



43

FOREST RESILIENCE, BIODIVERSITY, AND CLIMATE CHANGE

A Synthesis of the Biodiversity/Resilience/
Stability Relationship in Forest Ecosystems



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in Forest Ecosystems**

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Table of Contents

Glossary	4
Foreword.....	6
Summary for Policy-makers	7
1. Introduction.....	9
1.1 Forests, climate, and climate change.....	9
1.2 Definitions of and related to resilience.....	10
1.3 Components of biodiversity and definitions	12
1.4 Issues of scale and resilience	13
2. Genetic diversity and resilience to change.....	13
3. The relationships among biodiversity, productivity and function, and resilience and stability	17
3.1 Theoretical background.....	17
3.2 Evidence of a diversity productivity relationship in forests.....	18
3.2.1 Diversity-productivity relationships and forest resilience.....	21
3.3 Diversity and stability	22
3.3.1 Diversity and invasion of ecosystems	23
3.3.2 Diversity and insect pests.....	24
3.3.3 Diversity and stability of processes in forests	25
3.4 Summary of diversity-resilience processes	25
4. Resilience, biodiversity, and forest carbon dynamics	25
4.1 Forests and the global carbon cycle	25
4.2 Biodiversity and resilience of forest-carbon dynamics.....	27
5. Case studies of forest resilience and comparisons under climate change by forest biome.....	30
5.1 Boreal forest biome	30
5.1.1 Climate change and boreal forest resilience.....	31
5.1.2 Case-study: western North American lodgepole pine	31
5.1.3 Case-study: North American boreal mixedwoods	31
5.2 Temperate forest biome	34
5.2.1 Temperate Forests and Environmental Stressors	34
5.2.2 Case-study: Moist evergreen temperate forests.....	34
5.2.3 Case-study: southern Europe	37
5.2.4 Case-study: eastern North American deciduous forests.....	37
5.3 Tropical forests.....	39
5.3.1 Climate change and tropical forest resilience.....	41
5.3.2 Case study: Amazon rain forest.....	41
5.4 Summary among forest biomes.....	43
6. Conclusions and ecological principles	43
6.1 Ecological principles to foster forest ecosystem resilience and stability under climate change...44	44
7. Literature cited.....	46

Glossary

Term	Definition	Source
Adaptation	Adjustment in natural or human systems in response to actual or expected climatic stimuli or their effects, which moderates harm or exploits beneficial opportunities.	UNFCCC
Adaptive capacity	The ability of a species to become adapted (i.e., to be able to live and reproduce) to a certain range of environmental conditions as a result of genetic and phenotypic responses.	Dobzhansky 1968
Biodiversity or biological diversity	The variability among living organisms from all sources including terrestrial, marine, and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, among species, and of ecosystems.	CBD
Biomass	Organic material both above ground and below ground, and both living and dead, e.g., trees, crops, grasses, tree litter, roots, etc.	FAO 2006
Biome	A regional ecosystem with a distinct assemblage of vegetation, animals, microbes, and physical environment often reflecting a certain climate and soil	Helms 1998
Carbon sequestration	The process of removing carbon from the atmosphere and depositing it in a reservoir.	UNFCCC
Deforestation	The direct human-induced conversion of forested land to non-forested land.	UNFCCC - Marrakech Accords
Ecological resilience	The ability of a system to absorb impacts before a threshold is reached where the system changes into a different state.	Gunderson 2000
Ecosystem	A community of all plants and animals and their physical environment, functioning together as an interdependent unit.	Helms 1998
Ecosystem	A dynamic complex of plant, animal and micro-organism communities and their non-living environment interacting as a functional unit.	CBD
Ecosystem Services (also ecosystem goods and services)	The benefits people obtain from ecosystems. These include provisioning services such as food, water, timber, and fibre; regulation services such as the regulation of climate, floods, disease, wastes, and water quality; cultural services such as recreation, aesthetic enjoyment, and spiritual fulfillment; and supporting services such as soil formation, photosynthesis, and nutrient cycling.	Millennium Ecosystem Assessment
Engineering resilience	The capacity of a system to return to its pre-disturbance state	Gunderson 2000
Forest Degradation	Changes within the forest which negatively affect the structure or function of the stand or site, and thereby lower the capacity to supply products and/or services	FAO 2001
Forest Degradation	A degraded forest is a secondary forest that has lost, through human activities, the structure, function, species composition or productivity normally associated with a natural forest type expected on that site. Hence, a degraded forest delivers a reduced supply of goods and services from the given site and maintains only limited biological diversity. Biological diversity of degraded forests includes many non-tree components, which may dominate in the under-canopy vegetation.	UNEP/CBD

Forest state	Most commonly considered in terms of the dominant assemblage of tree species forming an ecosystem at a location, the functional roles those species play, and the characteristic vegetation structures (height, layers, stems density, etc.) at maturity.	This document
Functional groups	Assemblages of species performing similar functional roles within an ecosystem, such as pollination, production, or decomposition (i.e., trophic groups), hence providing some redundancy.	Hooper and Vitousek 1997
Fundamental niche	A geographic area with the appropriate set of abiotic factors in which a species could occur.	Hutchinson 1957
Genetic Diversity	Any variation in the nucleotides, genes, chromosomes, or whole genomes of organisms.	This document
Mitigation	In the context of climate change, a human intervention to reduce the sources or enhance the sinks of greenhouse gases.	UNFCCC
Modified natural forest	Forest/other wooded land of naturally regenerated native species where there are clearly visible indications of human activities. Includes, but is not limited to, selectively logged-over areas, naturally regenerating areas following agricultural land use, areas recovering from human-induced fires, areas where it is not possible to distinguish whether the regeneration has been natural or assisted.	FAO 2006
Monotypic stand	A forest stand containing one tree species.	This document
Plantation	Forest/other wooded land of introduced species and in some cases native species, established through planting or seeding, mainly for production of wood or non-wood goods	FAO 2006
Primary forest	Forest/other wooded land of native species, where there are no clearly visible indications of human activities and the ecological processes are not significantly disturbed.	FAO 2006
Productivity or production	The rate at which biomass is produced per unit area by any class of organisms.	Helms 1998
Resilience	The capacity of an ecosystem to return to the pre-condition state following a perturbation, including maintaining its essential characteristics taxonomic composition, structures, ecosystem functions, and process rates.	Holling 1973
Resistance	The capacity of the ecosystem to absorb disturbances and remain largely unchanged.	Holling 1973
Silviculture	The art of producing and tending a forest by manipulating its establishment, composition and growth to best fulfill the objectives of the owner. This may, or may not, include timber production.	Helms 1998
Succession	Progressive changes in species composition and forest community structure caused by natural processes (nonhuman) over time.	Helms 1998
Stability	The capacity of an ecosystem to remain more or less in the same state within bounds, that is, the capacity to maintain a dynamic equilibrium in time while resisting change.	Holling 1973

Foreword



The world's forest ecosystems provide environmental services that benefit, directly or indirectly, all human communities, including watershed protection, regional climatic regulation, fibre, food, drinking water, air purification, carbon storage, recreation, and pharmaceuticals.

Forests harbour an estimated two thirds of all terrestrial species, and a fascinating array of ecological processes. The ecological stability, resistance, resilience, and adaptive capacities of forests depend strongly on their biodiversity. The diversity of genes, species, and ecosystems confers on forests the ability to withstand external pressures, and the capacity to 'bounce back' to their pre-disturbance state or adapt to changing conditions. This review explores these relationships based on published scientific literature.

This publication is a direct response to a request by the ninth meeting of the Conference of the Parties to the CBD to explore the links between biodiversity, forest ecosystem resilience, and climate change. Its findings are relevant for the future implementation of the CBD, but also the United Nations Framework Convention on Climate Change (UNFCCC), the Forest Instrument of the United Nations Forum on Forests (UNFF), and other international and regional forest-related agreements. It provides a compelling rationale for the conservation and sustainable use of biodiversity in any forest-based climate change mitigation and adaptation efforts.

In the present debate on climate change, the carbon storage capacity of forests and their role in mitigation is receiving increasing attention. While the international climate change negotiations have now recognized the value of ecosystem-based adaptation, in reality ecosystem-based mitigation and adaptation are two sides of the same coin. Protecting primary forests and restoring managed or degraded forest ecosystems make a vital contribution to both reducing anthropogenic emissions and aiding societal adaptation to unavoidable climate change. It is the resilience inherent to intact forest ecosystems - fully functional units of plants, animals, micro-organisms, and fungi - that provides the best insurance against climate change and prospects for ensuring forests meet the needs of present and future generations.

Ahmed Djoghlaoui
Executive Secretary
Secretariat of the Convention
on Biological Diversity

Summary for Policy-makers

- Resilience is the capacity of a forest to withstand (absorb) external pressures and return, over time, to its pre-disturbance state. When viewed over an appropriate time span, a resilient forest ecosystem is able to maintain its 'identity' in terms of taxonomic composition, structure, ecological functions, and process rates.
- The available scientific evidence strongly supports the conclusion that the capacity of forests to resist change, or recover following disturbance, is dependent on biodiversity at multiple scales.
- Maintaining and restoring biodiversity in forests promotes their resilience to human-induced pressures and is therefore an essential 'insurance policy' and safeguard against expected climate change impacts. Biodiversity should be considered at all scales (stand, landscape, ecosystem, bioregional) and in terms of all elements (genes, species, communities). Increasing the biodiversity in planted and semi-natural forests will have a positive effect on their resilience capacity and often on their productivity (including carbon storage).
- The resilience of a forest ecosystem to changing environmental conditions is determined by its biological and ecological resources, in particular (i) the diversity of species, including micro-organisms, (ii) the genetic variability within species (i.e., the diversity of genetic traits within populations of species), and (iii) the regional pool of species and ecosystems. Resilience is also influenced by the size of forest ecosystems (generally, the larger and less fragmented, the better), and by the condition and character of the surrounding landscape.
- Primary forests are generally more resilient (and stable, resistant, and adaptive) than modified natural forests or plantations. Therefore, policies and measures that promote their protection yield both biodiversity conservation and climate change mitigation benefits, in addition to a full array of ecosystem services. Nevertheless, it must be recognized that certain degraded forests, especially those with invasive alien species, may be stable and resilient, and these forests can become serious management challenges if attempts are made to re-establish the natural ecosystem to recover original goods and services.
- Some forest ecosystems with naturally low species diversity nevertheless have a high degree of resilience, such as boreal pine forests. These forests, however, are highly adapted to severe disturbances, and their dominant tree species have a broad genetic variability that allows tolerance to a wide range of environmental conditions.
- The carbon pool is largest in old primary forests, especially in the wet tropics, which are stable forest systems with high resilience.
- The permanence of efforts under UNFCCC negotiations, such as reducing emissions from deforestation and forest degradation (REDD), and of other forest-based climate change mitigation and adaptation policies and measures, is linked to the resilience of forests, and thus to forest biodiversity. REDD activities therefore should take biodiversity conservation into consideration, as this will help maintain forest ecosystem resilience and the long-term stability of the carbon pool.
- The regional impacts of climate change, especially interacting with other land use pressures, might be sufficient to overcome the resilience of even some large areas of primary forests, pushing them into a permanently changed state. If forest ecosystems are pushed past an ecological 'tipping point', they could be transformed into a different forest type, and, in extreme cases, a new non-forest ecosystem state (e.g. from forest to savannah). In most cases, the new ecosystem state would be poorer in terms of both biological diversity and delivering ecosystem goods and services.
- Plantations and modified natural forests will face greater disturbances and risks for large-scale losses due to climate change than primary forests, because of their generally reduced biodiversity. The risks can partly be mitigated by adhering to a number of forest management recommendations:
 - o Maintain genetic diversity in forests by avoiding practices that select only certain trees for harvesting based on site, growth rate, or form.

- o Maintain stand and landscape structural complexity, using natural forests and processes as models.
- o Maintain connectivity across forest landscapes by reducing fragmentation, recovering lost habitats (forest types), expanding protected area networks, and establishing ecological corridors.
- o Maintain functional diversity and eliminate the conversion of diverse natural forests to monotypic or reduced-species plantations.
- o Reduce non-natural competition by controlling invasive species and reduce reliance on non-native tree crop species for plantation, afforestation, or reforestation projects.
- o Manage plantation and semi-natural forests in an ecologically sustainable way that recognizes and plans for predicted future climates. For example, reduce the odds of long-term failure by apportioning some areas of assisted regeneration for trees from regional provenances and from climates that approximate future climate conditions, based on climate modelling.
- o Maintain biodiversity at all scales (stand, landscape, bioregional) and of all elements (genes, species, communities) by, for example, protecting tree populations which are isolated, disjunct, or at margins of their distributions, source habitats, and refuge networks. These populations are most likely to represent pre-adapted gene pools for responding to climate change and could form core populations as conditions change.
- o Ensure that there are national and regional networks of scientifically designed, comprehensive, adequate, and representative protected areas. Build these networks into national and regional planning for large-scale landscape connectivity.

1. Introduction

This paper reviews the concepts of ecosystem resilience, resistance, and stability in forests and their relationship to biodiversity, with particular reference to climate change.

The report is a direct response to a request by the ninth meeting of the Conference of the Parties to the CBD, in decision IX/5¹, to explore the links between biodiversity, forest ecosystem resilience, and climate change. Forests are emphasized because they are major reservoirs of terrestrial biodiversity and contain about 50% of the global terrestrial biomass carbon stocks (IPCC 2007, FAO 2000). Emissions from deforestation and degradation remain a significant (ca. 18-20%) source of annual greenhouse gas emissions into the atmosphere (IPCC 2007), and therefore the conservation, appropriate management and restoration of forests will make a significant contribution to climate change mitigation. Further, forests have a certain natural capacity to adapt to climate change because of their biodiversity. Some animals have important roles in ecosystem processes and organization, such as pollination, seed dispersal, and herbivory, and the loss of these species has clear negative consequences for ecosystem resilience (e.g., Elmqvist et al. 2003). Here, however, we limit our discussion to botanical aspects of forests, with the exception of some discussion of insect pests and diseases as these influence forest resilience and stability.

Forests have many unique properties, related to their high rates of primary productivity and biodiversity, which distinguish them ecologically from other ecosystems. Such properties include biological structures that develop in vertical and horizontal layers of live and dead plants, complex processes at multiple vertical levels from within soil layers up to the canopy, the capacity for self-renewal in the face of constant small and large disturbances, co-evolved plant-animal and plant-plant interactions, and the influence forest landscapes can have on micro- and regional climates, especially in closed-canopy tropical forests. Forests are comprised of multiple ecosystems that are associated with variable edaphic and microclimate conditions across broad landscapes.

In the annex to decision II/9, the Conference of the Parties to the Convention on Biological Diver-

1. Decision IX/5 requests the Executive Secretary to: "Collect, compile and disseminate information on the relation between forest ecosystem resistance and resilience, forest biodiversity, and climate change, through the clearing-house mechanism and other relevant means."

sity recognized that "*Forest biological diversity results from evolutionary processes over thousands and even millions of years which, in themselves, are driven by ecological forces such as climate, fire, competition and disturbance. Furthermore, the diversity of forest ecosystems (in both physical and biological features) results in high levels of adaptation, a feature of forest ecosystems which is an integral component of their biological diversity. Within specific forest ecosystems, the maintenance of ecological processes is dependent upon the maintenance of their biological diversity*".

Humans are having long-term cumulative impacts on Earth's ecosystems through a range of consumptive, exploitive, and indirect mechanisms, even to the extent of influencing the global climate (IPCC 2007). The major impacts of humans on forest ecosystems include loss of forest area, habitat fragmentation, soil degradation, depletion of biomass and associated carbon stocks, transformation of stand age and species composition, species loss, species introductions, and the ensuing cascading effects, such as increasing risk of fire (Uhl and Kauffman 1999, Gerwing 2002). As a result, there has long been global concern about the long-term capacity of forests to maintain their biodiversity and associated rates of supply of goods and services (including carbon storage, food, clean water, and recreation). This concern has been amplified following observed impacts occurring to global forests as a result of climate change (e.g., Phillips 1997, Kellomaki et al. 2008, Phillips et al. 2009, Malhi et al. 2009).

1.1 Forests, climate, and climate change

Superimposed on the many other anthropogenic impacts on forest ecosystems noted above is human-forced global climate change. Climate has a major influence on rates of photosynthesis and respiration (Woodward et al. 1995, Kueppers et al. 2004, Law et al. 2007), and on other forest processes, acting through temperature, radiation, and moisture regimes over medium and long time periods. Climate and weather conditions also directly influence shorter-term processes in forests, such as frequency of storms and wildfires, herbivory, and species migration (Gundersen and Holling 2002). As the global climate changes, forest ecosystems will change because species' physiological tolerances may be exceeded and the rates of biophysical forest processes will be altered (Olesen et al. 2007, Kellomaki et al. 2008, Malhi et al. 2008).

