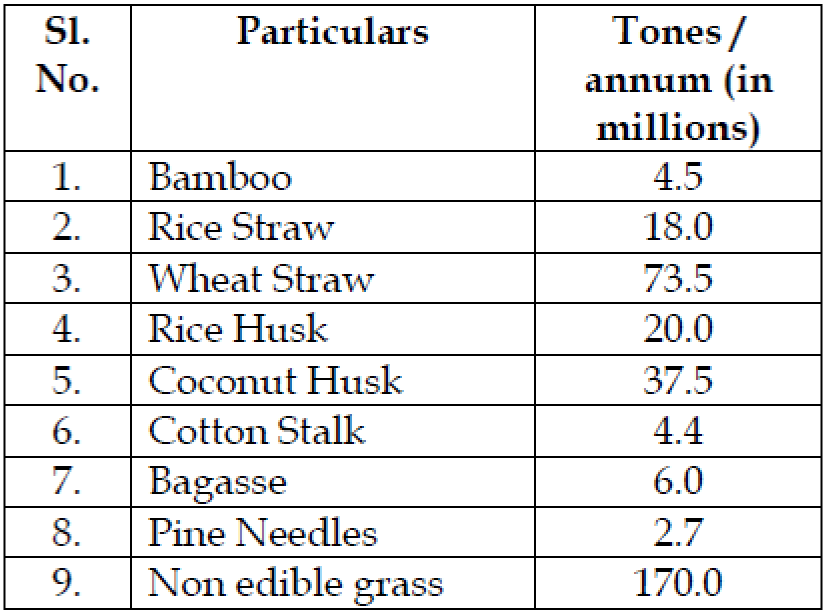
India is a vast country with vast fertile area under agricultural and forests to generate enough lignocellulosic materials which can be processed to panel and other component for substitution of wood and wood products. The main source of these materials is a) Non timber forest products b) Agricultural residues.

The range of wood based panel produced in the country has grown considerably during the last two decades of which plywood; particle/fibre boards constitute the major share. Various strategies identified to meet raw material shortfall for wood panel industries are improvements in conversion techniques, worker training, and utilization of non wood raw material and in the long term plantation of fast growing timber species. In the above context utilization of forest and agro residues for manufacturing particle board suitable for use under tropical climates assumes significance.

The greatest obstacle to increase the utilization of non wood fibres is the problem of the collection and storage and lack of suitable equipments for the purpose. There are also problem materials, which are available in sufficient quantities on site, but not used because of technical instability for alternate use consideration or both.

Table1 gives estimated availability of some non –wood lignocellulosic material in India.

Table 1 **Availability of Non-Wood Lignocellulosic Material**



Sl. No.	Particulars	Tones / annum (in millions)
1.	Bamboo	4.5
2.	Rice Straw	18.0
3.	Wheat Straw	73.5
4.	Rice Husk	20.0
5.	Coconut Husk	37.5
6.	Cotton Stalk	4.4
7.	Bagasse	6.0
8.	Pine Needles	2.7
9.	Non edible grass	170.0

Major Non-Timber Forest Products/Agricultural Products and their Industrial Processing

a. **Bamboo:** Bamboo is rightly called the “Green Gold” as it has immense potential for large scale value additions into plethora of panel products which can become game-changer for challenged and backward Economies. In this direction, significant Research & Development (R&D) efforts have already been made at the Indian Plywood Industry Research & Training Institute (IPIRTI), Bangalore which led to innovation of several bamboo composite products which can be broadly categorized into (1) Bamboo Mat Based Products; (2) Bamboo Strip Based Products; (3) Bamboo lumber based products besides; (4) Primary Bamboo Processing (5) Bamboo housing & other applications.

1. A range of **bamboo mat based products** are developed which are mainly Bamboo Mat Board (BMB), Bamboo Mat Veneer Composite (BMVC), Bamboo Mat Corrugated Sheet (BMCS), Bamboo Mat Ridge Cap (BMRC), Bamboo Mat Moulded Skin Board (BMMSB) etc. The Bamboo Mat Board (BMB) technology was commercialised in the 1985 in Angamally, Kerala which is still under manufacture. Subsequently, the BMCS technology was commercialised in the year 2002 in Byrnihat Megahlaya. Such value added bamboo products can contribute significantly in reducing energy consumption and carbon footprints by cutting down on non-renewable building materials viz. steel, concrete, aluminium etc.

2. **Bamboo strip based products** are so designed to behave like solid wood in properties and applications. The products have applications as flooring material as well as in furniture manufacture. IPIRTI has innovated several strip based bamboo products such as Bamboo Vertical Laminate; Bamboo Horizontal Laminate; Bamboo Floor Tiles and

Bamboo Flattened Board. Commercial production of bamboo strip based products started in 2011 in Kozhikode, Kerala.

3. **Bamboo lumber based products** are the third generation advance bamboo composites with potential to replace costly tropical hardwood such as teak for flooring and other applications. Commercial production of bamoo lumber started in 2015 in Agartala, Tripura.

4. **Primary processing** mainly includes cross cutting, knot removal, splitting, strip making, sliver making besides seasoning and chemical preservatives treatment. These processes have been done by hand for many generations. However, for making quality bamboo mat and for further processing into industrial products one of the important concerns is the uniform thickness of slivers and the thickness at the knot portions. To get good quality slivers process has been streamlined at IPIRTI.

5. IPIRTI has the expertise for the use of bamboo composites in prefabricated structures as well as developing low-cost earth quake resistant Bamboo-based IPIRTI-TRADA houses. Technologies are also available for bamboo particleboards, bamboo veneers etc.

