Biodiversity, ecosystem thresholds, resilience and forest degradation

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Following certain ecological principles in management of forests can enhance longterm forest resilience and aid adaptation to climate change.

orests comprise multiple ecosystems associated with variance in edaphic and microclimatic conditions across broad landscapes. The composition and nature of forest ecosystems vary over time, depending on natural disturbances and changes to the climate regime. However, they remain more or less the same within the bounds of natural variation (see Figure), referred to as a stable state. In a stable state, a forest can produce a range of associated goods and services that humans value.

Biodiversity underpins most forest ecosystem goods and services, and many tropical forests, in particular, maintain high levels of biodiversity. Loss of biodiversity may have considerable negative consequences for the productive capacity of forests (e.g. Thompson et al., 2009; Bridgeland et al., 2010; Cardinale et al., 2011) and for the provision of goods and services. Therefore, because forest degradation can be defined as the loss of the ability of a forest to produce the goods and services that are expected (e.g. FAO, 2009), the loss of biodiversity is a key criterion for measuring forest degradation. Conserving biodiversity is a cornerstone of sustainable forest management (e.g. Montreal Process, 2009) and a key to maintaining forest ecosystem functioning.

This article explores the ways in which forests maintain their stable states over time and outlines what happens when disturbances overwhelm the natural mechanisms of recovery. It describes how sustainable management of forests, including the conservation of biodiversity, is key to supporting a forest's recovery mechanisms, and presents ecological principles that can be applied to forest management.

RESILIENCE AND RESISTANCE Definitions

An important characteristic of forests is their resilience, which is the capacity to recover following major disturbances



or thresholds, in ecosystems

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(e.g. Gunderson, 2000). Under most natural disturbance regimes, forests maintain their resilience over time. Forest resilience is an emergent ecosystem property resulting from biodiversity at multiple scales, from genetic to landscape diversity (Thompson *et al.*,2009). To sustain the goods and services that humans derive from forests, forest ecosystems must recover after disturbances and not become degraded over time.

Related to the concept of resilience is resistance, which is the capacity of a forest to resist minor disturbances over time, such as the death of a few trees or a chronic level of herbivory by insects. Forests are generally stable and change little as a result of noncatastrophic disturbances. Minor changes are mitigated, such as when canopy gaps created by the death of individual or small groups of trees are quickly filled by new young trees. Forests may also be resistant to certain environmental changes, such as weather patterns over time, owing to redundancy among the functional species (redundancy refers to the overlap or duplication in ecological functions performed by a group of species; see Mechanisms) (e.g. Díaz and Cabido, 2001).

Ecosystems may be highly resilient but have low resistance to a given disturbance. For example, many boreal forests are not especially resistant to fire, but they are highly resilient to it and usually recover fully over a number of years. Generally, most natural forests, especially primary old forests, are both resilient and resistant to various kinds of changes. Loss of resilience may be

Hardwood forest composed primarily of trembling aspen in the boreal forest of northern Canada. Forests may not be particularly resistant to certain disturbances to which they are resilient

caused by the loss of functional groups (see Mechanisms and Tipping points) resulting from environmental changes such as large-scale climate change, poor forest management or a sufficiently large or continual alteration of natural disturbance regimes (Folke *et al.*, 2004).

Mechanisms

There is strong evidence that forest resilience is tied to the biodiversity that normally occurs in the ecosystem (e.g. Folke et al., 2004; Thompson et al., 2009). In particular, certain species and groups of species perform key functions in forests and so are essential for the forest to maintain all of its functional processes (Díaz and Cabido, 2001). For example, bird predation can maintain low abundances of insects in a forest, reducing the possibility of catastrophic levels of insect herbivory of trees, and thus increasing tree productivity (e.g. Bridgeland et al., 2010). Pollinators, including some insects, bats and birds, are also excellent examples of highly functional species in ecosystems, and without them, many plants could not reproduce. Forest resilience depends,

in large part, on these key species and the functions that they perform redeveloping as a forest recovers following disturbances, including forest management interventions.

At a genetic level, the capacity for resilience comes from the ability of a species to persist over a range of environmental variability, such as by tolerating a range of temperatures or a certain level of drought. At the species level, there are various behavioural and functional responses that can assist a species to repopulate a disturbed area or respond to environmental changes. Further, ecosystem assembly processes very much reflect the landscape pool of available species (e.g. Tylianakis et al., 2008), as well as landscape connectivity. At the landscape scale, heterogeneity among forest patches can provide a measure of redundancy among species and a source for colonizers that, as a forest begins to redevelop or recover after disturbance, should enable communities to converge on the original forest types. Hence, the consideration of resilience necessarily involves thinking from small to large scales.



Degraded juniper (Juniperus thurifera) forest in the High Atlas, Morocco

Loss of resilience and forest degradation

An ecosystem state is defined by the dominant floristic (tree) composition and stand structure expected for a given stand. A change in forest state results from a loss of resilience, with a partial or complete shift to a different ecosystem type from what is expected for that area. Such changes in state result in a reduction in the production of goods and services. Therefore, "change in ecosystem state" can be used as an indicator of degradation. For example, if a forest is expected to be of mixed species but is instead dominated by only a few species, or if it should be a closed canopy forest but is actually open or savannah, then the state has changed. These would be considered negative changes in state, as they degrade the forest, from a biodiversity perspective and from a production perspective, and would generally affect the level of goods and services available.