Forests can be usefully conceived as complex, self-organizing systems with multiple natural processes

that respond autonomously to internal and external drivers. For example, as available water becomes limiting, the height and density of the tree canopies is reduced because of basic ecophysiological relationships governing environmental controls on plant growth (Berry and Roderick 2002). If climate change results in a significant reduction in water availability, then the forest system will naturally change species composition (or state – see definition below). For example, the vegetation will reach a threshold beyond which the vegetation structure is not sufficiently tall and dense to comprise a forest, along with the concomitant changes in the dominant taxonomic composition of the plant community (Stephenson 1990). Under severe drying conditions, forests may be replaced by savannahs or grasslands (or even desert), while under increased temperature, open taiga can be replaced by closed boreal forests (assuming that there is sufficient moisture to support plant growth during the newly extended growing season) (e.g., Price and Scott 2006, Kellomaki et al. 2008).

Forests can also influence regional climates, depending on their extent and this is particularly true of the Amazon forest (Betts et al. 2008, Phillips et al. 2009). Hence, numerous feedbacks exist between climate and forests as the climate changes (Bonan et al. 2003, Callaghan et al. 2004, Euskirchen et al. 2009). These feedbacks are mediated through changes to albedo (Euskirchen et al. 2009), altered carbon cycle dynamics (Heath et al. 2005, Phillips et al. 2009), energy fluxes and moisture exchange (Wildson and Agnew 1992, Bonan et al. 2003), and herbivory, resulting in increased fires (Ayres and Lomardero 2000). Hence, maintaining forest resilience can be an important mechanism to mitigate and adapt to climate change.

1.2 Definitions of and related to resilience

We discuss several closely related terms throughout this paper and define them here, including resilience, resistance, state, and stability. We define **resilience** as the capacity of an ecosystem (i.e., forest type, in this paper) to return to the original state following a perturbation, maintaining its essential characteristic taxonomic composition, structures, ecosystem functions, and process rates (Holling 1973). Similarly, Walker and Salt (2006) defined resilience as the capacity of a system to absorb disturbance and still retain its basic function and structure, and therefore its identity (i.e., recognizable as the same by humans).

A forest ecosystem can respond in different ways to disturbances and perturbations. Depending on the

capacity of forests to cope with the degree of change, the characteristic taxonomic composition, vegetation structure, and rates of ecosystem processes may or may not be altered; that is, the resilience of the forest ecosystem may or may not be overcome. Forest characteristics can be used individually or in combination to define a forest ecosystem **state**. Most commonly, a forest state is considered in terms of the dominant assemblage of tree species forming an ecosystem at a location, along with the functional roles those species play, and the characteristic vegetation structures (height, layers, stems density, etc.) at maturity. So, a given mature forest type has a particular suite of characteristics that identify its state. (Note that we use the terms ‘system’ and ‘ecosystem’ synonymously throughout.)

A difference has been made in the scientific literature between “engineering resilience” and “ecological resilience” (Holling 1973, Peterson et al. 1998, Gunderson 2000, Walker et al. 2004). Engineering resilience is related to the capacity of a system to return to its more-or-less exact pre-disturbance state, and the assumption is that there is only one steady state. The latter concept has also been more recently referred to as equilibrium dynamics. Ecological resilience is defined as the ability of a system to absorb impacts before a threshold is reached where the system changes into a different state altogether. For example, in the case of increasing climatic drought, a resilient forest ecosystem according to the “engineering” definition is one that would recover from drought stress, with little or no change in species composition. If the ecological definition is used, then it is acknowledged that more than one stable system state is possible, with resilience being the measure of a forest ecosystem’s capacity to withstand a prolonged drought before being converted into a different vegetation ecosystem (e.g., non-forest); though it might go through several other different but stable forest states with new species compositions, before the conversion to grassland. Many of those successive forest states might be able to provide most or all of the goods and services provided by the initial state, and all would be recognizable as a forest type. This is also referred to as non-equilibrium dynamics.

Forests are engineering resilient in the sense that they may recover, after a period of time, from a catastrophic disturbance to their original, pre-disturbance state maintaining, more-or-less, the original species composition. The main ecosystem states of interest are defined by the dominant floristic (tree) composition and stand structure. However, it is also useful to consider the question of ecological

resilience with respect to the capacity of a forest to continue to provide certain (most or all) ecosystem goods and services, even if the forest composition and structure are permanently altered by disturbances.

Resilience is an emergent property of ecosystems that is conferred at multiple scales by genes, species, functional groups of species (see definition below), and processes within the system (Gunderson 2000,



Credit: A. Mosseler



Credit: A. Mosseler



Credit: A. Mosseler

Forest resilience as illustrated by the recovery of mixedwood forest in eastern Canada as a result of red pine plantation on a logged site, with natural infilling by deciduous species over a period of about 50-80 years.

Drever et al. 2006). Maintaining or restoring forest resilience is often cited as a necessary societal adaptation to climate change (e.g., Millar et al. 2007, Chapin et al. 2007). Drever et al. (2006) noted the importance of clarifying the questions: resilience of what and resilience to what? Here, the “of what” are particular characteristics of forest ecosystems (e.g., carbon sequestration, water use/yield), and the “to what” are environmental and human-caused disturbances, especially climate change. For example, an individual species’ physiological tolerances may be exceeded by natural environmental change or human-caused events. Consequently, the species composition of a forest may change while other ecosystem characteristics persist.

Forests are generally **resistant** to change, that is, they change little within bounds as a result of non-catastrophic disturbances, such as chronic endemic insect herbivory or minor blowdown and canopy gaps created by the death of individual or small groups of trees. Forests may also be resistant to certain environmental changes, such as weather patterns over time, owing to redundancy at various levels among functional species (as discussed further below, redundancy refers to the overlap and duplication in ecological functions performed by the diversity of genomes and species in an ecosystem). Ecosystems may be highly resilient but have low resistance to a given perturbation. For example, grasslands are not resistant, but are highly resilient, to fire. However, most well-developed forests, especially primary old forests, are both resilient and resistant to changes (e.g., Holling 1973, Drever et al. 2006).

Resistance is related to the concept of **stability** in the sense that, in response to minor perturbations, a forest ecosystem remains within a range of variation around a specified ecosystem state. Stability reflects the capacity of an ecosystem to maintain a dynamic equilibrium over time while resisting change to a different state. A stable ecosystem **persists** when it has the capacity to absorb disturbances and remain largely unchanged over long periods of time.

Species stability refers to consistent species composition over time. Drever et al. (2006) suggested that forest types that naturally progress through successional compositional changes are not necessarily changing state. On the other hand, a forest that was once dominated by a certain suite of species and that has changed as a result of new environmental conditions or human interference has changed ecosystem states. For example, if a harvested boreal spruce-pine-dominated forest regenerates to a mixedwood,

or if selective logging or disease eliminates species from a forest system, we would suggest that the system has indeed changed states. That is, even though it is still a forest, the ecosystem state, as defined by the dominant taxonomic composition of the canopy trees, has changed, along with various processes such as rates of growth and types of pollination. Furthermore, in this new state, some or many of the goods and services will also have changed and there may be effects on other elements of biodiversity resulting from changes in the provision of habitats and therefore the persistence of dependent animal species. Ecosystems may change states in response to disturbances, and the new state may or may not supply the same goods and services as the original state. Further, if species diversity is positively related to stability and resilience of forest systems, then species losses will likely have consequences for the long-term production of goods and services. Consequently, there is considerable interest in developing the capacity to understand and predict the mechanisms associated with resilience as it relates to the ways in which forests ecosystems respond to degradation, loss of species, and climate change (e.g., Kinzig et al. 2001, Scherer-Lorenzen et al. 2005).

1.3 Components of biodiversity and definitions

Biodiversity is often considered, especially within the forest management community, as simply a list of species present at a location. The term can also be used in the context of providing habitats for species of some particular value of interest to people, and in this sense biodiversity is a 'good' produced by the ecosystem. While **biodiversity** encompasses both these latter meanings, it is actually a broader term intended to encompass various measures of the full richness of life on Earth. As defined by the Convention on Biological Diversity, "biological diversity" means the variability among living organisms from all sources including terrestrial, marine, and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, among species, and of ecosystems. Allen and Hoekstra (1992) defined biodiversity even more broadly to include the variety of life at multiple scales of ecological organization, including genes, species, ecosystems, landscapes, and biomes.

Here we consider biodiversity in terms of specific components that are particularly relevant to forest ecosystems and equate them with the scale at which they are classified and mapped by humans. In so doing, we refer to standard metrics including genetic diversity and species richness

that relate to the dominant plant and animal species that characterize a given forest ecosystem. We also refer to terms that describe the vegetation structure (height, density, complexity) and age.

We make reference to functional redundancy, functional types or species, and functional groups. Several studies have established that resilience in ecosystems is related to the biological diversity in the system and the capacity that it confers to maintain ecosystem processes (Walker 1995, Peterson et al. 1998, Loreau et al. 2001, Hooper et al. 2005, Drever et al. 2006, Bodin and Wimen 2007). Most ecosystem processes are controlled by, or are the result of, biodiversity. However, not all species are necessarily equally important in maintaining these processes (Walker 1992, 1995, Diaz et al. 2003) and there is some redundancy at multiple levels within most ecosystems (Hooper et al. 2005). **Functional groups** are assemblages of species performing similar functional roles within an ecosystem, such as pollination, production, or decomposition, hence providing the ecosystem with a level of redundancy (e.g., see Hooper et al. 2002). As discussed further below, functional diversity is not necessarily correlated with species richness (Diaz and Cabido 2001, Hooper et al. 2005). Functional species that dominate ecosystem processes are not inevitably the most numerous species in the system (e.g., Hooper and Vitousek 1997, Diaz et al. 2003), and it is important to understand which species are contributing most to maintaining the flows of goods and services if management or protection is an objective. We are especially interested in functional diversity (within functional groups) in ecosystems because evidence has accumulated, especially in grassland systems, which implicates a relationship between functional diversity and ecosystem properties, including resilience and the related system attributes of stability and resistance (Diaz and Cabido 2001, Hooper et al. 2005). Under changed conditions, however, species that had a limited or no functional role ("passenger" species) may become functionally dominant ("driver" species), hence buffering the ecosystem against large changes and conferring resilience; that is, passengers can become the drivers (Walker 1995). This variable response has also been termed 'functional response diversity' and is critical to ecosystem resilience (Chapin et al. 1997, Elmqvist et al. 2003). Loss of functional species in the absence of redundancy has negative consequences for the ecosystem to the point of ecosystem collapse (Chapin et al. 1997). Hooper et al. (2005) noted that there is a clear need for continued research into the relationship between species richness and ecosystem stability.



Credit: B.J. Stocks, Canadian Forest Service

Many boreal conifer forests are prone to fire, however the species are well-adapted to this disturbance and the forest ecosystem rapidly regenerates. Hence, this kind of forest is not resistant to fire but it is highly resilient.

1.4 Issues of scale and resilience

Proper scaling is essential in the application of a theoretical framework. Most ecosystems are subject to disturbance regimes that occur across a range of temporal and spatial scales. Single communities in forests may occur across several tens to hundreds of hectares, while forests may be considered across hundreds to thousands of square kilometres. Forest stands may change continuously as a result of small-scale chronic disturbances that do little to affect the system, or they may change considerably at large scales owing to severe disturbances. Scaling is an important factor in defining ecosystem resilience, but scale and resilience are often investigated for different purposes. Resilience studies generally focus on how and why individual ecosystems maintain or change states, while scaling studies often examine ecological phenomena assuming steady-state ecosystems (Holling 1973). However, resilience is a scale-dependent phenomenon. Ecosystems are both temporally and spatially resilient when ecological interactions reinforce each other to reduce the impact of disturbances over time. This condition can be achieved through a range of mechanisms including species functional redundancy, or offsetting differences among species.

At larger scales in forests, there is also a level of potential role for species-level beta diversity (i.e. spatial turnover in species composition of communities) in enhancing ecosystem resilience in the face of large-scaled environmental change. Regional species pools provide a level of redundancy at large scales that may confer resilience if the capacity to migrate across the landscape persists. This concept has not been well-examined in the literature.

Defining resilience requires a temporal component that is related to disturbance frequency and recovery of the ecosystem. For most forests, we tend to consider resilience over many decades to centuries. While some existing terrestrial ecosystems seem to have persisted largely unchanged for thousands of years (Hopper and Gioia 2004), environmental change and disturbance of sufficient magnitude eventually alter all ecosystems. Resilient forest ecosystems, in response to a disturbance, follow a successional pathway that returns the ecosystem to its pre-disturbance state, at least structurally and functionally. This is particularly the case for forests dominated by small-scaled disturbances. A disturbance may be sufficiently severe to reorganize an ecosystem into a state, which in the short term (i.e., decades), may have a different resistance, but in the long term (i.e., centuries) may be equally as resilient as the original state. Furthermore, in the very long-term, the altered state of the ecosystem may simply be part of a long-term dynamical process.

Of course, ecosystems and forests are comprised of assemblages of individual species. Across regions, individual species' ranges reflect their physiological and ecological niches, with the latter reflecting the conditions where they have, among other things, a competitive advantage (Hutchinson 1958). Species with broad physiological niche requirements may be highly resilient to even significant global climate change. Likewise, species with a narrow ecological niche may be more resilient than they appear, if changed conditions provide them with an advantage at the expense of competitors. In either case, this only applies to species which have large enough gene pools and the ability to migrate. Where population sizes and genetic diversity have been reduced, and/or the mobility of species is restricted through habitat fragmentation or by natural lack of species mobility, the likelihood of successful adaptation to environmental change, such as climate change, is diminished.

2. Genetic diversity and resilience to change

While resilience can be attributed to many levels of organization of biodiversity, the genetic composition of species is the most fundamental. Molecular genetic diversity within a species, species diversity within a forested community, and community or ecosystem diversity across a landscape and bioregion represent expressions of biological diversity at different scales. The basis of all expressions of biological diversity is the genotypic variation found in populations. The individuals that comprise populations at each level

of ecological organization are subject to natural selection and contribute to the adaptive capacity or resilience of tree species and forest ecosystems (Muller-Starck et al. 2005). Diversity at each of these levels has fostered natural (and artificial) regeneration of forest ecosystems and facilitated their adaptation to dramatic climate changes that occurred during the quaternary period (review by: DeHayes et al. 2000); this diversity must be maintained in the face of anticipated changes from anthropogenic climate warming.

Genetic diversity (e.g., additive genetic variance) within a species is important because it is the basis for the natural selection of genotypes within populations and species as they respond or adapt to environmental changes (Fisher 1930, Pitelka 1988, Pease et al. 1989, Burger and Lynch 1995, Burdon and Thrall, 2001, Etterson 2004, Reusch et al. 2005, Schaberg et al. 2008). The potential for evolutionary change has been demonstrated in numerous long-term programmes based on artificial selection (Falconer 1989), and genetic strategies for reforestation in the presence of rapid climate change must focus on maintaining species diversity and genetic diversity within species (Ledig and Kitzmiller 1992). In the face of rapid environmental change, it is important to understand that the genetic diversity and adaptive capacity of forested ecosystems depends largely on in situ genetic variation within each population of a species (Bradshaw 1991). Populations exposed to a rate of environmental change exceeding the rate at which populations can adapt, or disperse, may be doomed to extinction (Lynch and Lande 1993, Burger and Lynch 1995). Genetic diversity determines the range of fundamental eco-physiological tolerances of a species. It governs inter-specific competitive interactions, which, together with dis-

persal mechanisms, constitute the fundamental determinants of potential species responses to change (Pease et al. 1989, Halpin 1997). In the past, plants have responded to dramatic changes in climate both through adaptation and migration (Davis and Shaw 2001).

The capacity for long-distance migration of plants by seed dispersal is particularly important in the event of rapid environmental change. Most, and probably all, species are capable of long-distance seed dispersal, despite morphological dispersal syndromes that would indicate morphological adaptations primarily for short-distance dispersal (Cwyner and MacDonald 1986, Higgins et al. 2003). Assessments of mean migration rates found no significant differences between wind and animal dispersed plants (Wilkinson 1997, Higgins et al. 2003). Long-distance migration can also be strongly influenced by habitat suitability (Higgins and Richardson 1999) suggesting that rapid migration may become more frequent and visible with rapid changes in habitat suitability under scenarios of rapid climate change. The discrepancy between estimated and observed migration rates during re-colonization of northern temperate forests following the retreat of glaciers can be accounted for by the underestimation of long-distance dispersal rates and events (Brunet and von Oheimb 1998, Clark 1998, Cain et al. 1998, 2000). Nevertheless, concerns persist that potential migration and adaptation rates of many tree species may not be able to keep pace with projected global warming (Davis 1989, Huntley 1991, Dyer 1995, Collingham et al. 1996, Malcolm et al. 2002). However, these models refer to fundamental niches and generally ignore the ecological interactions that also govern species distributions.