It may be argued that bamboo is no longer a poor man's timber due to its versatility and scope of utilization. India has started changing this concept by utilizing bamboo as raw material for value added products, like replacing timber with bamboo products for industrial use and floor boards etc. which has great demand as a substitute for timber. On a commercial scale, these products can cater to the growing markets of India and rest of the globe and have the potential to play a stellar role of game-changer for the challenged and backward economy of Bamboo-rich areas - especially the North East Region (NER) of India.

b. **Rice husk*:*** Among all the agricultural residues, the most abundantly available is rice husk. It is the by product of the most important agro based industry in the country, namely paddy milling. Rice husk is available in the country to the extent of 20 million tons per annum. With increasing population and more improved methods of cultivation, still larger quantities of rice husk will become available. Research work to find ways and means to utilize rice husk for the production of useful materials has been underway for the past three decades or so. However, because of its unique chemical composition, not many successful methods have been evolved. Of all the methods of utilization of rice husk developed so far, manufacture of boards by the admixture of suitable binding agents is undoubtedly the best method from the point of view of both value added and the complete utilization of the husk without any further secondary by-products.

c. **Coconut Husk:** India is one of the largest coconut growing countries with an annual production of about 6000 million nuts. The husk of a coconut weighs about 0.3 kg. The coarse and fine fibres are 30-43% by weight of the husk and the dust 57-70%. Out of the total husk available from coconuts only 50% is being utilized by the coir industry. Even if 10% of the remaining husk is converted into particle board, the production would be around 7 million sq/cm/yr of density 640 kg/m3 (19 mm thickness).

d. **Coconut coir wastes:** The coir fibre is extracted from coconut husk by the natural retting process and by mechanical decortications. It is a tough, strong, resilient and durable material. The bulk density of the fibre is between 0.25-0.5 g/cm 3 depending on the compactness. The use of these waste materials for building boards has been investigated by several researchers.

e. **Coconut coir pith:** The husk of mature coconut consists of numerous fibres embedded, in a soft cork like ground tissue usually referred to as pith. The bulk density of air dried pith is about 11042 kg/m 3. It is made up of pectins, tannins and other water soluble substances and hemi cellulose. Particle boards, insulation boards and hard boards have been successfully made with and without the use of binders.
f. **Areca nut husk:** Boards are made using the Asplund process and treating them with an alkali prior to forming to reduce moisture absorption and swelling. Asplund process consists of pre disintegration of the material - soaking in cold water screening and washing of the pulp-formation felt like sheets-pressing at 1000 C and 35 to 70 kg/m^2 pressure-driving and conditioning. The amount of husk available in country is roughly 75,000 tons per annum.
g. **Cotton stalks:** Indian has the largest area under cotton, accounting for one fourth of world’s area of cotton cultivation. The estimated yield of residue is 4.4 million tones per annum. The stalks are cellulose 42.7%, lignin 25.1%, pentosans 12.3%, moisture 13.7%, benzene alcohol 3.4%, and ash 2.3%. The first cotton stalk based MDF plant in the world with an installed capacity of 39000 tones/annum was established in India. However, due to poor market acceptance, high cost harvesting and transport and little technology back up this product could not stand in the market.
h. **Bagasse:** This waste in sugarcane processing consists partly of delignified cells and partly parenchymatic pith. The presence of pith as an unfavorable effect because it contain 33-38% pith and since the pith is hygroscopic, the panels made out of it will acquire high thickness swelling and water absorption and also decreases values of mechanical properties. To eliminate the pith, the diffusion process is adopted in which a large part of the pith gets separated from the fibre through disintegration process. After depithing it is advisable to add fungicide and termiticide. The technology for manufacture of panel product from bagasse is well established in India and FRI has done commendable work in this line. Even a particle board factory and been established in UP based on bagasse as raw material and was producing excellent product, but could not sustain for a longer period. Some of the problems faced by the industry are: The duration of sugar crushing season varies from year to year and therefore availability of mill run bagasse drops to 4-5 months in a year. Total area required for storage of mill run bagasse, depithed bagasse and pith at the peak loading level for 1100 TPA factory is 12,000 sq.m. Such a large storage area and subsequent movement of material is a serious problem. There is significant quality variation in respect of moisture content, silica content and fibre structure between materials obtained from different mills. Maintenance of consistent quality of the product is therefore difficult.

Technological Innovations

R.& D efforts should be made in selecting Genetically screened and siliviculturally managed tree species which can produce more volume of wood with desired properties. Technology should develop to reduce wastage of wood and process parameters should be the top priority for getting required inputs. Technology should be developed which are economically viable and commercially adopted.

With the technological innovation, the constraints mentioned above has been addressed with respect to both technology and machineries based on the new findings i.e. Eco-board in Maharastra has been successful in producing particle board from bagasse and market acceptance of the product is encouraging. In addition, Bajaj Eco-Tech Products Limited [BEPL], and other companies has planned to put up to produce Medium Density Fibre Board [MDF], High Density Fibre Board [HDF] and Particle Board [PB] plant based on agro-residues. One company in Madhya Pradesh and Centrury Plywood Industries Ltd are also planning to set up MDF plants based on bamboo.

Conclusion

Following are the main conclusions

- More use of non-traditional resources and application of green technologies will go a long way in tackling the problems of global warming and climate change mitigation
- Importance of development of high value added products from low value resources (planation wood, agro-residues and bamboo) is increasing due to dwindling wood resources and increasing demand for the wood products
- Development indigenous technologies may reduce import of similar product and minimizes the production cost.
- Utilization of agro-wastes/forest residues not only have potential to generate additional income to farmer but also reduces pressure on national forests and minimize air-pollution due to burning of crop-residues.
- Bamboo cultivation outside forest and application of value added technologies for bamboo may be a game changer to transform socio-economically challenged areas of the country such as NER, Chattisgarh, Orissa etc

forests

MDPI

Article

By 2050 the Mitigation Effects of EU Forests Could Nearly Double through Climate Smart Forestry

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Received: 3 November 2017; Accepted: 1 December 2017; Published: 6 December 2017

Abstract: In July 2016, the European Commission (EC) published a legislative proposal for incorporating greenhouse gas emissions and removals due to Land Use, Land Use Change and Forestry (LULUCF) into its 2030 Climate and Energy Framework. The Climate and Energy Framework aims at a total emission reduction of 40% by 2030 for all sectors together as part of the Paris Agreement. The LULUCF proposal regulates a "no debit" target for LULUCF (Forests and Agricultural soils), and regulates the accounting of any additional mitigation potential that might be expected of it. We find that the forest share of the LULUCF sector can achieve much more than what is in the regulation now. We elaborate a strategy for unlocking European Union (EU) forests and forest sector potential based on the concept of "climate smart forestry" (CSF). We find that to-date, European policy has not firmly integrated forest potential into the EU climate policy framework. Nor have climate objectives been firmly integrated into those of the forest and forest sector at either the EU or national level. Yet a wide range of measures can be applied to provide positive incentives for more firmly integrating these climate objectives into the forest and forest sector framework. With the right set of incentives in place at EU and Member States levels, we find the current literature supports the view that the EU has the potential to achieve an additional combined mitigation impact through CSF of 441 Mt CO_2/year by 2050. In addition, CSF, through reducing and/or removing greenhouse gas emissions, adapting and building forest resilience, and sustainably increasing forest productivity and incomes, tackles multiple policy goals.