Often, the degradation of forests results from the use of poor harvesting techniques over a period of time. However, forests can also become degraded for many reasons not involving logging. For example, forests may appear intact but be missing most large animal species as a result of over-hunting (e.g. Redford, 1992). As a result, there could be longterm consequences for forest health because of increased insect herbivory resulting from a lack of control by predators, or reduced seed dispersal, functions that the missing animals might have performed. Another example of degradation might be the successful establishment of an invasive species that out-competed endemic species, thereby constraining the goods available from the ecosystem.

In any of the cases described, if changes are severe enough to cause a change in state, the extent to which the forest



has been degraded can be determined through remote sensing. Using satellite data, Souza *et al.* (2003) mapped forest in the Amazon region of Brazil that had been excessively burned or heavily logged and burned, and Strand *et al.* (2007) reported on several cases in which remote sensing was used for monitoring forests affected by invasive tree species and insects from several regions of the world.

TIPPING POINTS

Forests may not always recover after severe and protracted disturbances. Thresholds exist for populations of individual species and for individual processes within ecosystems, and ultimately for the ecosystems themselves. The point at which the ecosystem loses its capacity to recover, or at which its resilience and integrity are lost, is referred to as a tipping point, or an ecological threshold. If there is too much disturbance, a cascade of effects with marked changes to the forest ecosystem will result, ultimately moving the forest to a new state. For example, severe drought and fire can convert a dry forest type to a savannah or even into grassland. Most often, the new state will provide a lower level of products and services to humans.

Tipping points can be reached rapidly or as a result of chronic change that wears away the capacity of an ecosystem to recover, such as through the gradual attrition of species over time. For example, forest fragmentation is a process that opens up continuous forests through multiple disturbances. A forest can readily tolerate some loss of spatial continuity and still maintain its species and functions, but studies suggest that certain levels of fragmentation are actually tipping points, with a resulting loss of forest biodiversity and function and a reduced capacity to produce goods and services (e.g. Andrén, 1994; Arroyo-Rodríguez et al., 2007).

Ecosystems can be used and harvested for services, but the derivation of those services cannot exceed sustainable levels, nor can goods be removed in a manner that destroys ecosystem processes (Figure). Once a tipping point is reached, changes to the ecosystem are large and nonlinear, often unpredictable, and usually dramatic (e.g. Scheffer and Carpenter, 2003). For example, parts of northern Africa underwent a rather spectacular change from dry forest to desert as a result of past climate change (Kröpelin *et al.*, 2008). Unfortunately, we often only recognize a tipping point once it has already been



Eastern Himalaya mountains, India. Biodiversity underpins forest resilience and is a key consideration for forest managers

reached and the generally negative consequences to the ecosystem have become obvious. Therefore, to manage a forest sustainably requires learning to identify possible tipping points in advance.

Climate change considerations

Superimposed on many other humancaused impacts on forest ecosystems is global climate change, which adds uncertainty to the identification of tipping points. Climate has a major influence on rates of respiration, production and other forest processes, acting through temperature, radiative forcing (increase in energy remaining in the atmosphere) and moisture regimes, over medium and long time periods. Climate and weather conditions also directly influence shorter-term processes in forests, such as wildfires, herbivory and species migration. As the global climate changes, forest ecosystems will change because the physiological tolerances of some species may be exceeded and the rates of many biophysical forest processes will be altered (e.g. Scholze *et al.*, 2006). Most studies suggest that many tropical forests may not be resilient to climate change over the long term, if the current and predicted trend continues, with reduced rainfall and increased drought (e.g. Betts, Sanderson and Woodward, 2008; Malhi *et al.*, 2008).

Forest ecosystems are composed of distinct assemblages of species. Across regions, the ranges of individual species reflect their physiological and ecological niches, which, in turn, reflect where environmental conditions are advantageous. Species with broad physiological tolerances may be highly resilient to even significant global climate change. Likewise, species with apparently narrow ecological niches might be more resilient than they appear, if changed conditions provide them with an advantage at the expense of competitors. In either of these two potential situations, this capacity would apply to species that have large and variable enough gene pools to adapt and the ability to migrate. However, for many species this is not the case. Where population size and/or genetic diversity have been reduced, or the mobility of species is restricted through habitat loss and fragmentation or is naturally low, successful autonomous adaptation to environmental change becomes less likely. Populations may be doomed to extinction if exposed to a rate of environmental change exceeding the rate at which they can adapt, or the rate at which individuals can disperse (e.g. Schwartz et al., 2006).

Most of the emphasis in negotiations on global climate change concerning forests has been on how to manage forests to mitigate climate change. Adaptation to climate change has received less attention. Adaptation of forests to climate change is primarily about maintaining forest resilience even if the ecosystem type may change. If ecosystems do change, there must be an understanding of how to respond through forest management. In most cases, some forms of active management will be necessary to enable forests to adapt to climate change. Maintaining forest resilience can be an important mechanism both to mitigate and to adapt to climate change.