In many tropical regions such as the Caribbean, forests are adapted to periodic major disturbances by hurricanes. The resilience of these tropical forests enable their rapid recovery of structural and functional attributes. These photos of El Yunque National Forest, Puerto Rico, were taken two months after Hurricane Hugo in 1989.

One of the best approaches, when dealing with an uncertain future, is diversification because no single approach will fit all situations, and this applies also to the development of forest management strategies (Ledig and Kitzmiller 1992, Millar et al. 2007). In the biological realm, maintaining species and genetic diversity addresses the need to be prepared for whatever environmental changes might happen, and this is fundamental to the concept of resilience. Species have two main means by which they adapt to change: they can either disperse by seed or vegetative propagules in the direction of a more favourable environment, or they can change their gene frequencies to favour genotypes (genetic constitutions) that are better adapted to the changed environment (Burdon and Thrall 2001, Reusch et al. 2005). Species may also adapt through phenotypic plasticity, if their genotype entails a range of permissible responses (with respect to the species morphological, physiological, behavioural or life history strategies and traits) that are suited to the new conditions (Nussey et al. 2005).

Seed and pollen dispersal, and gene frequency changes can occur simultaneously and interact in the process of adaptation. For instance, dispersal often promotes gene flow among highly fragmented tree populations; thereby maintaining within-population levels of genetic diversity and preventing the genetic drift and loss of genetic diversity that can occur through inbreeding within small, isolated or fragmented tree populations (Hall et al. 1996, Young et al. 1996, Nason and Hamrick 1997, Cascante et al. 2002, Rajora et al. 2002, Fuchs et al. 2003, Mosseler et al. 2004, Degen et al. 2006, Clouthier et al. 2007, O'Connell et al. 2007, Farwig et al. 2008). Seed dispersal can occur through wind and water, or via animals such as birds, mammals, etc. Operational forestry experience and observations have shown that seeds can be dispersed over surprisingly long distances over relatively short time frames. Seeds of light-seeded species, such as conifers, can travel long distances from the nearest population centres (Cwynar and MacDonald 1987). Conifers with semi-serotinous cones, such as black spruce (*Picea mariana*), red pine (*Pinus resinosa*), and pitch pine (*Pinus rigida*), for example, seem particularly well adapted for such long-distance dispersal over hard-packed snow and ice. Ritchie and MacDonald (1986) have suggested that wind dispersal over snow may also explain the rapid post-glacial migration rates of conifers that have non-serotinous cones, such as white spruce (*Picea glauca*). However, long-distance seed dispersal of typically wind-dispersed conifers could also be explained through dispersal by birds

(Wilkinson 1997). Large or heavy-seeded species, such as those found in mangroves (Geng et al. 2008), and especially those in highly fragmented environments, may have greater difficulty travelling across landscapes (e.g., walnuts [*Juglans spp.*], hickories [*Carya spp.*]). Nevertheless, oaks (*Quercus spp.*) (Skellam 1951, Davis 1981) and American beech (*Fagus grandifolia*) (Bennett 1985) are capable of rapid and widespread dispersal given the presence of certain animal species.

Generally, by dispersing their seeds and pollen, forest species can maintain their genetic diversity, and hence their long-term resilience to change over space and time, by re-establishing themselves elsewhere in favourable climates. However, anthropogenic changes to landscapes and gene pools may have reduced this capacity, and population fragmentation has the potential to adversely affect the genetic and reproductive status of populations.

We are also concerned with the idea of *in situ* resilience, based on the potential for genetic adaptation, that is, the ability of a forest to maintain itself *in situ* following a disturbance, and therefore we focus more specifically on the role of genetic diversity as a factor in the capacity to adapt to a disturbance. Adaptation in the genetic or evolutionary sense, whereby gene frequencies are changed to promote successful growth and reproduction in a changed environment, has both short- and long-term components. It is important to understand the different rates at which populations respond to environmental changes. Trees are among the most genetically diverse of all organisms (Hamrick and Godt 1990) and this diversity within natural populations provides the foundation for population stability in variable environments (Gregorius 1996). This concept has been well demonstrated with respect to adaptation to potential pollutants (Pitelka 1988, Berrang et al. 1989, Scholtz et al. 1989, Bazazz et al. 1995, Kull et al. 1996, Cantin et al. 1997), to pest populations (Burdon and Thrall 2001), and to various other physiological stresses. High levels of genetic diversity within a larger, local population or gene pool of a given tree species (e.g., typical boreal or temperate biome populations) allows for a relatively rapid adaptive response to an environmental challenge. Differential survival through natural selection pressures may result in a narrowing of the gene pool to promote those genotypes best able to survive disturbances, such as toxic chemicals, pest infestations or other types of interspecific competition, climate change, or soil water and nutrient conditions. In this sense, these local populations may contain a subset of genotypes that

are 'pre-adapted' (*sensu* Davis and Shaw 2001, Jump and Penuelas 2005) to environmental changes. Using experimental populations of yellow birch (*Betula alleghaniensis*), Bazazz et al. (1995) demonstrated the potential for populations to respond to varying levels of CO₂, and the genetic complexity and magnitude of genetic responses to population factors such as density and competitive interactions. Such experiments demonstrate the overall capacity for resilience of forest tree populations to anticipated increases in CO₂ or ozone (Berrang et al. 1989; e.g., in aspen [*Populus tremuloides*]) or combinations of these gases (Kull et al. 1996) based on extant levels of genetic diversity within populations at any given time. These kinds of experiments also indicate how difficult it is to predict the way in which species will respond to anthropogenically-caused changes (Bazazz et al. 1995), or to other environmental changes in the future (DeHayes et al. 2000).

Concerns have been expressed that predicted climate changes (IPCC 2007) may occur too quickly for species to adapt (Huntley 1991, Davis and Shaw 2001, Jump and Penuelas 2005), but genetically diverse species are capable of rapid evolution (Geber and Dawson 1993). Many species have adapted to rapid changes and have done so repeatedly over geological time through dispersal and genetic changes based on the extant genetic diversity within local or regional gene pools, suggesting long-term genetic-based resilience to change. There is considerable evidence for adaptation in the geological and fossil record (Bernabo and Webb 1977, Webb 1981, Davis 1983, Huntley and Birks 1983, and review by Geber and Dawson 1993). Such adaptation has been demonstrated by forest plants during or following past glacial and interglacial episodes, which were characterized by relatively rapid climate change (Huntley and Webb 1988).

Nevertheless, a common misunderstanding persists about the nature of genetic adaptation in species with long generation times. The general perception seems to be that, given the long-generation times of many long-lived tree species, trees are at a severe disadvantage in terms of a suitably rapid response to environmental challenges. However, trees are not entirely dependent on their generation time to demonstrate an adaptive or evolutionary response, but can respond reasonably rapidly based on the inherently high levels of genetic diversity that characterize most tree species. If evolution and adaptation in species with long generation times were dependent on generation time, there would be no trees left on Earth – with the possible exception of those that have

generation times approaching those of their predators and parasites (e.g., willows, *Salix* spp.) - many of which have generation times of less than a year. Understanding this point is crucial to understanding how trees adapt and why maintaining natural levels of genetic diversity is so important.

Genetic changes to the gene pool based on the actions of natural selection on the extant genetic diversity of *in situ* gene pools can follow a relatively rapid population decline or collapse following a disturbance, such as a major pest infestation. This process can then be reinforced by a longer-term process, whereby gene frequencies change more slowly in the directions forced by natural selection over many generations of subsequent breeding and reproduction. Individuals surviving a disturbance interbreed and propagate, favouring the gene frequencies of the surviving individuals. Over time, these gene frequency changes are enhanced and refined to create a better-adapted population. However, species that have inherently low levels of natural genetic diversity may not be able to adapt to relatively sudden challenges. For example, red pine is a tree species native to eastern North America that shows extremely low levels of detectable genetic diversity (Mosseler et al. 1991, 1992, DeVerno and Mosseler 1997). Natural populations of this species are vulnerable to pest infestations and infections by fungal pathogen such as *Armillaria* spp. and *Sclerroderris lagerbergii*, which can eliminate entire populations (e.g., McLaughlin 2001).

Diversity at the genetic level must also be complemented by diversity at the species level, particularly by species groups such as pollinators (e.g., insects, bats, birds) and seed-dispersal organisms (e.g., many birds and mammals) that may affect the long-term resilience of forest ecosystems. Without these associated species groups, tree species may be restricted



Evergreen trees on a mountainside in Banff National Park, Alberta, Canada



Natural regeneration of lowland Amazonian rainforest 18 years after clearcutting. Regrowth primarily from soil seed bank and resprouting of harvested trees. Porto Trombetas, Brazil.

in their ability to adapt to change through seed dispersal, pollination, and gene flow – important processes for maintaining genetic diversity and reproductive success within populations. For example, a certain amount of gene flow among populations is required to minimize the adverse effects of inbreeding and inbreeding depression on growth, reproduction, survival, and genetic diversity in small, isolated populations of species in highly fragmented landscapes. Small, isolated populations at the margins of the geographic range may also be of special importance to the resilience of forests under climate-change scenarios because such population islands often serve as well-adapted seed sources for population migration under environmental change (Cwynar and MacDonald 1987). It can be assumed that such populations at the geographic-range margins have experienced some physiological stresses while living at the limits of their eco-physiological tolerances. Such populations may have become adapted through natural selection and some degree of genetic isolation (Garcia-Ramos and Kirkpatrick 1997) and contain special adaptations that may enhance their value as special genetic resources for adaptation and resilience to change.

3. The relationships among biodiversity, productivity and function, and resilience and stability

We review published information on the relationship between biodiversity and productivity to provide an understanding of the mechanisms that may be important to function in forests systems. Through this review, we suggest below that there is a fundamental relationship among biodiversity, production, and resilience and stability in forests and that this

relationship is important with respect to adaptive management in forests under climate change. Here we consider climate, weather conditions, soil parent material as extrinsic (exogenous) physical inputs to terrestrial ecosystems and the role of species as intrinsic (endogenous) to ecosystem functioning. There is considerable ongoing debate over the role that biodiversity plays in ecosystem function and stability owing to the highly complex nature of the relationships among species and the synergistic roles of extrinsic factors and intrinsic factors, including genetic factors, in ecosystems (see e.g., Waide et al. 1999, Kinzig et al. 2001, Loreau et al. 2002, for summary discussions). Nevertheless, in the absence of biodiversity there would be no ecosystems and no functioning. Further, there is evidence that complex forest ecosystems are more productive than less diverse ones (under the same conditions) (e.g., Phillips et al. 1994), and generally that forest systems comprised of few species are highly prone to various catastrophes including disease and invasion (Scherer-Lorenzen et al. 2005).

3.1 Theoretical background

The relationship between diversity and productivity is variable (Waide et al. 1999) and dependent on the scale considered (Chase and Leibold 2002). Much of the work done to understand the relationship between species diversity, ecosystem processes, and production has necessarily been done in highly controlled low-diversity systems at small scales, especially using grasses (e.g., Tilman and Downing 1994, Tilman et al. 1996, Hector et al. 1999, Hector 2002), or in other controlled systems (e.g., Naeem et al. 1995). Few studies have examined more connected systems with multiple trophic levels and complex production webs, such as forests, nor have they considered larger scales. While the work on simple trophic systems has, at best, limited applicability in forests, it does present theoretical predictions for what species do in ecosystems and so is briefly discussed here. In particular, two main competing hypotheses have been identified to predict the relationship between biodiversity and productivity in ecosystems: the niche complementarity hypothesis (Tilman et al. 1996, Tilman and Lehman 2001) and the sampling effect hypothesis (Aarssen 1997, Doak et al. 1998). Under either hypothesis, a certain level of saturation is expected where no more effective use of resources can be achieved regardless of increased species richness (Hooper et al. 2005).

These hypotheses are related to some earlier alternate constructs, including: the rivet hypothesis,

where individual species are suggested to perform additive roles (Ehrlich and Ehrlich 1961); the keystone hypothesis, postulating that some species are substantially more important than others in controlling productivity, and which is closely related to the redundancy hypothesis, which suggests that most species live off excess energy in the system or play minor roles in production and so are largely insignificant in ecosystem function.

The niche complementarity (or niche differentiation) hypothesis (see above) predicts that as species are added to a system, the productivity in the system will increase until vacant niches are filled because of effective partitioning of resources. The coexistence of species then is assured through interspecific differentiation as a direct response to competition for resources. If species are able to avoid competition by occupying different niches, then production in the system will increase accordingly (e.g., Tilman and Lehman 2001, Tilman et al. 2002). Niche differentiation models also consider the concept of facilitation, where one or more species may enhance the capacity of another species to survive and reproduce (e.g., ectomycorrhizal fungi on tree roots or legumes in grasslands). However, few keystone functional roles among plants are known (e.g., C3 and C4 grasses, nitrogen fixers).

A competing model, the sampling (or selection) effect hypothesis, suggests that dominant competitors (“sampled” from the regional species pool) will play the greatest roles in ecosystem functioning and as diversity increases, functioning in the system will be controlled by these dominant species because of their greater likelihood of being present in a diverse system (e.g., Aarssen 1997, Huston 1997). This result is achieved because the best competitors will always control resources within a system. Niche differentiation models predict coexistence among species, while sampling effect models predict dominance by one or a few species, especially for systems in equilibrium. Various studies suggest support for one or the other of these models (e.g., Hooper and Vitousek 1997, Tilman et al. 2002, Hooper and Dukes 2004) or suggest that the capacity to conduct the experiments has been limited by almost intractable design problems or analysis constraints (e.g., Huston 1997, Allison 1999, Schmid et al. 2002).

These two competing hypotheses will be affected by scale of observation (Waide et al. 1999) and little information is available at large scales such as forest landscapes. Chase and Leibold (2002) working with production in pond systems found productivity

declined with species richness at a local scale (unimodal) but was monotonically increasing at regional scales, but these patterns differ depending on the ecosystem type (e.g., Waide et al. 1999). Measurement of forest production will be similarly influenced by the scale of measurement. Mechanisms for different responses at small and large scales might include regional heterogeneity in environmental or edaphic conditions, different forest communities, or multiple stable states for the same forest system.

3.2 Evidence of a diversity-productivity relationship in forests

Testing the theories of the relationship between diversity, productivity, and resilience in forests is difficult owing to the inability to control either extrinsic or intrinsic variables within these complex ecosystems. Furthermore, niche partitioning is well-known in forests (e.g., Leigh et al. 2004, Pretzsch 2005), with many uncomplicated examples such as tap and diffuse rooting systems, shade tolerant and canopy species, and xeric and hydric species. Some confounding effects also affecting production in forests include successional stage, site differences, and history of management (Vila et al. 2005). Species mixtures change with successional stage in forests, from those rapidly-growing species favouring open canopy environments to those capable of reproducing and surviving in a more shaded canopy environment. Various plant species are adapted to site types that are defined by soils, topography, and moisture levels, but opportunistically may be found across a range of sites. Many forests, including most temperate forests, have undergone many direct anthropogenic-related changes and so an understanding of community structure must be in the context of the human history related to the stand.



Forest fires in wet tropical forests can overcome the resilience of the ecosystem if they occur too frequently or over very large areas

For example, long-term selection harvesting may have reduced relative abundances among tree species in a given stand, thereby altering the competitive conditions and stand production. Developing a clear understanding of the species-productivity relationship in forests must take these several factors into account, use a very broad sampling approach, and/or test the relationship experimentally to control the various factors.

Several forest studies have found a positive relationship between diversity and production in stands, while fewer have not. Of the 21 studies considered in our review (excluding studies using herbicides, thinning, fertilization, and N-fixing facilitation to eliminate confounding effects), 76% suggested a positive effect of mixed species (i.e., number of species) on ecosystem production (table 1). In plantations, the effects of mixing species can be neutral owing to competition and so the results of such experiments can be directly related to the species mixtures that were selected. On the other hand, facilitation and additive effects on mean annual increment were seen in many studies (Kelty 2006, Piotto 2008), especially in studies where an nitrogen-fixing species was included (Forrester et al. 2006, Piotto 2008)

In Costa Rica, Ewel et al. (1991) experimentally developed forest communities on burned plots. Three treatments involved various successional communities, while a fourth limited production to a sequence of monocultures. They found that the multi-species plots developed much higher soil fertility over time than did monocultures, indicating superior production and nutrient retention in complex systems. Ewel et al. (1991) also noted much greater depletion of soil nutrients in short-lived monocultures than in stands using perennial plants.