Keywords: European forests; carbon sequestration; harvested wood products; bio-energy; climate smart forestry

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1. Introduction and Aim

In July 2016, the European Commission (EC) published a legislative proposal for incorporating greenhouse gas emissions and removals due to Land Use, Land Use Change and Forestry (LULUCF proposal) into its 2030 Climate and Energy Framework. The Climate and Energy Framework aims at a total emission reduction of 40% by 2030 for all sectors together as part of the Paris Agreement [1,2]. The LULUCF proposal regulates a "no debit" target for LULUCF (Forests and Agricultural soils) and an accounting framework to handle any additional mitigation potential. European Union Member

Forests **2017**, *8*, 484; doi:10.3390/f8120484 www.mdpi.com/journal/forests

States have negotiated with the European Commission over the respective approach by which forests will contribute to their overall goals. This has led to the incorporation of compensation mechanisms in case a debit would arise and complicates the regulation further in many country specific clauses [3].

Already in the negotiations leading up to the Kyoto Protocol in 1997, concerns about the consequences of incorporating the existing forest sink into the climate targets had the policy outcome of imposing significant limits on the forest climate change mitigation role [4]. In particular, requirements related to "caps", and "forest (management) reference levels" (FMRL now called FRL) were introduced over time in the UNFCCC framework, and this set of rules has now evolved further within the new EU-level LULUCF proposal [3]. We argue that the current LULUCF proposal limits the role of forests and the forest sector in climate policy and find that this role could be much greater than what was assessed in the initial Impact assessment report [5]. This is further substantiated in the Policy section below.

Against this backdrop, the aim of this paper is to elaborate a strategy for unlocking European Union (EU) forests and forest sector potential based on the concept of "Climate Smart Forestry" (CSF) which we see as a more specific (climate-oriented) form of the Sustainable Forest Management paradigm. The idea behind CSF is that it considers the whole value chain from forest to wood products and energy, and illustrates that a wide range of measures can be applied to provide positive incentives for more firmly integrating climate objectives into the forest and forest sector framework [6,7]. CSF is more than just storing carbon in forest ecosystems; it builds upon three main objectives; (i) reducing and/or removing greenhouse gas emissions; (ii) adapting and building forest resilience to climate change; and (iii) sustainably increasing forest productivity and incomes. These three CSF objectives can be achieved by tailoring policy measures and actions to regional circumstances in Member States forest sectors. The aim here is to quantify a realistic potential mitigation role of EU forests and the forest sector, and to devise a novel policy regime that tries to incentivize action according to the three main CSF objectives. Below we first quantify the mitigation role of EU forests and the forest sector towards 2050 taking into account its full impact along the forest ecosystem-wood products-energy value chain. We then devise an alternative policy regime, and last, we identify actions and actors, taking into account the high degree of variation across regional circumstances in the EU Member States.

2. Methods

For the quantitative part of this analysis, we conducted a literature search and review, searching in Google Scholar and online journal outlets. Search keywords were "Forest CO_2 sequestration/sink, EU LULUCF strategy, Member States national LULUCF/forestry strategies, forest measures for mitigation, LULUCF, forest and wood products value chain, forest value chain, carbon balance, cascade, and material and energy substitution". We selected articles that focused on the climate change mitigation potentials. We then quantified the full CO_2 impact of the forest and forest sector, although we are aware that in current accounting of the impacts of bioenergy, for example, the latter impacts are accounted in the energy sector. Thus, we regard the full impact along the forest ecosystem-wood products-energy value chain, using Intergovernmental Panel on Climate Change (IPCC) methods and conversion factors [8]. For the policy part of the study, we used existing public documents on LULUCF regulation, impact assessments [5], as well as EU workgroup meeting minutes together with scientific literature on the topic.

3. Results: The Mitigation Role of EU Forests and the Forest Sector through CSF

Based on our synthesis of the literature, we developed the CSF concept. It is derived from a more holistic and effective approach than one based solely on the goals of storing carbon in forest ecosystems. The core of CSF is that it considers the whole forest and wood product chain, including material and energy substitution and foremost takes regional circumstances into account. Furthermore, CSF not only aims at climate change mitigation, but tries to achieve synergies with other forest functions, such as adaptation to climate change, biodiversity conservation, ecosystem services and the bio-economy.

CSF through (1) reducing and/or removing greenhouse gas emissions; (2) adapting and building forest resilience; and (3) sustainably increasing forest productivity and incomes, tackles multiple policy goals. The greater the synergies and the fewer the trade-offs between climate policy and other societal, forest-related goals, the more likely climate objectives will be effectively implemented in practice.

Given that the EU aims at an ambitious 80% emission reduction by 2050, it will be essential to involve all the sectors and thus to include EU forests and the forest sector in order to achieve this aim (Figure 1). Although EU forests cover 40% of the land, the scientific literature has occasionally pointed to a limited, but additional mitigation role for EU forests on the order of 90–180 Mt CO_2/year by 2040 [6]. We find, however, that with adjustments to the LULUCF policy framework, and with CSF implementation, EU forests and the forest sector can play a much larger role than previously thought.

The current annual mitigation effect of EU forests via contributions to the forest sink, material substitution and energy substitution is estimated at 569 Mt CO_2/year, or 13% of total current EU emissions [4,9–14]. With the right set of incentives in place at EU and Member States levels, we find, based on a literature review (and accounting for regional circumstances (Table 1), that the EU has the potential to achieve an additional combined mitigation impact through the implementation of CSF goals, of 441 Mt CO_2/year by 2050 (see Appendix Tables A1 and A2). In this estimate, we simply consider the total impact of forests and the forest sector on the atmosphere from a climate perspective. We arrive at this number based on the four following measures (see also Table 1).

Table 1. Summation of the Climate Smart Forestry mitigation effect. All numbers are approximations.