MANAGING FORESTS TO AVOID TIPPING POINTS

Sustainable forest management is ecosystem management of forests that, in large part, has an underlying objective to enable the natural resilience to continue. One of a forest manager's main tasks is to help forests recover after harvesting of timber or other products, through sustaining the properties of the ecosystem over the long term. In recent years this task has become more complicated through the additional stress of climate change on terrestrial ecosystems. While proper, biologically sound sustainable forest management is a major part of maintaining forest resilience, response to climate change requires additional planning and actions. If we understand ecosystems better and can accurately predict at what level of use thresholds might exist, the management of forest goods and services can be more benign.

Maintaining biodiversity

Maintaining biodiversity is a key to maintaining forest resilience and avoiding tipping points. The biological diversity of a forest is linked to and underpins the ecosystem's productivity, resilience, resistance, and its stability over time and space. A reduction in biodiversity in forest systems has clear, often negative, implications for the functioning of the systems and the amounts of goods and services that these systems are able to produce.

Understanding how biodiversity supports local forest resilience and resistance provides important clues to improve forest management. For example, while it is relatively simple to plant trees and produce a short-term wood crop, it is much more difficult to recover a forest ecosystem. The lack of diversity at all levels (gene, species of flora and fauna, and landscape) in simple plantation forests reduces resilience and resistance to disturbances, degrades the provision of services and many goods that the system can provide and renders it vulnerable to catastrophic disturbance. Through the application of ecological forest management principles, forest plantations can provide much more than just a wood crop, and forest ecosystems can be restored at the same time that the productive capacities of the forest for the chosen product are improved (e.g. Parrotta and Knowles, 1999; Brockerhoff et al., 2008).

Understanding thresholds

Forest ecosystems change continuously in response to short- and long-term environmental pressures, resulting in inherent variance over time. As a result, measures of function, such as production of given goods, also fluctuate over time. Therefore, thresholds should be perceived as a range in values to accommodate both this fluctuation and the statistical uncertainty associated with insufficient understanding of ecosystem functioning. To avoid forest ecosystem degradation, forest managers require some basic understanding of how local biodiversity is related to productivity and the levels of disturbance that their ecosystems can tolerate.

Suggested actions

As forests change after logging or insect attack, or because of climate change or extreme weather events, managers need to be concerned with bringing the forest back to a condition that will supply the goods and services that were desired from that forest. A key aspect of any plan to maintain a flow of forest goods and services is an understanding of local forest ecology on which to base sustainable forest management, and how the forest may change in response to changes in climate. The following suggested actions were developed from ecological principles that can be employed to maintain and enhance long-term forest resilience, and especially to aid adaptation of forests to climate change:

- Plan ahead to maintain biodiversity at all forest scales (stand, landscape, region) and of all elements (genes, species, communities) based on an understanding of thresholds and of expected future climate conditions. This means basing actions on ecological principles and expert knowledge to conserve biodiversity during and after forest harvesting.
- 2. Maintain genetic diversity in forests through management practices that do not select only certain trees for harvesting based on site type, growth rate and superior form.
- 3. Do not reduce the landscape-scale populations of any tree species to the extent that self-replacement is not possible.
- 4. Maintain stand and landscape structural complexity using natural forests as models and benchmarks. When managing forests, managers should try to emulate the processes and composition in natural stands, in terms of species composition and stand structure, by using silvicultural methods that relate to the major natural disturbance types.
- 5. Maintain connectivity across forest landscapes by reducing fragmentation, recovering lost habitats (forest types), and expanding protected area networks. Intact forests are more resilient than fragmented forests to disturbances including climate change.
- Maintain functional diversity (and species redundancy) and minimize the conversion of diverse natural forests to monotypic or reducedspecies plantations.
- 7. Reduce non-natural competition by controlling invasive species (and

entry pathways), and reduce reliance on non-native tree crop species for plantation, afforestation, or reforestation projects.

- 8. Reduce the possibility of negative outcomes by apportioning some areas of assisted regeneration with trees from provenances and from climates of the same region that approximate expected conditions in the future. For example, in areas projected to become more dry, consider also planting tree species or provenances that may be moredrought-resistant than local species and provenances, with special consideration to regional species.
- 9. Protect isolated or disjunct populations of species, such as populations at the margins of their natural distribution ranges, as possible future source habitats. These populations may represent pre-adapted gene pools for responding to climate change and could form core populations as conditions change.
- 10. Ensure that there are national and regional networks of comprehensive and representative protected areas that have been established based on scientifically sound principles. Incorporate these networks into national and regional planning for large-scale landscape connectivity.
- 11. Develop an effectiveness monitoring plan that provides data on natural disturbances, climate conditions and consequences of post-harvest silvicultural and forest management actions. Adapt future planning and implementation practices as necessary.

The capacity to conserve, sustainably use, and restore forests rests on our understanding and interpretation of patterns and processes at several scales, the recognition of thresholds, and the ability to translate knowledge into appropriate forest management actions in an adaptive manner. ◆



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