Also in Costa Rica, tree species richness was correlated to increased production in afforestation experiments by Montagnini (2000), a result also reported by Erskine et al. (2006) for Australian tropical plantations of individual and mixed species. In one of the few published studies not to report a positive relationship between production and diversity, Finn et al. (2007) found that Australian tropical plantations that had been invaded by endemic species from nearby natural forests did not result in increased production, presumably because of inter-specific competition effects. Parrotta (1999) was able to show facilitation effects in mixed plantings of tree species in experimental tropical plantations, with mixed species plots producing



Following natural or anthropogenic disturbances creating forest gaps, regeneration from soil seed banks play a critical role in recovery of biodiversity in tropical forests. Location – Porto Trombetas, Pará State, Brazil.

almost double the biomass. Pretzsch (2005) and Jones et al. (2005) provided separate examples of complementarity between tree species in long-term, simple two species mixture experiments. Vila et al. (2005) found that overall production in Catalonian open canopy forests was superior for mixed species stands than for pure stands, although individual production within the dominant species was not higher, indicating an ecosystem rather than an individual response. Schulze et al. (1996) found no evidence that mixed species had a positive effect on production in European temperate stands and Enquist and Niklas (2001) reported no relationship between plant diversity and total biomass in their stands. Using experimental tropical tree plantations, Healy et al. (2008) used redundancy analysis to suggest that diversity explained 23-30% of the variance in productivity (environmental factors explained the rest). In boreal forests, jack pine (*Pinus banksiana*) was observed to have greater diameter when growing in mixedwood stands, as opposed to in pure stands on similar sites and at the same ages (Longpré et al. 1994), suggesting a level of complementarity. Wardle et al. (1997) found a relationship between increasing plant functional diversity and forest production (including biomass accumulation) following varied fire frequency, on island systems in hemiboreal Sweden. Caspersen and Pacala (2001) found a positive relationship between carbon storage and high tree species diversity, compared to lower carbon storage in stands with low tree species diversity, across multiple types of forests.

Table 1. Summary of published studies in forests that tested the relationship between species richness and some measure of production (e.g., biomass increment, soil C, etc.).

Studies testing effects of herbicides, thinning, fertilization, and nitrogen-fixing plant facilitation were excluded. Observational refers to studies where data were gathered from existing forest stands and experimental refers to directed planting or removal experiments. See text for details of individual studies.

Effect of multiple species on stand production				
Author/year	Forest type	Observational or Experimental	Positive	Neutral
Prokopenv 1976	Boreal	Expt	X	
Ewel et al. 1991	Tropical	Expt	X	
Longpré et al. 1994	Boreal	Obs	X	
Schultze et al. 1996	Temperate	Obs		X
Wardle et al. 1997	Temperate	Expt		X
Parrotta 1999	Tropical	Expt	X	
Enquist and Niklaus 2001	Temperate	Obs		X
Casparsen and Pacala 2001	Temperate	Obs	X	
Schroth et al. 2002	Tropical	Expt	X	
Petit and Montagnini 2004	Tropical	Expt	X	
Pretsch 2004	Temperate	Expt	X	
Jones et al. 2004	Temperate	Expt	X	
Vilà et al. 2004	Temperate	Obs	X	
Erskine et al. 2006	Tropical	Expt	X	
Bristow et al. 2006	Tropical	Expt	X	
Finn et al. 2007	Tropical	Expt	X	
Kirby and Potvin 2007	Tropical	Obs		X
Healy et al. 2008	Tropical	Expt	X	
Murphy et al. 2008	Tropical	Expt		X
Piotto 2008	Meta-analysis of 14 plantation studies	Expt	X	

They concluded that forest managers should attempt to retain species diversity to increase production and especially manage for species that maximize functions of interest, such as carbon storage.

Some of the above studies are within-site types and some are across-site types. Across-site comparisons provide more variable results than do the within-site comparisons, as might be expected because larger scales include potentially confounding effects of habitat variability, range boundaries, and different climates. Depending on scale, these studies provide evidence that more diverse forests are generally more productive than forests with low species diversity. Further, many studies indicated that carbon sequestration, a frequently measured variable among the studies, is enhanced by the presence of multiple complex levels of functional groups in forests. This notion is further supported by several recent studies showing that complex old-growth forests provide high-value carbon sinks and may continue to do so for centuries in all forest biomes, unless disturbed (Phillips et al. 1998, Baker et al. 2004, Luysaert et al. 2008, Lewis et al. 2009). In only one of these cases (table 1) was the direct additive or synergistic relationship between number of species (or functional species) and ecosystem productivity quantifiable, owing to the complexity of these systems. The experimental data (table 1) all come from two-or few-species plantations, somewhat similar to the evidence from highly controlled grassland systems. Nevertheless, it is doubtful that evidence of a biodiversity-productivity relationship in forests can be derived experimentally in natural forests through removal experiments, owing to the large number of uncontrollable variables, such as site differences and tree densities.

Mechanisms of complementarity effects observed in mixed species forest stands may be nutritional, as a function of improved soil condition (e.g., Ewel et al. 1991, Brantberg et al. 2000, Hattenschwiler 2005), or related to improved partitioning of resources through different rooting patterns and depths (Schmid and Kazda 2001). While Scherer-Lorenzen et al. (2005) suggested that diversity matters less than expected with respect to its contribution to biogeochemical cycles, Hooper et al. (2005) concluded that certain combinations of species are indeed superior in terms of soil nutrient retention and production. Clearly more evidence is required to reduce the uncertainty associated with how complementarity operates in forests. Arguably these various results may support either the niche differentiation hypothesis or the sampling effect hypothesis and the evidence

supporting one over the other is sparse. However, the common theme from most studies is that diverse forests are more productive than low-richness forests and that functional diversity within systems matters considerably. The evidence broadly supports the concept that diverse forests provide more goods and services than do forests with low species richness, especially planted forest monocultures (e.g., Pearce and Moran 1994, Srivasteva and Velland 2005, Diaz et al. 2005, Dobson et al. 2006).

Many authors have advocated, and indeed demonstrated, that it is not diversity *per se* that influences production and resource dynamics but rather it is the number of functional species (or functional diversity) that is important (e.g., Phillips and Gentry 1994). While studies have indicated a link between plant species richness and ecosystem productivity (Phillips and Gentry 1994, Symstad et al. 1998, Wardle et al. 1999, Schwartz et al. 2000, Schmid et al. 2002, Tilman et al. 2002, Hector 2002), species richness and functional richness are not necessarily correlated (Diaz and Cabido 2001, Hooper et al. 2005). Certainly, some species play much greater functional roles in systems than do others (Walker 1994, Schlapfer and Schmid 1999, Chapin et al. 2000, Diaz and Cabido 2001), but species-specific functional roles may be idiosyncratic, with different key species among similar ecosystems (Phillips et al. 1994, Hooper et al. 2005). Nevertheless, most data and almost all examples in the summary by Diaz and Cabido (2001) come from manipulated controlled systems, especially relatively simple grasslands. The concept of functional diversity is compatible with either the niche complementarity or sampling effect hypotheses. Different functional types could compete for the same resource or be sufficiently dissimilar to occupy different niches within the same system.

3.2.1 Diversity-productivity relationships and forest resilience

Stone et al. (1996) concluded that more productive ecosystems are more resilient than less productive ones, and hence recover more rapidly from disturbances. Functional diversity in forests is related to production in the ecosystem (Chapin et al. 1997, Diaz and Cabido 2003), and many species in forests appear to be redundant in terms of total production (Pretzche 2005). Redundancy, which is also referred to as the insurance hypothesis (Naeem 1998, Yachi and Loreau 1999), appears to be a common and important trait in most forest systems, contributing to their resilience following

various disturbances, protecting against effects of species loss, or responding to environmental change. For example, several tree species have been lost, or substantially reduced in abundance, in temperate forest ecosystems, with little or no loss of productivity in that broad forest system (e.g., Pretzsch 2005), suggesting compensation by other species. Therefore, the redundancy provided resilience in terms of maintaining productivity in the face of species loss. Redundancy can also confer system resilience and/or resistance in response to the impact of disease and pests (see below: Jactel et al. 2005, Pautasso et al. 2005). The resilience that redundancy provides in maintaining system productivity in response to species loss, disease and pests, may not necessarily compensate for other ecosystem goods and services. For example, loss of a particular species that had specific cultural or economic importance would mean a less valuable forest (e.g., Hooper et al. 2005). Furthermore, there may not necessarily be redundancy for certain functional species, such as nitrogen-fixers, and their loss would then have consequences for ecosystem processes (Brown et al. 2001).

While the evidence above supports the notion that mixed-species forest ecosystems are more resilient than monotypic stands, some natural monotypic, or nearly monotypic, forests do occur. For example, in the boreal biome, natural stands of jack pine (*Pinus banksiana*), Scots pine (*P. sylvestris*), lodgepole pine (*P. contorta*), and Dahurian larch (*Larix gmelinii*) are commonly dominated by single species. These stands self-replace usually following fire over large landscapes, with no change in production over time. Similarly, in wet boreal systems where fire is absent, monotypic stands of a single species of fir (*Abies* spp.) occur and generally self-replace following insect-caused mortality. Generally, these monodominant boreal forest ecosystems tend to be relatively short-lived and are prone to fire or insect infestation, and so while not very resistant (relative to other forest types), they are highly resilient ecosystems despite their lack of functional types and redundancy. The high degree of seasonality in boreal forests may contribute to the resilience among boreal monotypic stands, compared to in temperate and tropical biomes (Leigh et al. 2004), where forest species richness is considerably higher (greater than an order of magnitude) than in the boreal biome. Only a few types of monodominant canopy stands are also found in temperate forest types, such as pines and eucalypts, or in tropical forests (e.g. *Gilbertiodendron* sp.).

3.3 Diversity and stability



Credit: J. Veilleux

Cloud of smoke rising from the Anгора forest fire in south Lake Tahoe, California

For a system to have resilience, the state of interest (e.g., the mature forest type) must be stable over a certain time period. Considerable research has explored the concept that species diversity enhances stability, defined as variation within defined bounds (time and space) or dynamic equilibrium, in ecosystem processes in response to environmental change (e.g., Loreau 2000, Hughes et al. 2002). The relationship between diversity and stability is complex and may resist generalization. Confusion over this issue stems from debate over whether stability refers to individual populations within ecosystems or the stability of ecosystems and their processes. For example, relatively recent work has suggested that as diversity increases, stability within individual population declines (e.g., Moffat 1996, Tilman and Lehman 2001).

Ecosystems respond to environmental change through functional compensation, or the dynamic capacity of systems to maintain production, even though levels of output among individual species may change (e.g., Loreau 2000). This concept is closely linked to that of functional redundancy in diverse ecosystems (Naeem 1998, Yachi and Loreau 1999). Dynamic responses in diverse ecosystems that maintain stability to environmental change over time may occur at genetic, species, or population levels. There appears to be low variability among ecosystem properties in response to change in diverse systems compared to those systems with low diversity, where higher variance is observed (Hooper et al. 1995, Ives et al. 1999, Lehman and Tilman 2000, Hughes et al. 2002).

Loreau et al. (2002) noted the importance of regional species richness that enables migration into systems as a means to enhance ecosystem adaptability to change over time. Immigration could enhance both genotypic and phenotypic responses to

environmental change enabling resilience in the system through compensation. Overall, the evidence is consistent with the concept that diversity enhances the stability of ecosystem processes (Hooper et al. 2005) and the flow of goods and services.

Ecosystems may exist in more than one stable state (Holling 1973), a fact supported by some experimental evidence largely from closely controlled experiments (Schroder et al. 2005). Drever et al. (2006) provided several examples of alternate stable states among the forest biomes. It seems intuitive that forest ecosystems have multiple stable states that depend on the kinds of disturbances that forests regularly undergo (Marks and Bormann 1972, Mayer and Rietkerk 2004, Schroder et al. 2005) and that many or all of these alternative states may deliver similar goods and services. For example, regeneration trajectories following wildfire differ in many forest types depending on previous disturbances, intensity of the fire, time since last fire, whether or not a fire occurs in a year with abundant tree seed, level of endemic insect infestation, age of the trees, and many other factors (Payette 1992, Little et al. 1994, Hobbs 2003, Baeza et al. 2007). While the engineering resilience may be low, in that the identical or similar species mix may not result following recovery from the disturbance, the ecological resilience is high because a forest ecosystem is restored. Lack of convergence to pre-disturbance floristic composition does not necessarily imply a lack of resilience with respect to other forest system characteristics. Rather it implies that successional patterns differ depending on circumstances but that the system is ecologically resilient, even though the dominant canopy species composition has changed along with certain ecological processes.

The capacity of an ecosystem to stay within stable bounds is related to slow processes that can move the system to another state, sometimes a state that is undesirable, from a human perspective (Scheffer and Carpenter 2003). Folke et al. (2004) suggested that biodiversity is one of those slow-changing variables that have consequences for ecosystem state, acting primarily through species with strong functional roles. The capacity of systems to maintain stability in the face of environmental change is also related to the capacity of individuals within species to meet challenges and to the possibility that other species may increase their functionality under changed regimes (biodiversity as insurance). A major factor impeding the recovery and stability of forest ecosystems is degradation and loss of functional species and reduced redundancy caused by land

use practices, including unsustainable harvesting. Degradation results in the ecosystem moving to an undesirable state that may have its own high resilience but be undesirable in terms of the reduced goods and services that it provides.

3.3.1 Diversity and invasion of ecosystems

Another measure of stability, and ultimately of resilience in the case of forest pests, is the capacity of an ecosystem to resist invasion by non-local species (i.e., community invasibility). Various factors, both extrinsic and intrinsic to an ecosystem, such as availability of niches, system degradation, and fragmentation, may affect the capacity of alien species to invade. Another factor which may promote invasion is the lack of enemies of the invading species in the new range (Williamson 1996). Most experimental evidence of a diversity-stability relationship in ecosystems again comes from highly controlled experiments using grasses, and many studies are the same as those assessing the diversity-production relationship (e.g., Tilman 1996, Levine 2000, Symstad 2000, Kennedy et al. 2002). Loreau et al. (2002) reviewed numerous studies of the relationship between resistance, diversity, and invasibility, and found that most supported a negative relationship, with the majority again in grasslands. Many of these studies have been criticized based on uncontrolled effects (e.g., Huston 1997, and see Loreau et al. 2002, Vila et al. 2005, Fridley et al. 2007 for summaries of critiques). Liao et al. (2008) conducted a meta-analysis of the effects of plant invasion into various ecosystems, including many forest systems. They found profound effects of invasion on the carbon and nitrogen-related processes in all systems, usually positive in terms of carbon sequestration rates with both positive and negative effects for nitrogen. They did not provide information about the levels of past disturbance in the systems, but for these results to have occurred, the invading species apparently occupied vacant niches, possibly made available from past disturbances. Thus evidence relating resistance to invasion success is based on the capacity of species in more diverse systems to better use and/or partition resources, compared to simple systems, where vacant niches are likely available (e.g., Elton 1958, Post and Pimm 1983, Levine et al. 2002, Hooper et al. 2005).

Invasion by non-native (alien) plant species into forests is occurring globally. Numerous examples of introduced trees invading forest ecosystems exist (Richardson 1998), suggesting that most forests are not especially resistant to invasion and that

many invading species are superior competitors to many key endemic species and/or that forest plant communities are not saturated. However, Simberloff et al. (2002) suggested that in undisturbed tropical forests, at least, invasions are rare. Lack of resistance to invasion, especially in temperate forests, may be a long-term result of a reduced number of endemic species following ice ages coupled with loss of species owing to invasive diseases anthropogenic effects, which have resulted in vacant niches (Simberloff et al. 2002, Petit et al. 2004). Some examples, among many, of successful invasions include: Norway maple (*Acer platanoides*) into eastern US deciduous forests (Webb et al. 2000) and into western US riparian zones (Reinhart et al. 2005), Monterrey pine (*Pinus radiata*) invasion into Australian eucalyptus forests (Williams and Wardle 2007), and wattles (*Acacia* spp.) invading into various South Africa forest and *fynbos* ecosystem types (Richardson and van Wilgen 2004). It should be noted that in all cited cases, the forests had been disturbed by unsustainable forest management. Sakai et al. (2001) suggested that fire and forest management reduce the capacity of forests to resist invasion, acting through fragmentation, degraded habitats, and altered moisture conditions, for example.