Main Category of Forest Management Measure	Sub Measure	Mitigation Effect (Mt CO_2 a^{-1})
1. Improved forest management		172
	1a. fullgrown coppice	56
	1b. enhanced productivity & improved management	38
	1c. reduced disturbances, deforestation, drainage	35
	1d. material substitution wood products	43
2. Forest area expansion		64
3. Energy substitution		141
4. Establish forest reserves		64
Total		441

3.1. *Improved Forest Management in Existing Forests and Wood Chains*

Projections of forest resources under alternative management and policy assumptions indicate that carbon storage in existing EU forests could continue to increase, providing additional sequestration benefits of approximately up to 172 Mt CO_2/year by 2050 [15–20] (see Table A2 for calculations). Measures could include enhanced thinning of stands leading to additional growth and higher quality raw material, regrowth with new species, planting of more site-adapted species, and regeneration using faster growing species. For example, large areas of low productivity hardwoods previously only used for firewood production (some 350,000 km^2 of old coppice forests), could be regenerated and replaced by more productive mixed deciduous and coniferous forests, generating an additional sink of ~56 Mt CO_2/year [21]. This can be done by using new provenances better adapted to future climates, without the need for exotic species. Furthermore, we recommend this measure only be carried out on sites with lower biodiversity values. Some coppice sites are highly valuable for nature conservation strategies arising out of centuries old cultural historical management [22].

An increase in the productivity of forests through the above measures is feasible on ~700,000 km^2 of forest land, yielding increased stemwood growth of ~1 m^3/ha/year [16,23]. Converting this area into carbon measurements using IPCC standards (Table A1), the additional growth could potentially yield an addition to the forest sink of ~38 Mt CO_2/year (see country examples in [18,19,24,25]). Moreover, serving as a support for the EU Bioeconomy strategy, this measure would add ~35 million m^3 of future harvest potential (see Appendix Table A1 factor "harvest rate of additional wood growth") to the EU's current fellings of 522 million m^3 [26], although possible trade offs with other services should always be kept in mind [27].

Harvested wood products: Not only the carbon in forest ecosystems plays a role in climate change mitigation. The long-term use of harvested wood products (HWP) can also contribute to mitigation. Using wood resources in this way can substitute for the use of fossil fuels—in particular for CO_2—and energy-intensive materials like steel and concrete in the construction sector. According to meta-analysis estimates, for example, each additional ton of wood products substituted for ordinary Portland cement, helps to avoid an average of 2 tons of CO_2 emissions [21]. Favoring wood-use in the construction sector (when carried out in synergy with the above-mentioned production increase) could therefore potentially help avoid future emissions on the order of ~43 Mt CO_2/year [11,28]. With the additional implementation of cascaded use for quality wood products, only post-consumer wood products would be used for energy production; this strategy would provide additional substitution impacts [18]. Currently, however, 25% of all EU harvested wood is used directly in non-commercial low efficiency household fire places [29]. We acknowledge that there is still much new research needed to improve the substitution multipliers, so that we will be able to provide more accurate estimates of the potential mitigation impacts.

Combining adaptation with reduced emissions: Emissions occur in European forests as well. Annual deforestation, as exemplified by land use conversions to infrastructure of close to 1000 km^2/year, causes emissions of ~15 Mt CO_2/year [12].

Further, natural disturbances such as wind storms and forest fires [30–32], on average, cause emissions of ~18 Mt CO_2/year. Draining of peat soils under forests emits ~20 Mt CO_2/year [10]. Forest management and the improved protection of forest areas in Europe can aim to reduce all of these emissions. In Spanish forests, for example, a more active management regime that also aims at introducing more adapted species could significantly reduce fire risk and thus land-use change. If we conservatively assume that 2/3 of the above emissions can be avoided, this would reduce emissions by a further ~35 Mt CO_2/year.

3.2. Forest Area Expansion

Some 150,000 km^2 of farmland are projected to be abandoned in the EU by 2030 [33]. These lands are in remote locations, currently with low biodiversity value, on land that is unprofitable for agriculture and where labor is not easily available. In such areas, forestry represents a good option without leakage of agriculture to developing countries. Using new tree species that easily achieve stem wood growth of ~8 m^3/ha/year, and using IPCC conversion factors, the expansion of forests onto this area could provide an additional sink of ~64 Mt CO_2/year and could further provide the additional spinoff benefit of an additional harvesting potential of ~60 million m^3 with spinoffs to the HWP pool etc.

3.3. Producing Biomass for Bioenergy

Currently, woody biomass already provides 7% of total EU energy needs [17,34]. Because of this bioenergy contribution, fossil fuel emissions have currently been reduced by 190 Mt CO_2/year. The potential, however, is larger. Based on EU domestic woody biomass availability, secondary residues and low-quality thinning wood, estimates suggest that a sustainable additional 200 million tons of woody biomass can be produced. This represents an additional 5% of total EU energy needs and potential avoided emissions of ~141 Mt CO_2/year [35–38]. Projects like Biomassfutures and Biomasspolicies [36,37] have paid a lot of attention to the sustainable management of the forest resources preserving soil quality and nutrient levels, thus arriving at the carefully assessed estimates provided above.

3.4. Forest Reserves

Setting up strict forest reserves—which currently cover 2% of European forests [26] will strengthen short term CO_2 sequestration. NGOs have continuously asked for an overall goal of 10% of EU forests to be set aside as strict reserves. If we assume that 2/3 of this goal (a 7% share of EU forests for set-aside forests) can be achieved by 2050, an additional CO_2 sequestration of ~64 Mt CO_2/year could be achieved on ~120,000 km^2 (Tables A1 and A2). This would benefit the EU Biodiversity Strategy and the EC Natura2000 network of protected areas.

4. The EU LULUCF Proposal and How to Approach Reform

The LULUCF proposal [1] places forestry together with agricultural land-CO_2 into one compartmentalized sectoral package (the LULUCF "Pillar"), with very limited flexibility and potential for exchange with other sectors. A no-debit rule applies for the combined LULUCF forestry and agricultural land-CO_2, meaning that these quantities together should not result in net emissions (i.e., create more emissions), and should ideally contribute to a continuously increasing sink. Emissions from agricultural land may be compensated by change in the forest sink, but only above a forest (management) reference level (a baseline sink, FMRL, FRL), and only up to a maximum 3.5% of a country's total, economy-wide, base year emissions, in sum 160 Mt CO_2/year for the EU as a whole. However, due to high reference levels and/or small caps in individual Member States, many of them will be inadequately encouraged to achieve this potential [4]. The proposal further allows for a small exchange with the Effort Sharing Decision (ESD) sectors, which sets reduction targets for the transport and housing sectors, and non-CO_2 emissions from agriculture. The exchange, however, is capped at 280 Mt CO_2/10 years and can only be achieved through specific activities such as afforestation and cropland management—the forest management activity has been excluded from this quantity, for now, although it is under discussion. Because of the limited set of allowable measures, this maximum is not likely to be achieved either. Thus, we find, based on the quantitative estimates provided above, that the EU climate policy framework should ideally provide improved incentives that strengthen the forest and forest sector likelihood of contributing to climate change mitigation. Furthermore, the overall strategy should be greatly simplified in order to avoid unnecessary technical complications and costs. The current web of caps, reference levels, targets and pillars have the effect of marginalizing incentives for forests, wood products and energy-related mitigation efforts.