Generally, there have been equivocal results when the number of native plants in a system is compared to the number of introduced plant species in a system (e.g., Levine 2000, Macdonald et al. 1989, Keeley et al. 2003). The issue of invasion, however, is complicated by the level of disturbance in a given ecosystem, the extent of the undisturbed area owing to edge effects, and the scale of measurement, for example, and, as a result, deriving a general hypothesis for forests is confounded. Evidence clearly indicates that disturbed systems are more prone to invasion than undisturbed systems and that



Black wattle has become an invasive species, altering riparian forest communities in many areas, such as South Africa

diverse tropical ecosystems are not prone to invasion (e.g., Lonsdale 1999, Fridley et al. 2007).

The scale at which invasion is measured appears to complicate the pattern resulting in an invasion paradox. At small scales (i.e., m^2), there is a negative relationship between native diversity and exotics, while at large scale (i.e., $>1 km^2$) there is a positive relationship (e.g., Fridley et al. 2007). These latter authors concluded that high diversity areas also had high exotics but that a decrease in native species resulted in a consequent increase in exotics, across a wide range of ecosystems. However, at very large scales (i.e., 100s of km^2), intact diverse tropical forests support very few exotics (Sax 2001).

3.3.2 Diversity and insect pests

One type of disturbance that is universal in forests is insect herbivory. There may be an inverse relationship between insect infestation and stand diversity (Elton 1958, McCann 2000). Reviews by Gibson and Jones (1977), Barthod (1994), and Jactel et al. (2005) supported the hypothesis that monotypic stands, especially plantations, are more prone to herbivore infestations than are diverse forests. On the other hand, Powers (1999) and Gadgil and Bain (1999) noted that many non-native plantation monocultures had low incidences of pests or diseases, which they attributed to intensive management and the lack of native insect pests to attack the trees.

Natural monotypic stands are fairly common in boreal forests, suggesting that these forests, at least, are resilient to insect attack over the long term, although they may have low resistance in the short term (e.g., Porter et al. 2004). Certainly the relationship between natural old-age boreal forests, insect infestation, and forest fire has been discussed at length (Bergeron and Leduc 1998, McCullough et al. 1998). Jactel et al. (2005) used a rigorous meta-analysis procedure to indicate that the effect of invasion and herbivory was significantly higher for planted monocultures as opposed to the effect observed from mixed-species stands. Their results were positive regardless of forest biome but greatest in boreal forests. There are several likely mechanisms to explain this observation including: greater concentration of uniform food resources in monotypic stands (Karieva 1983); concealment of particular host plant species (Watt 1992) or emission of multiple chemicals (Zhang et al. 2001) in mixed stands; phenological mismatch of insect life history and bud-burst in mixed stands (Jactel

et al. 2005); increased predators and parasitoids in diverse systems (Root 1973); or possible absence of alternative hosts in monotypic stands (Jactel et al. 2005). Diverse forest landscapes (multiple types of ecosystems across a landscape) are also expected to reduce forest pest damage based on metapopulation dynamics (Pimm 1991). Similarly, Pautasso et al. (2005) suggested that the evidence broadly supports the concept that diversity of tree species in a stand reduces the susceptibility of the stand to disease. Trembling aspen (*Populus tremuloides*) has the largest range of any North American tree species, but its monotypic natural and clonal reproductive strategy make monotypic ecosystems of this tree less resilient than mixed tree species ecosystems. Large areas of aspen forest may all be connected via their integrated root system (Mitten and Grant 1996). Therefore, any root born insect or disease (e.g. *Armillaria*) could destroy an entire stand (i.e., lowered resistance), with stand regeneration hampered by the continued presence of the disease, resulting in lowered forest resilience (e.g., Brandt et al. 2003). Clearly, at stand and landscape scales, diversity can reduce the effects of damage by pests and diseases to forests, suggesting stability and resistance are a characteristic of diverse forests but lacking in planted monotypic stands.

3.3.3 Diversity and stability of processes in forests

Forests are dynamic mixtures of ecosystems over time and across landscapes. Stability of ecosystem processes in the face of disturbances may be positively related to diversity in these ecosystems (Pimm 1984, McCann 2000). Good examples come from removal experiments in soil decomposer communities that resulted in no net effects on rates of decomposition, indicating a high level of redundancy in the system (Ingham et al. 1985, Liiri et al. 2002). This is related to the disturbance or 'passengers and drivers' hypotheses, whereby certain species may assume greater functional roles under different environmental conditions (Walker 1995, Loreau et al. 2002). Brown and Ewel (1987) found support for the insurance hypothesis in tropical forest plantations, but a study by Berish and Ewel (1988) did not support a diversity effect, as measured by the production of fine roots in successional tropical forests. Hooper et al. (2005) suggested that the majority of evidence supports the notion that a range of species, which respond in different ways to changes, confer stability to ecosystem processes. Nevertheless, there is only limited evidence on the relationship between diversity and stability of production in forests.

3.4 Summary of diversity-resilience processes

In reviewing the various concepts about, and relationships between forest biodiversity and related ecosystem processes from the case-studies, we have identified a summary set of scale-related biodiversity attributes and processes that confer resilience on forests (table 2). Some of these attributes relate to theories that account for species richness, others to properties of biodiversity that emerge at particular scales. Others are natural attributes of populations or community organization and can constitute feedbacks between the biota and physical environment.

4. Resilience, biodiversity, and forest carbon dynamics

The ecosystem service of most current interest to the international community is the role of forests in carbon sequestration and storage. This section considers the questions: 1.) how important to regulating atmospheric greenhouse gases is the carbon sequestered and stored by terrestrial forest ecosystems; and 2.) in what ways does biodiversity confer resilience on this ecosystem process? To answer these questions we first provide a brief overview of the role of forests in the global carbon cycle.

4.1 Forests and the global carbon cycle

The main reservoirs of carbon are fossil fuel reserves, the atmosphere, oceans, ocean sediment, and terrestrial ecosystems. The biospheric flux and storage in terrestrial ecosystems and oceans is a highly significant component of the carbon cycle. Terrestrial ecosystems currently store about 2,400 Gt C and have an annual gross carbon exchange with the atmosphere of some 200 Gt C (IPCC 2002). About 50% of terrestrial carbon stocks reside in forest ecosystems (biomass living and dead, both above and below ground; and soil carbon) (FAO 2000, IPCC 2002), with much of the remainder in peatlands and wetlands. About half the world's forests have been converted to agriculture and other land uses (Ravindranath et al. 2008); as have substantial areas of other carbon dense ecosystem types. Therefore, given this conversion and emissions associated with degradation, the current terrestrial stock of ~2,400 Gt is possibly about 40% below the natural reservoir when at equilibrium with current climate.

Oxygenic or photosynthetically-based ecosystems have persisted on Earth for at least 2.8 billion years, and forests will continue to uptake and store carbon

Table 2. Summary of biodiversity attributes and related processes that confer resilience on a forest ecosystem

a) see text for description and examples of types; b) the scale at which the attribute or process operates, where stand, landscape, regional scales are comparable to alpha, beta, gamma diversity, respectively; c) the potential impact of climate change on the effectiveness of the characteristics and processes to confer resilience. Note that whether the impact is positive or negative for resilience will depend on the direction and magnitude of change in regional climatic conditions, particular in terms of rainfall (annual total, seasonality) and evaporation.

a) Biodiversity attribute or process	b) Spatial scale	c) Potential impact of climate change
Niche selection or differentiation	Stand	<ul style="list-style-type: none"> • Changes conditions shift outside driver species optimal conditions, making passenger species more competitive • Changed conditions produce new niches
Functional complementarity	Stand	<ul style="list-style-type: none"> • Loss of historic synergies and development of new ones with changing climatic stress
Functional diversity	Stand	<ul style="list-style-type: none"> • Loss of historic diversity and development of new ones with changing climatic stress, some ‘passengers’ become ‘drivers’
Adaptive selection	Stand	<ul style="list-style-type: none"> • Changed environmental stresses could be too rapid for natural adaptive selection to occur
Phenotypic plasticity	Stand	<ul style="list-style-type: none"> • Changed conditions induce structural changes in dominant canopy species
Microevolution	Stand/ landscape	<ul style="list-style-type: none"> • Driver species evolve new adaptive traits that enable them to remain competitive in face of changed conditions
Microhabitat buffering	Stand/ landscape	<ul style="list-style-type: none"> • Changes in canopy density from new climatic conditions alters environmental conditions for ground-dwelling fauna habitats
Source habitats	Landscape/ Regional	<ul style="list-style-type: none"> • Changed climate may disrupt viability of historic source habitats or make them more productive
Refugia habitats	Landscape/ Regional	<ul style="list-style-type: none"> • Under new climatic conditions, previously common habitat becomes reduced to a network of locations where topography provides microhabitat buffering, and populations can persist
Regional species pool	Regional	<ul style="list-style-type: none"> • Migration from source habitats may not be able to keep pace with rapidly changing climate
Synergistic interactions	Stand/ landscape/	<ul style="list-style-type: none"> • Unknown interaction of stress on ecosystem resilience are likely but difficult to predict

so long as there is adequate water and solar radiation for photosynthesis; even though the genetic and taxonomic composition of forest ecosystems changes over time (Des Marais 2000). In the past, increase in the size of the terrestrial buffer has occurred naturally as a negative feedback response to increasing CO₂ levels and associated global warming and wetting (there is ~5% increase in global rainfall for every 10K degree increase temperature) (Zhang et al. 2007).

Humans are forcing the global carbon cycle into disequilibrium by increasing the atmospheric pool of greenhouse gases at a faster rate than it can be reduced by removal of CO₂ through natural processes. About 70% of the additional CO₂ in the atmosphere is the result of burning fossil fuel while 30% is from land conversion. Currently, emissions from deforestation are estimated to contribute ~17% of annual anthropogenic emissions (IPCC 2007).

The lifetime of the airborne fraction of a CO₂ pulse is surprisingly long; about 300 years for 75%, with the remaining 25% continuing to interact with the climate system for thousands of years (Archer et al. 2009). The exchange of carbon between the atmosphere and both terrestrial ecosystems and the ocean provides a vital buffering capacity that reduces atmospheric CO₂ concentrations. The residency time of carbon in long-lived trees and non-labile forms of soil carbon ($1 \times 10^2 - 10^4$; e.g. Roxburgh et al. 2006a, 2006b) is sufficiently long to enable forests to have a significant regulatory influence on the global carbon cycle. Furthermore, the less carbon there is stored in forests, the more there is circulating through the atmospheric-ocean exchanges and the sooner the ocean's buffering capacity is exceeded.

The significance of the forest carbon reservoir is such that protecting the current stock of carbon in forests and other natural ecosystems is necessary, along with deep cuts in fossil fuel emissions, if total global anthropogenic emissions are to be reduced to a level that avoids dangerous climate change (Cramer et al. 2001, Lewis 2006). Given the significance of the forest carbon stock, the increasing disruptions to it from human land-use activities, and the prospects for climate change impacts, there is special interest in the role that biodiversity has in conferring resilience on forest-carbon dynamics and on the stability of forest carbon stocks.

4.2 Biodiversity and resilience of forest-carbon dynamics

At the global scale, the role of biodiversity in the

resilience of forest-carbon dynamics is evidenced by the specialized species that have evolved and characterize the distinctive forest ecosystems found in the major climatic and forest domains – tropical, temperate, and boreal (Figure 1). Over time, evolution results in new plant traits, which through the filter of natural selection, and aided by ecological processes such as dispersal, result in forests comprising species that function optimally under the climatic conditions and disturbance regimes prevalent in each domain.

Forest-carbon dynamics (the rate of fluxes and the stock resulting from net carbon exchanges) are driven by the climatic inputs which govern the rates of photosynthesis and respiration/decay. Rates of photosynthesis scale with increasing water availability, so long as thermal and radiation regimes are sufficient to support plant growth. Holding wetness constant results in respiration-decomposition rates scaling with temperature; generally, the rate of biochemical processes doubles with every degree Celsius. Differences in the chemical and physical characteristics of substrates also influence growth rates due to locally-scaled variations in sub-surface water availability and soil parent material mineral nutrient status (Law et al. 2002, Chambers et al. 2000).

At the level of biome recognized by the IPCC, major differences occur in forest carbon dynamics (Table 3). Tropical forests have the least dead and soil biomass carbon because of higher respiration and turnover rates associated with increasing temperature, while boreal have the converse (note that the Table 3 default biome values represent spatial averages). Particular forest ecosystems can store significantly more carbon in both living and dead biomass as the result of local conditions, and carbon stocks can be low due to the impacts of land-use history (Keith et al. 2009).

Tropical forests have higher levels of biodiversity than temperate and boreal forests. Various hypotheses have been proposed to explain this diversity, including the metabolic theory of ecology (Brown et al. 2004), neutral theory, Hubbell (2005), and landscape heterogeneity (Ruokolainen et al. 2005); all of which probably contribute in some way to the overall understanding. Stand-level (alpha diversity) richness of tree species is between 100-300 in tropical forests, with regional (gamma) species richness of 4,000+ (Ruokolainen et al. 2005). Geographic variation in tropical forest biodiversity has been shown to be correlated with

climatic, substrate and topographic gradients, indicating species distributions to some extent reflect environmental optima (Condit et al. 2005, Mackey 1994, Schneider and Williams 2005). Such high levels of species richness at all spatial scales means that many of the biodiversity-related processes detailed in table 2 operate in a powerful way in tropical forests, especially niche selection, functional complementarity, and functional diversity.

Micro-habitat buffering plays a critical role in all forests but perhaps reaches its strongest expression in tropical forests (Kennedy 1997, Malhi et al. 2009). Primary tropical forests create a microclimate that virtually eliminates the probability of fire, whereas secondary growth forests in the eastern Amazon area were found to burn after 8 to 10 rainless days (Uhl and Kauffman 1990). The synergistic effects of biodiversity on primary productivity are also most evident in primary tropical forests with respect to nutrient cycling. Many tropical forests naturally form on nutrient-poor substrates. However, these ecosystems have developed through natural selection such that they can harvest from rainwater the nutrients lacking in the soils. Furthermore, through retention and recycling they build up the stock of nutrients needed to support the high levels of plant growth enabled by moist tropical climates. Plants have special adaptations that serve to conserve nutrients and a myriad of other fungal, bacterial and animal species aid in their efficient and rapid recycling (Golley 1983). Overall, biodiversity-related processes serve to

increase the productivity and resilience of carbon dynamics in tropical forests.

The role of biodiversity in conferring resilience to forest-carbon dynamics varies between climatic domains, and climate change will alter forest-carbon dynamics with respect to rates of both photosynthesis and respiration-decay, and thus carbon stocks. However, whether total ecosystem carbon increases or decreases, or whether there are changes in the size of living biomass, dead biomass and soil carbon, will depend on (1) the magnitude of increase in temperature and (2) the direction and magnitude of change in climatic wetness (i.e., rainfall minus evaporation). While regional trends in temperature can be projected with reasonable reliability, there is greater uncertainty around wetness. Projected regional changes in climatic wetness are highly variable and for many regions models differ in the direction of change (IPCC 2007, Lim and Roderick 2009). However, models suggest significant regional-scaled impacts are likely (Malhi et al. 2009).

In summary, within a given biome, diverse forests are more biologically productive and provide larger and more reliable carbon stocks, especially in old-age stable forest systems (see table 1 and associated text above). Hence, protecting and restoring biodiversity serves to maintain resilience in forests, in time and space, and their ongoing capacity to reliably sequester and store carbon. Carbon sequestration is an ecosystem service that provides a vital contribution to climate change mitigation and this service can be enhanced by maintaining ecosystem resilience in space and time.

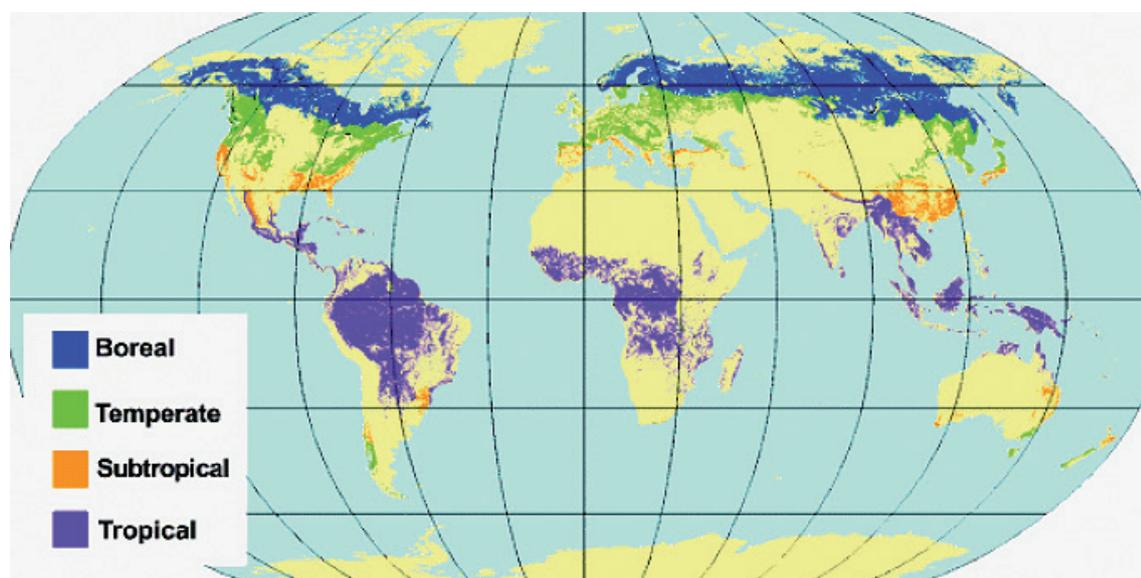


Figure 1. Distribution of the world's forests by major ecological zone. Source: FAO 2001, Figure 1-4.

Table 3. Default biomass carbon values for major forest biomes, exclusive of soil carbon.

Source: Adapted from Keith et al. (in press, 2009) and compiled from IPCC (2006, 2003).

	Climate region	Aboveground living biomass carbon (tC ha⁻¹) biome default values	Root+dead biomass carbon (tC ha⁻¹) biome default values	Total living+dead biomass carbon (tC ha⁻¹) biome default values
Tropical	Tropical wet	146	67	213
	Tropical moist	112	30	142
	Tropical dry	73	32	105
	Tropical montane	71	60	112
Sub-tropical	Warm temperate moist	108	63	171
	Warm temperate dry	75	65	140
	Warm temperate montane	69	63	132
Temperate	Cool temperate moist	155	78	233
	Cool temperate dry	59	62	121
	Cool temperate montane	61	63	124
Boreal	Boreal moist	24	75	99
	Boreal dry	8	52	60
	Boreal montane	21	55	76

5. Case-studies of forest resilience and comparisons under climate change by forest biome

Forests are all variously driven by disturbances, whether the disturbance is in the form of minor blowdown events at a scale of <1 ha or landscape-altering wildfires affecting hundreds of thousands of hectares. Species that occur in these systems must necessarily be adapted to such changes because they recur over time and space and individual species adaptations to disturbance types are legion. Some forest ecosystems that have been disturbed by humans may exhibit engineering resilience, or equilibrium dynamics, to the disturbances under many conditions in all forest biomes (Attiwill 1994, Drever et al. 2006, Phillips et al. 2006, Norden et al. 2009). However, any ecosystem may change states when disturbed by a novel and/or severe disturbance, under altered interval time between disturbances, or with multiple simultaneous disturbances. Climate change may present such a serious challenge to the resilience of forest ecosystems globally.

Concentrations of atmospheric CO₂ have been rising for >150 years (IPCC 2007) largely as a result of fossil fuel burning (IPCC 2007). In addition to reducing anthropogenic CO₂ emissions, land managers are assessing the potential to increase forest carbon sequestration and storage as a mitigation strategy. In theory, improvements in ecosystem management should allow forests to sequester more CO₂ as the forest growth rate improves, and thus help to mitigate anthropogenic CO₂ emissions.

Biological processes accelerate as air temperature increases. Increases in tree respiration and metabolism can shorten leaf retention time as temperature increases. Litter decomposition, soil nitrogen mineralization, and soil nitrification also increase with increasing temperature (Mellio et al. 1982), so climate change could significantly affect all of the biological functions of forests. Increased air temperature is projected to increase fire risk and return interval (Dale et al. 2001). Episodic drought will favour more drought tolerant species over more water demanding ones (Dale et al. 2001). Even if a forest remains intact (albeit with possible changes in the mix of dominant species), many functional aspects of the forest and its goods and services are likely to change. As the spatial scale increases, the potential for climate change alterations in ecosystem structure and function increases. Therefore, changes in water use and yield, and carbon storage in some

sites, stands or even watersheds may be highly resilient to climate change, while bio/ecoregionally these processes will almost assuredly be less resilient.

Below we consider a set of case-studies that examine the resilience of a sample of the world's forests. We have selected the case-studies by major forest biome and assess resilience to current climate and the normal disturbances in the system, and follow this for each by assessing the changes that are predicted to occur as a result of climate change. These studies, in one way or another, reflect the amount of change and the capacity of the ecosystem biodiversity to maintain the system in the face of predicted effects of climate change.

5.1 Boreal forest biome

The circumpolar boreal biome occurs across North America, Europe and Asia and has 33% of the Earth's forested area. Boreal forests are characterized by a small number of common tree species, any of which may dominate over a vast area (Mooney et al. 1996). Annual temperature ranges from -5 to 5°C with annual precipitation ranging from 300-1500 mm. The mean maximum of the warmest month is 10°C. Forests in the boreal biome are relatively young, assembling after the quaternary ice ages, and so may be <7000 years old (Liu 1990). Boreal forests are primarily driven by disturbance at landscape scales where, depending on the moisture conditions, fire interval ranges from 50-500+ years (Johnson 1992, Li 2000) and several major insect pests are chronic to regularly epidemic (Drever et al. 2006, Soja et al. 2007). As a result, boreal forests are highly ecologically resilient under current conditions because the species in these systems are adapted to recover following regular disturbances (niche selection, table 2). In North America, between 0.5 and 2% of the overall boreal landscape burns annually in wildfires of various sizes and intensities (Johnson 1992).

5.1.1 Climate change and boreal forest resilience

The boreal forest biome is predicted to undergo the greatest increase in temperature under climate change scenarios (IPCC 2007). Using global climate change scenarios 'growth' (>+4-5°C) and 'stable' (+2-3°C), Fischlin et al. (2009) and Sitch et al. (2003), reported predicted broad gains northward for boreal forest distribution, although with conversion of boreal forests to temperate forests and grasslands at southern and central areas of Canada and Russia. Soja et al. (2007) summarized

published predicted changes for the boreal forest as: increased fire, increased infestation, northward expansion, and altered stand composition and structure. To that list we add reduced old-growth forest and conversion to grasslands and steppe of southern-central dry forests (Thompson et al. 1998, Price and Scott 2006). Warming climate has been implicated as a cause for current extensive outbreaks of mountain pine beetle (*Dendroctonus ponderosae*) in western Canada and the USA (Taylor et al. 2006). Productivity is expected to rise, but net carbon losses are likely to occur before the end of the century, owing to increased disturbances and higher rate of respiration (Kurz et al. 2008). However, significant stocks of biomass and soil carbon will remain. The net exchange and resultant standing stock will depend on, among other things, changes in fire regimes and forest management activities (Chen et al. 2008). Some areas of the boreal forest are predicted to become wetter and others drier, with consequently more or less fire (Johnson 1992, Bergeron and Flannigan 1995, Kellomaki et al. 2008). Generally fire frequency has been predicted to increase in the boreal biome (Flannigan et al. 1998) and evidence has accumulated confirming this prediction in North America and Russia (Gillette et al. 2004, Soja et al. 2007). Our first case-study on lodgepole pine (*Pinus contorta*) reflects that prediction (table 4).

5.1.2 Case-study: western North American lodgepole pine

Lodgepole pine forests are a self-replacing, fire-driven ecosystems (Brown 1975) and climate change is generally predicted to reduce the fire interval over much of their distribution (Flannigan et al. 2005). However, ecosystem models suggest that stands may remain as carbon sinks even under increased fire regimes, in part because of the increase in production in response to temperature, but also depending on the model selected and the climate change regime that is modelled (Kashian et al. 2006, Smithwick et al. 2009). Insect infestation, notably mountain pine beetle (*Dendroctonus ponderosae*) can significantly alter the dynamic influence of fire, to the point of being the dominant factor responsible for stand renewal over huge landscapes (Logan and Powell 2001), and the combination of fires and insect infestation may lead to new forest states (Shore et al. 2006). If the insect-killed stands do not burn, then a large amount of carbon would enter the detrital pool. In lodgepole pine forests, the impact of climate change on carbon stocks may be marginal depending on infesta-



Lodgepole pine (*Pinus contorta*) killed by the mountain pine beetle (in red) in British Columbia, Canada

tion levels and this forest ecosystem may be resilient during at least the next 50-100 years.

5.1.3 Case study: North American boreal mixedwoods

A second boreal case-study is from a moister ecosystem where fire has an influence but the fire regime is much more protracted, resulting in broad expanses of mixed species (hardwood and softwood) forests (table 5). Here, the relatively large number of species, relative to many other boreal types, appears to increase the resilience of these forests (Girard et al. 2008). However, even in these more moist systems, fire frequency is predicted to increase by 50-80% in boreal mixedwoods in the next 50+ years, in North America (Krawchuk et al. 2009). Under a high disturbance regime, carbon stocks in mixedwood forests are predicted to be about 16-50% or more of current stocks, depending on location (Price et al. 1999, Bhatti et al. 2001, Ni, 2002, Yarie and Parton 2005). These forests will still provide habitat and most of the same goods and services, but they will most likely change states in response to the increased disturbance regime. While the case-study presented is from central Canada, in Finland, increased moisture and elevated temperatures are expected to result in an increase in production and carbon sequestration (Kellomaki et al. 2008).

5.2 Temperate forest biome

Temperate deciduous forests can be found across central-western and eastern North America, central and western Europe, and northern Asia. These forests have a four distinct seasons, and a growing season lasting 150-200 days. The continental climate is subject to a wide range of air temperature variation (i.e. 30°C to -30°C), and annual precipitation of 750

Table 4. A case study of expected forest resilience in boreal lodgepole pine (*Pinus contorta*) forests of western North America under current climate (A) and expected under climate change (B).

Numbers refer to time (yrs) to recover from disturbance (i.e., resilience). A zero suggests that the forest will only recover to a new state and/or not recover the attribute in question.

Biome: Boreal

Ecosystem: Boreal lodgepole pine forest ecosystem

A. Current Climate

Natural disturbance regimes:

(a) Fire - stand replacing fires <100 years, 200 -100,000 ha

(b) Epidemic insect infestations.

Resilience to natural disturbance or sustainable forest management:

Resilient at ≤ 50 yrs, ≤100 yrs, >100 yrs, 0=not resilient (state change)	Spatial scale		
	Attributes that are indicators of system change	Site/stand (species and structures)	Landscape and/or wa- tershed (stand mixtures and age structure)
Dominant canopy spe- cies	≤100	≤100	Resilient
Stand structure (canopy height + density; layers)	≤50	>100	Resilient
Ecosystem services			
1. Total carbon	≤50	Resilient	Resilient
2. Water	≤50	≤50	Resistant
3. Habitat	≤100	Resilient	Resilient

B. Expected under Climate Change

Natural disturbance regimes: Fire - stand replacing fires <50 years, 200-500,000 ha

Resilience is relative to the 2000 expectation

Resilient by ≤ 50 yrs, ≤100 yrs, >100 yrs, 0= not resilient (state change)	Spatial scale		
	Attributes that are indicators of system change	Site/stand	Landscape and/or watershed
Dominant canopy spe- cies	≤50	≤50	≤ 50
Stand structure (canopy height + density; layers)	0	0	0
Ecosystem services			
1. Total carbon	≤50 (+9 to -37% of original C stocks)	≤50	≤50
2. Water	≤ 50	≤ 50	≤ 50
3. Habitat	≤100	≤100	≤100

Table 5. A case-study of expected forest resilience in boreal mixedwoods forests of central Canada, under current climate (A) and expected under climate change (B).

Numbers refer to time (yrs) to recover from disturbance (i.e., resilience). A zero suggests that the forest will only recover to a new state and/or not recover the attribute in question.

Biome: Boreal

Ecosystem: Boreal upland mixedwood forest ecosystem, central Canada

A. Current Climate

Natural disturbance regimes:

a) Fire - stand replacing fires >100 years, 200 -100,000 ha

b) Epidemic insect infestations on conifer component

Resilience to natural disturbance or sustainable forest management:

Resilient at ≤ 50 yrs, ≤100 yrs, >100 yrs, 0=not resilient (state change)	Spatial scale		
	Attributes that are indicators of system change	Site/stand (species and structures)	Landscape and/or wa- tershed (stand mixtures and age structure)
Dominant canopy spe- cies	>100	>100	Resilient
Stand structure (canopy height + density; layers)	>100	>100	Resilient
Ecosystem services			
1. Total carbon	>100	Resilient	Resilient
2. Water	≤ 50	≤ 50	Resistant
3. Habitat	>100	Resilient	Resilient

B. Expected Climate

Natural disturbance regimes: Fire - stand replacing fires <100 years, 200-500,000 ha

Resilience is relative to the 2000 expectation.

Resilient by ≤ 50 yrs, ≤100 yrs, >100 yrs, 0= not resilient (state change)	Spatial scale		
	Attributes that are indicators of system change	Site/stand	Landscape and/or watershed
Dominant canopy spe- cies	≤ 50	≤ 50	≤ 50
Stand structure (canopy height + density; layers)	0	0	0
Ecosystem services			
1. Total carbon	0 (ca. 50% of original C stocks)	0	0
2. Water	≤ 50	≤ 50	resilient
3. Habitat	0 (50% of original habi- tat values)	0	0

to 2500 mm is evenly distributed during the year) (Whittaker 1970). While these conditions typify much of the temperate forest region, some areas of the temperate forest region have less distinct seasons, more or less rain, and less variation in annual air temperatures. Temperate forests generally have a high number of dominant tree species compared to the tropics (many species with few that dominate) or boreal forests (few species and most can dominate) (Mooney et al. 1996). The high number of dominant species is a significant factor contributing to resilience in temperate forests.

Goods and services from temperate forests are important in large part owing to the large number of people living in close proximity to these forests. Clean water, wood products, and recreation opportunities have been some of the primary products from temperate forests. While these goods and services remain important, forest carbon sequestration is a newly valued service that these forests provide, in the wake of increasing atmospheric CO₂ levels and global warming. Major ecosystem perturbations can significantly and often negatively alter an ecosystem's productivity capacity and affect the flows of goods and services.

5.2.1 Temperate forests and environmental stressors

History is replete with both naturally- and anthropogenically-induced disturbances leading to an altered re-stabilization of forest processes at a different and often lower state (i.e., less timber productivity, less water demand, less biodiversity). Natural climatic change has previously caused some forest areas to become more or less productive over time. For example, 6,000 years before present (BP), the Northern Chad region of the Sahara was a tropical rain forest, but over the course of <4,000 years these forest areas were completely converted to desert (Kröpelin et al. 2008).

Over the past 4,000 years, climate change, unsustainable forest use, and land clearing has led to significant changes in global temperate forest cover. The Caledonian forests of Scotland originally may have covered as much as 1.5 million ha. However climate change (4,500 BP), and probably land clearing (starting ca. 4,000 BP) removed the vast majority of this forest type, and the forests have never recovered. Forest vegetation is only now beginning to return to some of these areas following changes in land management practices over 150 years ago (Hobbs 2009). The resilience of a forest

is a function of the absolute ability of the forest to recover from a wide range of environmental stresses and disturbances. From the previous examples, it is clear that forest resilience can be overcome and that not all forest types or tree species recover equally well to all forms and combinations of stressors. Under a changing climate, some stress and combinations of stressors, such as temperature and drought, may become more or less common or severe over time.

5.2.2 Case-study: Moist evergreen temperate forests

Moist evergreen temperate forests, as their name suggests, occur at the wetter end of the temperate forest climatic domain, with total annual rainfall of 1,000mm+. In addition to southeastern Australia, moist temperate forests are also found on the Pacific coast of North America, Chile, and New Zealand. While taxonomic composition differs among these forests due to their evolutionary biogeography, they share similar levels of biodiversity, climatic conditions, rates of primary productivity and respiration, and thus comparable forest-carbon dynamics. They are the most carbon-dense forests on Earth, having larger living and dead biomass stocks compared even to tropical forests, even though they are far more fire prone than tropical forests (Keith et al 2009).