The range of earlier concerns toward including LULUCF in the climate targets was primarily related to uncertainty in reporting on the forest sink, opposition to using the forest sector as a tool for "offsetting" industry-level emission reduction commitments, a strong interest in preserving "environmental integrity", and questions regarding the relative permanence of forest-based carbon sequestration. Many or most of these (earlier) concerns hampered innovation in the LULUCF policy framework. However, many of these concerns have been sidelined by important changes since the early 1990s. Continuous increased growth in European forests over the last several decades [39], as well as continuous improvement in forest inventory reporting practices since the initial UNFCCC reporting requirements were agreed, have helped to reduce concerns related to uncertainty and permanence.

To deal with the concerns regarding environmental integrity, the 2011 Durban inclusion of forests in the UNFCCC effectively turned a baseline sink into a forest sector commitment that has been added on top of the regular commitment framework. This baseline sink is now called the Forest Management Reference Level (FMRL) and must be achieved before any additional forest sector achievements can be counted. The structure of these rules essentially enforces the additive role of the forest contribution. Despite this raised ambition (existing commitment + the FMRL commitment) and the presence of additional emission reduction pathways, forests continue to play a marginal role in the climate policy framework.

As soon as Member States fail to achieve this baseline (the FMRL), they are debited for the shortfall. For many Member States, this may represent a significant obstacle to their mitigation goals, in particular the increasing use of bioenergy. Though countries are likely permitted additional harvesting in their

FMRL (management intensity) projections, this placement of constraints on how additional annual growth in European forests can be used may have unintended consequences. First, forest owners invest resources in productive forests. Perceived limits on the use of these productive resources (through the implementation of reference levels) may well create disincentives for future forest investments. Second, additional forest and forest resource use (rising harvesting levels as in the bio-economy case of Finland and Sweden) may in the short-term lead to a reduced sink. Even though these countries will likely continue to have a net sink, they will be debited for any shortfall. Finally, the difficulty in projecting future demand for bioenergy resources over longer periods of time is only likely to exacerbate these tensions.

We thus find there is every reason to propose better ways to encourage future forest investments and promote climate-friendly uses and the ecosystem services of forests and forest-based resources. Imposing limits on the potential use of forest resources—in particular, where these can negatively impact cost-efficient climate change mitigation strategies—does not represent a wise use of existing resources.

Therefore, we propose the following four policy revisions:

A. Eliminating caps and the current reference levels.

Our alternative policy approach is based on incentivizing ambition, in particular through elimination of the limits on access to carbon credits. Removing limits, in particular, on the cap, can provide an immediate financial incentive framework as well as the appropriate resources for stimulating additional forest-related CSF efforts. This can provide opportunities for Member States to develop strategies that build upon other efforts e.g., the EU's Biodiversity Strategy [40], and provide the potential availability of additional resources for the Bio-economy Strategy [41]. In contrast to the Impact Assessment (IA) of the LULUCF regulation [5] carried out by the Commission, we especially look for alternative policy incentives outside the current scope of the regulation. The IA only looked for small alternatives within the scope of the Regulation.

A core of our approach is to set higher ambitions for the LULUCF sector: Member State forest and forest resource-based climate mitigation targets can be determined through a joint effort by the European Commission and the Member States, based on principles of fairness, the state and size of forest resources, current forest sinks, Gross Domestic Product, as well as cost-efficiency. Moreover, these targets can and should be set to further raise ambition and strengthen CO_2 mitigation. However, the placement of these targets in the forestry sector through the creation of a forest "Pillar" immediately gives rise to concerns about the future use of the forest resource and encourages lobbying focused around the setting of the FMRL. If these targets are instead added on top of the economy-wide emission reduction commitment and the FMRL is removed, these targets will no longer directly impinge upon actions within the forest sector. Doing this would thereby facilitate the decoupling of forest emission reduction targets from future potential forest resource uses (e.g., wood raw material flows), the confounding of which has been a cause for great concern.

Removing the FMRL would thus make it possible to eliminate the cap and thereby free up the right to claim carbon credits for additional carbon sequestration in standing forests. With this achieved, Member States would then be able to more freely incentivize climate-friendly forest actions. When forest sector targets are set together with this type of enabling framework for promoting investments in forest management, this will make it possible to further incentivize forest growth. The long-standing debate over "whether to store more carbon, or use the forests", misdirects attention away from the real challenge, which is how to stimulate additional forest growth, such that it becomes possible to both maintain and increase harvest, while at the same time maintaining the sink. Such an approach is entirely in line with the IPCC 4AR (2007) which concluded "In the long term, a sustainable forest management strategy aimed at maintaining or increasing forest carbon stocks, while producing an annual sustained yield of timber, fibre or energy from the forest, will generate the largest sustained mitigation benefit".

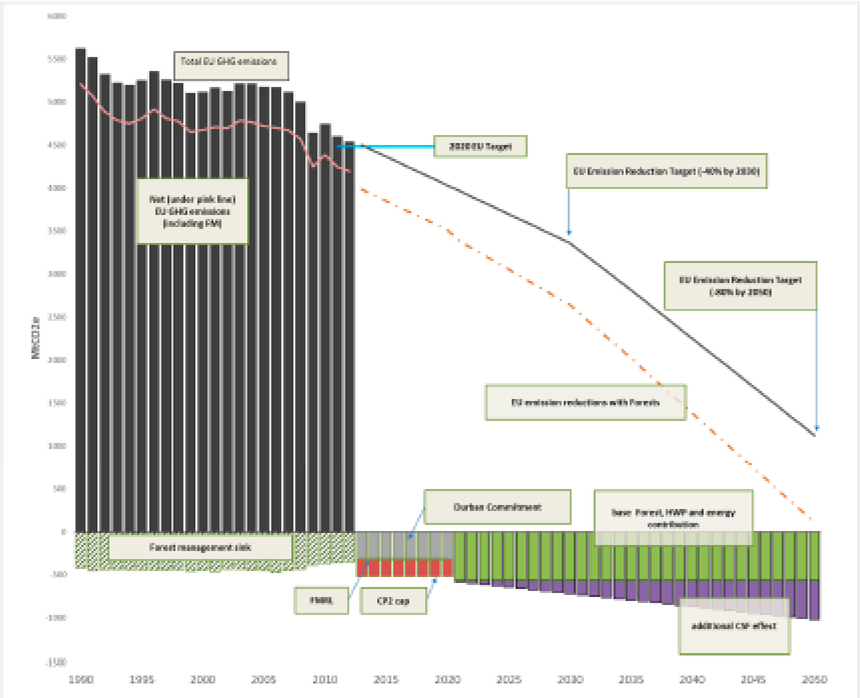

Figure 1. Total Projected European Union (EU) Emission Reductions by 2050, with and without climate Smart Forestry. Reported data were used through to 2012 (emissions of all sectors positive and sinks negative). The expected impact of both the Durban commitment created by the introduction of the Forest Management Reference Level (FMRL), and the cap for the second Commitment Period (CP2 cap), through 2020 is projected by the red and grey bars. Further, we project the potential forest contribution from climate smart forestry from 2020 to 2050 through bright green and purple bars. These consist of forest (net removals), harvested wood products and bio-energy. The green bars provide the projected base forest contribution from 2020 to 2050. The purple bars are the additional Climate Smart Forestry (CSF) effect based on the potential introduction of additional incentives as described in this article. These total potential contributions from CSF forestry on net EU emissions (displayed as negative bars) is then copied by the brown and purple line and suggests a significant impact compared to the EU's current 80% emission reduction target by 2050. GHG: Greenhouse gases; FM: Forest management

The potential climate-friendly use of forest resources would thus be unrestricted (Member States could thus choose more effectively between the most appropriate climate-friendly actions, as well as being free to fulfill their emission reduction commitments by other means). Motivated either by the ability to claim credits or receive additional financing, forest owners would be more strongly encouraged to pursue additional climate-friendly forest management efforts. This in turn would create powerful motivation for providing additional forest growth without necessarily impinging upon the potential use of the existing forest resources.

B. Investments, economic incentives, and carbon price.

Member States currently dedicate very few resources to forestry. On average, they spend some 26€ per ha per year [26], mostly on State Forest Services and for supporting private owners with management plans and tree regeneration. However, the EU currently has a number of programs that could potentially provide additional financial resources for EU forests and the forestry sector. These include: the Emissions Trading Scheme (ETS), the Rural Development Program (RDP), the Common Agricultural Policy (CAP), and for knowledge generation the Framework Program for Research and Innovation (Horizon 2020). Further, Member States (e.g., Austria, France, Finland, Germany, Italy, Netherlands, Spain and Sweden) also have national programs for their forests that can provide additional support.

Under the current trend of reducing state budgets, Member States may find it difficult to financially support additional forest measures. The above-mentioned programs suggest, however, that funds are available at the EU level. EU funding strategies and mechanisms have previously and primarily been directed at renewable energy strategies and the development of new renewable technologies. Thus, funding for climate-friendly, forest resource-based activities has been far more limited. With relatively modest changes to existing EU programs, however, it is possible to introduce a CSF-based strategy to provide support to Member States and/or forest owners, and to encourage additional forest-based carbon sequestration efforts. Because a CSF strategy will mobilize both Member States and forest owners, it may prove more effective at promoting flexibility, resilience and additional forest revenues than the current European Forest Strategy proposed by the Commission. This would require, however, the Commission and the Member States to undertake efforts to weave forests and forest-based CSF measures more firmly into the current mitigation (and adaptation) framework, which is possible under the current Article 10 of Decision no 529/2013. Under Article 10, Member States must submit information on their most relevant current and future LULUCF actions in land use activities such as afforestation, forest management, cropland and grassland management, and wetlands management. CSF can be an overarching measure reported under Article 10.

Additional revenues for motivating forest mitigation efforts and providing an improved support framework for private sector investment could also be funded through the EU emissions trading system (ETS). In its updated EU ETS Directive, the European Commission is proposing to increase revenues for climate mitigation for the next ETS commitment period (2021–2030). Growing numbers of countries are implementing carbon taxes (e.g., Denmark, Finland, France, Great Britain, Ireland, Netherlands, Portugal and Sweden), and the revenues from these taxes could also be partly redirected to climate-friendly, CSF-based forest sector investments. The new activities funded by this would also help generate more public revenue and could help encourage urgently needed joint ventures between Member States and bottom-up private interests in undertaking additional mitigation efforts [42]. Income thus generated—if spent on forest climate measures—would represent an important motivation for the 16 million private forest owners, industry, and public forest owners in the EU to implement CSF.

C. Flexibility.

As the EU regionally encompasses a large variety of forest types and forest-sector characteristics, a forest related target should allow adequate flexibility across the full range of mitigation options. Member States are capable of deciding how best to meet their national and LULUCF sector targets, and establishing best strategies and measures for meeting these overall commitments—in conjunction with forest and forest sector bio-economy and biodiversity goals.

The EU and the Member States can set a facilitating framework by providing the appropriate setting for encouraging additional forest growth through EU Bioeconomy, Biodiversity and CSF goals. Removing limits on the right to claim carbon credits could likewise further provide the impetus Member States need to provide latitude for promoting national level incentive strategies. Flexibility can be further increased by raising the degree of fungible exchange across climate change mitigation sectors in the EU climate policy framework (in particular across LULUCF, the Effort Sharing Regulation and possibly also the EU ETS), thereby enhancing mitigation in activities where the marginal costs of mitigation are lowest. Flexibility should not compromise the transparency and effectiveness of climate policy. However, neither should we forego the opportunity for a more rapid, efficient and cost-effective mitigation strategy, especially when it can help raise ambition and ease progress toward the climate goal.

D. Actors and synergies.

Forest policy is drawn-up and implemented at the Member States level and ideally builds an effective link between national level goals and the interests of actors at other levels. This is the level that can best take account of local circumstances. Forest owners, the forest industry and NGOs are the actors that can implement actions to achieve productive and resilient forest ecosystems and fulfill biodiversity objectives (see Table 2). They must also achieve an economically viable forest value chain that provides forest products, income, energy and jobs. The regularly managed forests and forest sectors in Europe provide a good basis for achieving these goals. If the major regional actors do not support the policy, it will bear the burden of not succeeding in practice.

Table 2. Examples of measures for implementing Climate Smart Forestry and their local synergies.