While Australian moist temperate evergreen forests experience shorter mean fire intervals than tropical forests, they are among the most resilient to fire of any ecosystem type (table 6). The canopies of these forests are dominated by the *Eucalyptus* genus. Most eucalypt species are highly resistant to fire and can rapidly regenerate leaves from stem and branch epicormic growth. A few species, in particular, *E. regnans*, which dominate certain tall wet forests in south-eastern Australia, will die if their entire canopy is scorched but then shed seeds that germinate in the post-fire ash beds. A long evolutionary history means that these forests are dominated by species that are optimal for prevailing environmental conditions, and the relatively high levels of tree species richness (there are >700 *Eucalyptus* species), along with networks of relictual and refugia habitats, provide a rich regional pool of species that can potentially fill new niches under changing change.

Most temperate forests are expected to continue increasing their carbon sequestration for at least the next two decades (e.g. Fischlin et al. 2009). Models predict continuing trends of modestly increasing forest productivity in eastern North America and

western Europe over the next century (Field et al. 2007, Alcamo et al. 2007, Alo et al. 2008). Regional declines in forest productivity have also been seen in some areas of temperate forests due primarily to limitations of water related to recent droughts in Australia (Pitman et al. 2007) and in western North America (Breshears et al. 2005).

As the drier regions of the temperate domain covering semi-arid to subhumid climates in regions adjacent to the subtropical domain continue to experience more droughts, productivity is expected to decrease in those forests. However, as noted earlier, regional-scale prediction of changes in future climatic wetness come with a high degree of uncertainty, in many cases, about even the direction of change.

Biological processes accelerate as air temperature increases. Increases in tree respiration and metabolism can shorten leaf retention time as temperature increases. Litter decomposition, soil nitrogen mineralization, and soil nitrification also increase with increasing temperature (Mellio et al. 1982). Therefore, climate change could significantly affect the biological function of temperate forests. Increased air temperature is projected to increase fire risk and return interval (Dale et al. 2001). Episodic drought will favor more drought tolerant temperate species over more water demanding ones (Dale et al. 2001). The wide geographic range of the temperate forest types will provide a large selection of species that can adapt to changing environmental conditions.

However, even if a temperate forest remains intact (albeit with a possible changes in the mix of dominant species), many functional aspects of the forest and its goods and services are likely to change. For example, some areas of this biome are projected to receive reduced annual and or growing-season precipitation (IPCC 2007). Although, precipitation may still be sufficient to allow for the continued existence of most of the tree species that were present before the onset of anthropogenically induced climate change, there may be insufficient soil moisture to maintain the current species density. As trees die, the gaps created may not be filled or be filled more slowly than has historically occurred. A reduction in stand leaf area would (all other factors being equal), reduces forest evapotranspiration, and increases water yield from the forest (Lu et al. 2005, Sun et al. 2005). Additionally, increases in atmospheric CO₂ concentrations may further improve forest water use efficiency offsetting some of the water yield

reductions that would be associated with reduced precipitation (McNulty and Swank 1995).

Water is one of the principle determinants of ecosystem type. Average annual precipitation in temperate forests ranges from 500 to 2500 mm per year (Whittaker 1970). Millennia of plant competition have favored vegetative species that best adapt to limited resources (including water). Short-term (i.e., <2 years) drought can cause reduced ecosystem productivity (Hanson and Weltzin 2000) and reduced leaf area (Gholz 1990). Long-term (i.e., >2 years) droughts can cause additional ecosystem disruptions. Long-term droughts have all of the characteristics of short-term drought (described above) plus the potential for tree mortality due to water stress (Kloppel 2003), increased insect outbreak potential (McNulty and Boggs, In press), and increased fire risk (Flannigan and Wotton 2001). A shift in the either insect species, insect or fire return interval, or severity could shift competitive advantages among temperate tree species and thus make some species and forest types less resistant.

5.2.3 Case-study: southern Europe

Southern European forests tend to be dry and driven over the long term by fire and over the short term by blowdown (Schelhaas et al. 2003). As climates warm, the prediction is for fire to increase in some of these forests, especially in the Mediterranean area (Milne and Ouijen 2005, Dios et al. 2007). As a result, Morales et al. (2007) suggested that there will be a net loss of forest area and of total carbon from these systems. As the forests burn, more will likely change states to savannahs or grasslands suggesting little habitat resilience. Similarly, Lindroth et al. (2009) suggested that increasing blowdown will reduce overall production in temperate forests.

Although temperate deciduous forests are the most widely distributed of the temperate forest type, there are other temperate forest types such as the Mediterranean Forest. While high moisture characterizes many areas of the temperate forest biome, the Mediterranean area is an especially dry temperate system as illustrated in the following case-study (table 7). Like moist conifer forests, Mediterranean forests have a dry period during the summer months. However, Mediterranean forests are more similar to dry conifer forests with regard to total annual precipitation. The combination of precipitation is concentrated in winter, and totals <1000 mm per year (Whittaker, 1972).

Table 6. A case-study in moist temperate forests of Australia under current and expected climate regimes.

Numbers refer to time (yrs) to recover from disturbance (i.e., resilience). A zero suggests that the forest will only recover to a new state and/or not recover the attribute in question.

Biome: Temperate

Ecosystem: Mountain Ash forest, Victoria, Australia

Climate scenario: Current climatic conditions

Natural disturbance regimes: a) Intense tree killing fire frequency 75-150 years

b) Annual area burnt up to 70,000 ha (Mackey et al. 2002)

Resilience is relative to the 2000 expectation

Resilient by ≤ 50 yrs, ≤ 100 yrs, >100 yrs, 0=not resilient (state change)

Attributes that are indicators of system change	Spatial scale		
	Site/stand	Landscape and/or watershed	Bio(eco)region
Dominant canopy species	Resilient if intense fire frequency $>20 < 400$ years ^a	80% catchment remains <i>E. regnans</i> if mean intense fire interval 26-290 years	Resilient
Stand structure (canopy height + density; layers)	Resilient if mean interval of all fires (not just intense tree killing fires) ~ 50 assuming ~ 35 trees survive fires	Resilient	Resilient
Ecosystem services			
1. Total carbon Keith et al. (2009)	Around 90% of total carbon can remain after an intense fire, but significant amount of biomass carbon will be moved from living to dead biomass pools	Resilient	Resilient
2. Water Australian Government (1994)	(not a site-level processes)	Decreasing water flows for ~ 30 follow in intense fire; after 130 years water flow returns to pre-disturbance state ^b	Resilient because of patchiness in fire regimes at bioregional scale
3. Habitat	Maximum habitat value obtained if mean intense-fire interval $>150-250$ years ^c	Resilient due to network of fire refugia (areas burnt less intensely or frequently) enabling persistence of habitat resources	Resilient

^a Reproductive age of *E. regnans*

^b High rates of transpiration by dense regeneration reduces catchment water flow

^c Large number of hollow-dependent vertebrate fauna and habitat hollows do not start forming in *E. regnans* until trees are $\sim 120-150$ years old

Potential climate change impacts on Ash forests: The Mountain Ash forests which are the focus of this case-study are located about 120km N.E. of the city of Melbourne, the capital of the Australian State of Victoria. These forests are located in a region called the Central Highlands of Victoria. In general terms, under high emission growth scenarios, this region's climate is expected to change by 2070 as follows: the greatest increases in temperature will occur in summer (3°C warmer); the greatest decreases in rainfall are expected in spring (21% decrease); there will likely be few rainy days (-19%) but increasing rainfall intensity (+4.5%); and runoff into the major river systems is expected to decrease by around 50%. Mackey et al. (2002) showed that, whilst the empirical relations are tenuous, FFDI and annual area burnt in this region scale with daily 3 p.m. temperature and annual rainfall respectively. The projected climate change for the Central Highlands will therefore likely alter fire regimes, all other factors being equal. Reductions in the mean fire interval as the result of increasing temperatures and dryness may therefore cause, over the course of time, changes in the forest composition towards more fire-tolerant cohorts of other *Euclayptus* species such as Messmate (*Euclayptus obliqua*); with subsequent changes in the abundance of tree hollows, carbon dynamics and water flow.

Long summer droughts predispose the region to fires so the forests of Aleppo pine (*Pinus halepensis*), stone pine (*P. pinea*), maritime pine (*P. pinaster*), Corsican pine (*P. nigra*), and Turkish pine (*P. brutia*) are all fire adapted species, meaning that they usually require fire for reproductive success (i.e., cone opening). Additionally, these pines have very high concentrations of resin and therefore burn readily when fires occur. While intense fires will kill the mature pines, they may also kill other tree species, and thus provide both needed nutrients (via the ash and substrate created) and reduced competition for limited water supply for the emerging pine seedlings. The eucalypt (*Eucalyptus regnans* and *E. delegatensis*) of Australia use a similar survival strategy.

As an alternative survival mechanism, the evergreen sclerophyll oaks (e.g., holm oak (*Quercus ilex*), cork oak (*Q. suber*, *Q. coccifera*) have developed morphological traits that reduce their susceptibility to wildfire (i.e., increased resistance as opposed to increased resilience). The thick bark of cork oak protects the cambial layer from moderate intensity fires, increasing the probability of tree survival. If the fire is sufficiently intense to burn the above-ground vegetation, dormant buds will be activated and regenerate new shoots and sprouts following the fire.

As in dry coniferous forests, increased air temperature could lead to increasing wildfire severity and occurrence. However, unlike those of the dry coniferous forests, the tree species of the Mediterranean forests have two alternative survival strategies. The pine species may become competitively disadvantaged compared to the oak species if fire reoccurrence intervals do not allow for the regeneration of reproductive age pines. Alternatively, the oaks have both a primary (i.e., thick bark) and a secondary (stump sprouting) survival mechanism. Therefore, the oak species may be more resilient than the pine species to a change in the fire regime.

The oaks and pines of the Mediterranean forest type are well-adapted to these harsh environmental conditions and are historically resilient to disturbance (table 7). The slow growth rates require a longer time for these forests to return to a pre-disturbance productivity or carbon state, but the ecosystem is ecologically stable. Climate change will likely increase the severity of environmental conditions in these forests. As the environment changes, so may ecosystem resilience. These forests have evolved under very harsh conditions, and in that sense, they

are adapted to cope with some additional stress from climate change. However, there are limits to even ecological resilience. Mediterranean deciduous forests will unlikely be able to maintain their current stand structure, and total carbon sequestration and storage potential owing to increased drought and fire, and it is likely that these forests may change states considerably under climate change (table 7).

5.2.4 Case-study: eastern North American deciduous forests

During the first decade of the twentieth Century, the chestnut blight fungus (*Cryphonectria parasitica*) was introduced to the eastern USA and Canada. Prior to the introduction, American chestnut (*Castanea dentata*) was a dominant tree species in North American temperate deciduous forests ecosystems (Douglass and Severeid 2003). However, over the course of a few decades, virtually all of the stands with mature chestnuts were killed. The blight largely affects older trees, so chestnut is still present across much of its former range but was reduced to an understory tree (i.e., shrub/sapling). Even as the chestnut was being removed as a major ecosystem component, oaks (*Quercus* spp.), maples (*Acer* spp.), ashes (*Fraxinus* spp.), and other species were filling the gaps left by the chestnuts. *Fraxinus* sp., *Quercus* sp., *Carya* sp., and *Acer* sp. all have wide natural ranges and each is highly adaptable to individual site conditions. These forests regenerated quickly following the disturbance, and over time, tree species replacement within the stand filled the functional role of lost species, suggesting high engineering resilience. Additionally, these forests exist within a relatively stable climate zone, not prone to extremes in temperature or precipitation. Adequate moisture reduces the reoccurrence interval for wildfire (Westerling et al. 2006). The combination of moderate climate tolerance and functional overlap of many dominant species explains why North American temperate deciduous forests are so resilient. At the stand and watershed levels, most stand attributes and ecosystem services return to pre-disturbance conditions within 50 years (table 8).

Xiao et al. (2008) estimated that the temperate forests in the USA sequestered 200 to 800 grams of carbon per square metre per year, amounting to a total carbon uptake of 0.51 to 0.70 petagrams (Pg) per year from 2001-2006. The variation in inter-annual carbon sequestration is a function of variable growing conditions and disturbance impacts (Xiao et al. 2008), in part because releases of carbon from

Table 7. Case-study of temperate Mediterranean forest resiliency under current climate (A) and expected under climate change (B).

Numbers refer to time (yrs) to recover from disturbance (i.e., resilience). A zero suggests that the forest will only recover to a new state and/or not recover the attribute in question.

Biome: Temperate

Ecosystem: Mediterranean forest

A. Current Climate

Natural disturbance regimes:

- a) Fire - stand replacing fires > 100 years, 200-10,000 ha
- b) Wind <100 ha

Resilient at ≤ 50 yrs, ≤100 yrs, >100 yrs, 0=not resilient (state change)	Spatial scale		
	Attributes that are indicators of system change	Site/stand (species and structures)	Landscape and/or wa- tershed (stand mixtures and age structure)
Dominant canopy spe- cies	>100	>100	Resilient
Stand structure (canopy height + density; layers)	>100	>100	Resilient
Ecosystem services			
1. Total carbon	>100	Resilient	Resilient
2. Water	≤ 50	≤ 50	Resilient
3. Habitat	≥100	Resilient	Resilient

B. Expected Climate

Natural disturbance regimes:

- a) Fire - stand replacing fires < 100 years, 200- 20,000 ha
- b) Wind <100 ha

Resilient by ≤ 50 yrs, ≤100 yrs, >100 yrs, 0= not resilient (state change)	Spatial scale		
	Attributes that are indicators of system change	Site/stand	Landscape and/or watershed
Dominant canopy spe- cies	0	0	0
Stand structure (canopy height + density; layers)	>100	>100	0
Ecosystem services			
1. Total carbon	0	0	0
2. Water	<50	<50	<50
3. Habitat	0	0	0

wildfires and hurricanes can significantly affect long-term carbon budgets. Felzer et al. (2005), predicted that future climate variability, CO₂ fertilization, nitrogen deposition, and ozone pollution would enhance plant growth in temperate ecosystems and increase carbon sequestration. However, other studies have suggested that increasing extreme climate events and disturbances are likely to more than offset such fertilization effects in the USA (McNulty 2002), and actually exert a positive feedback to the climate (Gruber et al. 2004). Temperate deciduous forests should continue to provide most of the same goods and services under climate change as currently, although the state, especially the species composition, will be altered (e.g., Fischlin et al. 2009), suggesting at least ecological resilience.

5.3 Tropical forests

Tropical forests are found between 25°N and 25°S and cover an area of about 17.5 million km² (Fischlin et al. 2007). Tropical forests are characterized by high alpha diversity, with few highly dominant species, especially in rainforests (Mooney et al. 1996). These forests range from wet to dry and include evergreen rainforests, tropical seasonal drought-deciduous forests (moist savannahs), and tropical dry forests (dry savannahs). Rainforests are characterized by an annual mean temperature above 24°C and ≥ 2.5 m/yr regular precipitation during the year, while other tropical forests remain above 15.5°C throughout the year (Prentice et al. 1992). Precipitation in rainforests is at least twice the potential evapotranspiration (Fischlin et al. 2007). Nevertheless, not all rainforests receive the same precipitation, with African forests being considerably drier than many parts of the Amazon, for example. Even within the Amazon basin, there exist gradients in precipitation. Tropical seasonal forests receive most of their rainfall during a wet season and have a ratio of precipitation to potential evapotranspiration between 2 and 1. Seasonal forests are found in tropical monsoon regions or other seasonal tropical wet-dry climate zones and are moist deciduous, i.e., the trees shed their leaves in the dry season. Tropical dry forests are characterized by a precipitation to potential evapotranspiration ratio < 1 (Fischlin et al. 2007, 2009). Tropical forests are found in Australia, Asia, Africa, and South/Central America.

Tropical forests provide a wide range of goods and services, many of which are of global significance. In particular, rainforests are estimated to support the highest biodiversity of all terrestrial ecosystems (e.g. Gentry 1992, Leigh et al. 2004), including

an estimated half of terrestrial and 25% of global biodiversity (Myers et al. 2000). This biodiversity provides a vast array of goods and services to people (e.g. Fearnside 1999), including shelter, food, and fuel in local communities. Tropical forests contribute 30% of the global net primary production (Field et al. 1998). A key service provided by tropical forests is globally significant climate regulation and production of oxygen. For example, the Amazon rainforest alone is suggested to produce about 20% of the global oxygen (Hakoum and Souza 2007). Tropical forests regulate continent-wide climates by sustaining higher precipitation levels compared to regions without a forest canopy (e.g. Laurance and Williamson 2001, Betts et al. 2004, Malhi et al. 2008). Primary tropical forests are a significant global carbon sink and the rate is currently increasing (Lewis et al. 2009). In the Amazon, the above-ground carbon sequestered has increased by an estimated at 0.5 to 0.8 Pg C/yr (Phillips et al. 2008) and for African tropical forests, the increase is estimated to be 0.34 Pg C/yr. The mean total sequestered for all tropical forests is currently about 1.3 Pg C/yr (Lewis et al. 2009). Malhi et al. (2008) found that intact primary tropical forests provide the best carbon sink, compared to second-growth or fragmented tropical forest stands. This carbon sink is dramatically altered by land-clearing for agriculture and plantation forests, which sequester and maintain far less carbon than primary forests (e.g., Cramer et al. 2004, Malhi et al. 2008, Lewis et al. 2009). Furthermore, Bunker et al. (2005) suggested that tropical forests depleted of species will have much lower carbon storage capacity than the original forests.

5.3.1 Climate change and tropical forest resilience

Most evidence suggests that tropical forests may not be resilient to climate change over the long term, primarily owing to a predicted reduction in rainfall and increased drought (IPCC 2007, Malhi et al. 2009). In the short term, evidence suggests a positive effect of CO₂ fertilization on tropical forest production as a result of present climate change (Boisvenue and Running 2006, Lewis et al. 2009), although importantly this has involved some changes in species composition, indicating resilience to current change. Future capacity of these forests to maintain this service is highly uncertain (Cramer et al. 2004) as a result of altered moisture regimes possibly leading to increased fire and drought (e.g., Malhi et al. 2009). Loss of tropical forests will have consequences for global hydrology, among other consequences of global relevance (Fischlin et al. 2009).

Table 8. A case-study of forest resilience in temperate deciduous forests under current climate (A) and expected under climate change (B).

Numbers refer to time (yrs) to recover from disturbance (i.e., resilience). A zero suggests that the forest will only recover to a new state and/or not recover the attribute in question.

Biome: Temperate

Ecosystem: North American Deciduous Forest

A. Current Climate

Natural disturbance regimes:

a) Fire - stand replacing fires >100 years, 200 -10,000 ha

b) Wind – blowdown events annual single tree to 10,000 ha (related to disease)

Resilience to natural disturbance or SFM:

Resilient at ≤ 50 yrs, ≤100 yrs, >100 yrs, 0=not resilient (state change)	Spatial scale		
	Attributes that are indicators of system change	Site/stand (species and structures)	Landscape and/or wa- tershed (stand mixtures and age structure)
Dominant canopy spe- cies	>100	>100	Resilient
Stand structure (canopy height + density; layers)	>100	>100	Resilient
Ecosystem services			
1. Total carbon	>100	Resilient	Resilient
2. Water	≤ 50	≤ 50	Resistant
3. Habitat	>100	Resilient	Resilient

B. Expected Climate

Natural disturbance regimes:

a) Fire - stand replacing fires <500 years, 200-20,000 ha

b) Blowdown, storms, drought, herbivory (especially invasive species)

Resilience is relative to the 2000 expectation

Resilient by ≤ 50 yrs, ≤100 yrs, >100 yrs, 0= not resilient (state change)	Spatial scale		
	Attributes that are indicators of system change	Site/stand	Landscape and/or watershed
Dominant canopy spe- cies	>100	>100	0
Stand structure (canopy height + density; layers)	>100	>100	Resilient
Ecosystem services			
1. Total carbon	0	0	0
2. Water	≤50	≤50	Resilient
3. Habitat	>100	Resilient	Resilient

There is considerable evidence that climate change may lead to large losses in biodiversity in all tropical forests (e.g. Bazzaz 1998, Miles et al. 2004, Possingham and Wilson 2005, Rull and Vegas-Vilarrubia 2006, Fitzherbert et al. 2008, Malhi et al. 2008), with consequent effects on the flow of goods and services from these forests. This will be especially true for montane and cloud forests, owing to a lack of surrogate habitats for species, and where evidence of biodiversity loss has already accumulated (Bunker et al. 2005, Rull and Vegas-Vilarrubia 2006, Colwell 2008). Wilson and Agnew (1992) provided an example of permanent regime shift in tropical cloud forests following unsustainable harvesting that resulted in a negative feedback involving the needed condensation moisture for remaining trees to survive; climate drying would have an identical effect. Tropical forests are at a substantial risk for biodiversity loss under climate change for several reasons including disruptions to complex ecosystem dynamics, the high degree of specialization and narrow niches for many tropical species, and because climate change will exacerbate an already high rate of deforestation (Bazzaz 1998). Large-scale loss of biodiversity will have dramatic negative effects on carbon sequestration capacity by tropical forests (Cramer et al. 2004, Fischlin et al. 2009).

5.3.2 Case-study: Amazon rain forest

The Amazon rain forest is an extensive forest system about as large as the United States occurring in eight South American countries. It contains many forest types, depending on soils, topography, and climate, but there is a large area of evergreen forest with little seasonality where 200-900 cm of rain falls annually. These forests are highly resilient to the chronic disturbances of herbivory and blowdown typical of the region (table 9). However, land-clearing and logging had reduced the original extent of the Amazon forest by 15% by 2003 (Soares-Filho et al. 2006). Recent occasional drought episodes have exacerbated the human impacts by increasing forest fires (Malhi et al. 2008). Climate change is predicted to have long-term effects on forest structure and function by changing the mortality and growth rates of trees and increase the frequency of disturbances, especially an increasing fire frequency under a drier climate regime (Malhi et al. 2008, Phillips et al. 2008). Increased carbon dioxide concentrations seem to be having a direct positive impact on the productivity and relative competitive success among tropical plant species (Baker et al. 2004, Malhi et al. 2009).

Modelling global warming of $>3^{\circ}\text{C}$, as expected in tropical areas, reduces the tropical forest sink by mid-century, and results in a net carbon source towards the end of this century (Scholze et al. 2006, Fischlin et al. 2009). The most likely impact of climate change on Amazon forests will be drought and the development of seasonality in the rainforest (Malhi et al. 2009, Phillips et al. 2009), although models are far from certain in their prediction of rainfall. The predicted decreased rainfall and ground moisture will increase the likelihood of fire and shift the rainforest into drier seasonal forest. This process has a positive feedback owing to the loss the rainforest canopy that otherwise tends to maintain regional moisture levels (Laurance and Williamson 2001). As a result, much of the rainforest will change states to drier and possibly more open forests, reducing habitats, lowering regional water supplies, and becoming a far less productive forest (Malhi et al. 2009, Cochrane and Barber 2009). Climate change will exacerbate the many negative effects of ongoing deforestation and forest loss (Laurance 1998, Cook and Vizy 2008, Cochrane and Barber 2009), and the forests will be considerably different than at present.

5.4 Summary among forest biomes

All forest types will undergo some change as a result of altered climate conditions; some of these changes are already occurring but widespread change is expected over the next 50-100 years (e.g., Alcamo et al. 2007, Fischlin et al. 2009). From the case-studies, it is clear that some forests are considerably more vulnerable (less resilient) than others as a result of altered disturbance regimes that are predicted under climate change. This is especially the case for forests where previously rarely-seen disturbances will become more common, such as fire in rainforests. In some cases, even ecological resilience will be overcome and forests are expected to change states to non-forest or savannah (IPCC 2007), as has happened in many areas previously, such as the northern Sahara area of Africa (Kröpelin et al. 2008). In many cases, forests will change states, however, at least among most boreal and some temperate forests, ecological resilience is expected. In many tropical forests, however, many rainforests may become dry tropical forests with reduced carbon storage capacity (case-studies, Fischlin et al. 2009). The diversity in these tropical regions suggests that some form of forest will continue to exist even with severe disturbance, but that many of the functions will change owing to the lack of resilience and new states, in general, will produce considerably less goods and services while supporting less biodiversity than at present.

Table 9. Amazon rain forest resiliency under current climate (A) and expected under climate change (B).

Numbers refer to time (yrs) to recover from disturbance (i.e., resilience). A zero suggests that the forest will only recover to a new state and/or not recover the attribute in question.

Biome: Tropical

Ecosystem: Amazon rain forest ecosystem

A. Current Climate

Natural disturbance regimes: a) Wind – up to 10,000 ha; events infrequent
b) Herbivory

Resilient at ≤ 50 yrs, ≤100 yrs, >100 yrs, 0=not resilient (state change)	Spatial scale		
	Attributes that are indicators of system change	Site/stand (species and structures)	Landscape and/or wa- tershed (stand mixtures and age structure)
Dominant canopy spe- cies	<50	<50	Resilient
Stand structure (canopy height + density; layers)	>50	>50	Resilient
Ecosystem services			
1. Total carbon	<50	Resilient	Resilient
2. Water	≤50	≤50	Resilient
3. Habitat	<50	Resilient	Resilient

B. Expected Climate

Natural disturbance regimes: a) Fire - stand replacing fires <50 years, 200-20,000 ha
b) Drought - common
c) Wind – up to 10,000 ha; events more frequent
d) Increased herbivory

Resilience is relative to the 2000 expectation

Resilient by ≤ 50 yrs, ≤100 yrs, >100 yrs, 0= not resilient (state change)	Spatial scale		
	Attributes that are indicators of system change	Site/stand	Landscape and/or watershed
Dominant canopy spe- cies	0	0	0
Stand structure (canopy height + density; layers)	0	0	0
Ecosystem services			
1. Total carbon	0	0	0
2. Water	0	0	0
3. Habitat	0	0	0

6. Conclusions and ecological principles

The biodiversity in a forest is linked to and underpins the ecosystem's productivity, resilience, and stability over time and space. Biodiversity increases the long-term resilience and resistance of forest ecosystem states, increases their primary production, and enhances ecosystem stability at all scales. While not all species play important functional roles in ecosystems, many do, and we may not know or understand the role of a given species. Further, under changed environmental conditions, species with previously minimal functional responsibilities may become highly functional. The persistence of these functional groups within ecosystems is essential for ecosystem functioning and resilience. Capacity for resilience and ecosystem stability is required to maintain essential ecosystem goods and services over space and time. Loss of resilience may be caused by the loss of functional groups, environmental change such as climate change, or alteration of natural disturbance regimes (Folke et al. 2004). Loss of resilience results in a regime shift, often to a state of the ecosystem that is undesirable and irreversible. Resilience needs to be viewed as the capacity of natural systems to self-repair based on their biodiversity, hence the loss of biodiversity could mean a reduction of that capacity. This review, together with those of Loreau et al. (2001), Hooper et al. (2005), and Drever et al. (2006), suggested strong support for the following concepts specific to forest ecosystems and their resilience:

1. Resilience is an emergent ecosystem property conferred at multiple scales by the biodiversity in the forest system. More specifically, forest resilience is related to genetic diversity, functional species diversity, and ecosystem diversity (beta diversity) across a forest landscape and over time (table 2).
2. Most natural forests are highly resilient ecosystems, adapted to various kinds of perturbations and disturbance regimes; but if disturbance exceeds the capacity of the forest to recover (forest degradation owing to human use, for example, which reduces functional components), the system will recover to a different state that may or may not also be highly resilient, but which is unlikely to provide the former level of goods and services.
3. Complex forest ecosystems are generally more productive and provide more goods and services than those with low species richness. Productive forests dominated by mature trees are generally

highly stable ecosystems.

4. There is niche differentiation among some tree species in a forest, as well as competition, leading to complexity and variability within and among forest ecosystems and their processes. Some of this variability is caused by small local changes in site conditions across a forest.
5. Redundancy of functional species is common in complex forest ecosystems and is directly related to ecosystem resilience. Redundancy provides insurance against changing environmental conditions, and species with limited functions under one set of conditions may become driver species under an altered set of conditions.
6. Diverse forest systems are more stable (within defined bounds) than less diverse systems and this is partly related to a robust regional species pool and the beta diversity among ecosystems.
7. Nevertheless, even high diversity is no guarantee for ecosystem resilience once climate conditions move beyond those experienced by most of the component species.
8. Although a forest may change states in response to disturbances, the flow of goods and services may not necessarily be highly altered, suggesting that the ecosystem is ecologically resilient, even though the forest community structure may have changed. Ecological resilience is unlikely, however, in a system that has low redundancy, such as degraded forests.
9. There is a negative relationship between species diversity, landscape diversity, and the capacity of a forest system to be invaded, especially by pests and diseases.
10. Not all forest ecosystems are equally resilient to disturbances, including climate change. Effects of climate change will vary in forests depending on biome, tree species composition, natural disturbance regime, and moisture, temperature and edaphic responses to climate change.
11. Resilience is necessary to maintain desirable ecosystem states under variable environmental conditions.

6.1 Ecological principles to foster forest ecosystem resilience and stability under climate change

Forests have a capacity to resist environmental change owing to their multiple species and complex multiple processes. However, a reduction in biodiversity in forest systems has clear implications for the functioning of the system and the amounts of goods and services that these systems are able to produce. While it is relatively simple to plant trees and produce a short-term wood crop, the lack of diversity at all levels (i.e., gene, species of flora and fauna, and landscape) in these systems reduces resilience, degrades the provision of goods and services that the system can provide, and renders it vulnerable to catastrophic disturbance.

Specifically, with respect to mitigating CO₂ emissions from deforestation and degradation, maintaining long-term stable forest ecosystems will be critical, as opposed to for example, rapidly growing simple low diversity forests that have limited longevity, resistance, resilience or adaptive capacity. Further, the application of ecological sustainability principles in the recovery of degraded forests to redevelop their resilience and their former goods and services will provide part of a long-term approach to mitigating and adapting to climate change (e.g., Lamb et al. 2005, Innes et al. 2009). Hence, maintaining resilience in forests, in time and space, is important to maintain their function as an important “buffer” in the global carbon cycle by maximizing their potential to sequester and store carbon; along with the ongoing capacity to provide the other goods and services that humans require. To this end, human use of forests will need to change in order to ensure their conservation, sustainable use, and restoration.

In managed forests, it is imperative that biodiversity and ecosystem resilience be maintained. The principles of sustainable forest management are to maintain ecosystem processes by matching management practices to natural processes (or expected processes, modified under climate change) at multiple scales (e.g., Attiwill 1994, Perera et al. 2004). Restoration of degraded forest landscapes can take advantage of the linkage between biodiversity and ecosystem resilience, by planting to enhance species richness and through the addition of functional species (e.g., N-fixing species) where known (see: Lamb et al. 2005, Brockerhoff et al. 2008, for management recommendations). Various options for policies and measures are available to promote forest conservation and biodiversity, particularly at landscape and regional scales, in addition to conventional protected areas, including payments for land stewardship and ecosystem services (USDA 2007), connectivity conservation

programmes (Crooks and Sanjayan 2006), and schemes built around recognition of Indigenous and traditional lands (Australian Government 2007).

The capacity to conserve, sustainably use and restore forests rests on our understanding and interpretation of pattern and process at several scales, the recognition of thresholds, and the ability to translate knowledge into appropriate management actions in an adaptive manner (Frelich and Reich 1998, Gauthier et al. 2008). Caring for forests in ways that maintain their diversity and resilience is being made even more complex owing to climate change (e.g., Chapin et al. 2007, Kellomaki et al. 2008). We suggest the following as ecological principles that can be employed to maintain and enhance long-term forest resilience, especially under climate change (e.g., Thompson et al. 2002, Fischer et al. 2006, Millar et al. 2007, Innes et al. 2009):

1. Maintain genetic diversity in forests through practices that do not select only certain trees for harvesting based on site, growth rate, or form, or practices that depend only on certain genotypes (clones) for planting (see e.g., Schaberg et al. 2008).
2. Maintain stand and landscape structural complexity using natural forests as models and benchmarks.
3. Maintain connectivity across forest landscapes by reducing fragmentation, recovering lost habitats (forest types), and expanding protected area networks (see 8. below).
4. Maintain functional diversity (and redundancy) and eliminate conversion of diverse natural forests to monotypic or reduced species plantations.
5. Reduce non-natural competition by controlling invasive species and reduce reliance on non-native tree crop species for plantation, afforestation, or reforestation projects.
6. Reduce the possibility of negative outcomes by apportioning some areas of assisted regeneration with trees from regional provenances and from climates of the same region that approximate expected conditions in the future.
7. Maintain biodiversity at all scales (stand, landscape, bioregional) and of all elements (genetic, species, community) and by taking specific actions including protecting isolated or disjunct populations of organisms, populations at margins

of their distributions, source habitats and refugia networks. These populations are the most likely to represent pre-adapted gene pools for responding to climate change and could form core populations as conditions change.

8. Ensure that there are national and regional networks of scientifically designed, comprehensive, adequate, and representative protected areas (Margules and Pressey 2000). Build these networks into national and regional planning for large-scale landscape connectivity.

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