Forest Management Measure	Regional Specific Climate Smart Forestry Incentive (+Actor (in Bold))	Synergies Achieved
Regenerate full grown coppice forest areas with more productive and climate adapted species	Create tax incentives for regeneration with improved provenances. **National and regional governments, industry.**	Synergy with climate change adaptation can be achieved. It will also enhance woody biomass flow for the Bio-economy and the Renewable Energy Directive. Resilient forests will also function in synergy with biodiversity goals
Stimulate ecosystem service promotion and preservation	Encourage explicit attention to the benefits of harmonizing carbon, water, soil and forest interactions. Award CO_2 credits and other payments for ecosystem services. **Private sector with interest in e.g., recreation, pollination or water and soil protection.**	A resilient forest ecosystem will hold a sustainable carbon balance and will protect the water and soil resources underneath, which will optimize forest-based mitigation and adaptation efforts.
Enhance regeneration in older declining (drought susceptible Norway spruce (*Picea abies* L. H. Karst.) forest and stimulate establishment of climate adapted species	Award CO_2 credits for creating a more productive, resilient mixed forest ecosystem. Paid from CO_2 taxes. **Member States with private sector and large forest owners.**	The regenerated and mixed forest can be managed in synergy with climate change adaptation and will enhance woody biomass flow for the Renewable Energy Directive. Also, regenerated resilient forests will function in synergy with biodiversity goals.
Merge or stimulate cooperation between fragmented forest owners that are now avoiding investment nor mobilise wood	Create tax exemptions when an adjacent property is bought. The budget can be derived from CO_2 taxes and rural development programmes. **EU + national governments, forest owner associations, certifiers.**	This is in synergy with wood mobilization strategies for an enhanced bio-economy and with rural development strategies. Furthermore, larger owners and cooperatives have more opportunities to invest in regeneration and thus in climate-adapted forest estates.
Reduce drainage of low productive drained peatlands	Reduce drainage of formerly drained peatland and award CO_2 credits. **Forest owner associations, NGOs.**	In synergy with biodiversity objectives and an increase in CO_2 sink.
Reduce disturbance risks in storm or fire prone forest areas and regenerate with drought resistant species	Reduce growing stock through harvest and regeneration or through thinning, producing wood for bioenergy. Funding derived from rural development budgets. **EU & Member States, State forest services, large forest owners, industry.**	This reduces the chance of CO_2 emissions, reduces forest owner vulnerability to climate events and stimulates adaptation to climate change through regeneration with new species. This measure is also in synergy with an increased wood flow for the bio-economy, creating jobs in synergy with rural development and the Renewable Energy Directive.
Improve transparency of the regional wood raw material market, aiming at improved cascading	Better insight and open access to data on wood resources and qualities leading to most optimal uses of wood. R&D budget. **Research creating improved databases, education, outreach organisations.**	This measure leads to more optimal uses of woody raw material, avoiding carbon debts and aiming at higher value chains. It can be achieved in synergy with jobs and rural development.
Promote wood use in building sector	Stimulate wood use through tax exemptions when using wood, or CO_2 taxing when using steel or aluminum etc. **National governments, Public procurement to favor wood in construction, education of builders and architects.**	In synergy with greenhouse gas emission substitution, environment-friendly buildings, improved city environment.

Table 2. *Cont.*

Forest Management Measure	Regional Specific Climate Smart Forestry Incentive (+Actor (in Bold))	Synergies Achieved
Afforest abandoned farmland	Improved mapping and land use databases in combination with afforestation schemes. Designate budget in Common Agricultural Policy and derive funds from CO_2 credits and CO_2 taxes. **EU & Member States, industry, investors.**	An increased CO_2 sink can be achieved in synergy with the production of additional woody raw material from new forest areas, and will create new bio-economy opportunities. Will help climate change adaptation through e.g., forest corridors. Jobs will be created by interactions between rural development and Natura 2000.
Establish large strict forest reserves in remote areas and/or low-productivity areas	Award CO_2 credits for introducing large connected reserves in existing forests paid from CO_2 taxes. **Forest owner associations, EU + Member States, State Forest Service, NGOs.**	In synergy with Natura 2000 and Biodiversity strategy and in line with increase CO_2 sink in the forest ecosystem.

5. How to Implement CSF

Too little work has been done on connecting the forest policy framework at the EU level with national level strategies directed at land and forest owners. We highlight synergies that can potentially provide leverage between these levels and the private sector in Table 2. Forestry has always been characterized by a long-term planning horizon. Given these long-cycle patterns of forest management and in order to give actors time to respond, the LULUCF timetable should extend beyond 2030. A forest-related strategy should aim, for e.g., at 2050, with an initial learning and implementation phase taken up in the five year cycles of the Indicative Nationally Determined Commitments (INDC)

Politically realistic climate-friendly forest and forest sector policy strategies that are taken up in practice by forest sector actors require an implementation strategy that adequately links the interests of these forest sector actors with the over-arching Member States and EU level policy framework. To-date, such linkage is either partially or entirely missing [43]. Moreover, while both national and EU level strategies envision important emission reductions by the year 2030 and 2050, the failure to provide appropriate strategies for motivating forest owners essentially means they may be more likely to respond to other kinds of incentives (e.g., economic concerns), irrespective of their climate impact.

Finding synergies between a forest climate target and other forest related concerns like biodiversity loss, forest fire, loss of peat carbon, forest health problems under climate change, fragmented ownership, low demand for wood raw material, etc., will help provide the levers to make things happen (Table 2). As suggested in Table 2, this requires balancing climate change mitigation measures with goods and services provision; biodiversity, water services, forest resilience, surface cooling, adaptation, and the bio-economy. Likewise, different regional options and strengths are needed to achieve mitigation in the forest sector and forests. For example, in drought and fire prone regions, CSF is geared to creating a fire-resistant landscape. Or in industrial forestry countries, CSF measures are more geared toward the bio-economy and new biomaterials. Table 2 provides examples of a potentially much more extensive list of measures adapted to regional circumstances.

6. Discussion

How certain are the above quantifications and suggested impacts of policy change? Of course these do contain uncertainty. Projecting the large (diverse) European forest resources, its management and wood demand in the future is uncertain [44] and thus we are not certain even how the baseline sink may develop. Further, our method was a literature review building on quite a wide range of other applied methods or modelling studies. Naturally those studies portray a range of possibilities and a range of quantified mitigation potential. Still, many studies point in the same direction of a significant additional potential.

Further, how the suggested policy changes will be elaborated and implemented and what the impacts will be, is also uncertain. However, such uncertainties also surround the other sectors and are no reason to do nothing. The climate change problem is grave enough to make any effort in a sector worthwhile. To avoid disappointments, we highlight synergies with other targets, such as biodiversity, a resilient ecosystem and a productive forest sector.

It is increasingly being acknowledged that reaching the Paris Agreement climate targets will require fundamental changes in economies and societies, and therefore climate policy should be planned in connection with this systemic change [45]; this also applies to land use and forestry. Can CSF really work and have the additional 441 Mt CO_2 mitigation impact as outlined in this article? Yes, we think it can, but it will require effort (like in any other sector) and it will only work when climate policy builds upon interconnections with other societal policy goals and minimizes trade-offs. Without achieving this, there is a danger that climate policy targets will not be politically possible to implement.

7. Conclusions

In conclusion, Figure 1 provides a graphical representation of the potential mitigation impact that both the revisions suggested in this article and the introduction of CSF measures could potentially have on the EU's Climate and Energy Policy Framework. The graph shows that towards 2050 the total mitigation impact of the forest and forest sector reaches close to 20% of total EU emissions in the base year. A very significant impact with many synergies can be achieved, provided the effort is made.

Acknowledgments: This work has been financed by European Forest Institute's Multi-Donor Trust Fund. We thank the Governments of Austria, Finland, France, Germany, Ireland, Italy, Norway, Spain and Sweden who support this Fund. The Lab of Forest Economics contributed through LabEX ARBRE ANR-11-LABX-0002-01. Hetemäki acknowledges financial support from the FORBIO project (No. 14970) funded by the Strategic Research Council at the Academy of Finland. Nabuurs acknowledges the FP7 SIMWOOD project (No. 613762) and the ERA-NET GAS project FORCLIMIT for contributing to the writing stages of the paper. We thank Annalisa Savaresi and Martin Nesbit for contributing to the EFI report FSP2. We thank two anonymous reviewers and Geerten Hengeveld for very helpful comments.

Author Contributions: G.-J.N. did the conceptual thinking of the paper idea, as well as the quantitative part and much of writing; P.D. collaborated in quantitative part and co-writing; D.E. did the conceptual thinking of the paper idea, the policy ideas and much of writing; M.H. collaborated in quantitative part and co-writing; L.H. did the conceptual thinking of the paper idea, and co-writing; M.L. collaborated in quantitative part and co-writing.

Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

Table A1. Annex.

Conversion Factors	Value	Unit	Reference
Convert from stemwood volume to dry matter	0.45	tonne dry matter/m^3 stemwood	[19]
Convert from dry matter to carbon	0.5	unitless	[19]
Convert from stem carbon to whole tree carbon	1.3	unitless	[19]
Convert from carbon to CO_2	3.67	unitless	[19]
Harvest rate of additional wood growth	0.5	fraction	Assumed based on current harvest rate in Europe of 70% [26]
Carbon (C) stock in deforested forest average for EU	40 [1]	ton C/ha	[26]
Material substitution factor for wood use instead of steel, aluminium etc.	0.28	ton C/m^3 wood product	[21]
Wood going into structural use every year	169	Mm^3/y	[29]
Additional woody biomass potential from primary, secondary and tertiary residues	88	Million tonnes oil eq.	[36]

Average carbon stock in the whole EU forest is 61 ton C/ha. We assume that the deforested forest (i.e., land use change) are not the best sites. E.g., shrub-like, half-open forest in the Mediterranean. Therefore 40 ton C assumed/ha.

Table A2. Calculations Table, with Explanations in Footnote References.

		Area (ha)	Additional Stemwood Volume Growth (m^3/ha year)	Additional Sink/Substitution (Mt CO_2/year)
1a	Full grown coppice	35,000,000 [1]	1.5	56 [9]
1b	Enhanced productivity	70,000,000 [2]	1 [6]	38
1c	reduced natural disturbance (fire/wind)			12 [10]
	reduced deforestation	100,000 [3]		10 [11]
	reduced drainage of peat soils			13 [12]
1d	Material substitution wood products			43 [13]
2	Forest area expansion	15,000,000 [4]	8 [7]	64
3	Energy substitution			141 [14]
4	Establish forest reserves	12,000,000 [5]	5 [8]	64 [15]

[1] McGrath et al 2015 [46]. [2] Eggers et al [16] apply measures on 95 Mha. We assume measures are only feasible on 3/4 of this based on share of EU forests in the hands of larger forest owners, e.g., 40% of EU forests are in the hands of state owners. Then another 30–35% is in the hands of large industry or large private owners. These respond, respectively, to regulations and price incentives. [3] Current deforestation in EU forests (i.e., land use change) is 100,000 ha per year. [12] [4] Keenleyside & Tucker 2010 [33]. [5] Although the aims of NGOs differ quite a lot, an often voiced aim is to set aside 10% of European forests as strict reserves. [47]. 18% of Europe's land is now under Natura 2000 [48]. However, the Natura2000 designation is not a strict protection. Less than 2% of current forests are now in "strict reserves" (IUCN class 1.1) [26]. We have assumed that in the studied time frame, an additional 6–7% of forest land under strict reserves can be achieved. This equals 12 Mha's. [6] Eggers et al 2008 [16] find a 20% increase in increment when management is improved. 20% of the current EU average of 5 m^3/ha year is 1 m^3/ha year. [7] Average increment of plantations is assumed 60% higher than average increment of total existing forests in EU, which is now 5 m^3/ha year [26]. [8] Average increment of total existing forests in EU is now 5 m^3/ha year [26]. [9] Assumed that additional growth is harvested at a rate of 50% during the studied time frame. So factor "harvest rate of additional wood growth" also applied. [30,32]. [10] Emissions from disturbances are ~5 Mton C/year = 5 × 3.66 = 18 Mt CO_2/ year [30]. Assumed effective on 2/3rds of forests. [11] Assumed deforestation can be brought back with 2/3. [12] EU CRF submission to UNFCCC: emissions from peat soils under forests are 20 Mt CO_2/year. Assumed effective on 2/3 of land. [13] Assume one quarter of sawnwood ends up in structural longer term use, displacing steel, aluminium, etc. [14] Elbersen gives 88 million tonnes oil equivalents as realistic additional potential. This is 5.23% of total energy use in EU (1683 Million tonnes oil equivalents). Because of the large mix of energy use, we assume that this will lead to a reduction of total emissions of the same amount; 5.23%. Thus 5.23% of emissions from 4500 Mt CO_2 = 235 Mt CO_2. The EU requires a 60% saving of emissions when applying renewables. We assume the same 60% efficiency. 0.6 × 235 = 141. [15] Additional growth is not harvested in this time frame.

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