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SYNTHESIS & INTEGRATION

Viewing forests through the lens of complex systems science

Elise Filotas,[1,14,†] Lael Parrott,[2] Philip J. Burton,[3] Robin L. Chazdon,[4] K. David Coates,[5] Lluís Coll,[6,7] Sybille Haeussler,[8] Kathy Martin,[9] Susanna Nocentini,[10] Klaus J. Puettmann,[11] Francis E. Putz,[12] Suzanne W. Simard,[9] and Christian Messier[1,13]

[1]*Centre for Forest Research, Department of Biological Sciences, University of Québec, Montréal, Québec H3C 3P8 Canada*
[2]*Departments of Earth and Environmental Sciences & Biology, University of British Columbia, Okanagan Campus, Kelowna, British Columbia V1V 1V7 Canada*
[3]*Department of Ecosystem Science and Management, University of Northern British Columbia, Terrace, British Columbia V8G 1K7 Canada*
[4]*Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, Connecticut 06269-3043 USA*
[5]*Ministry of Forests, Lands and Natural Resource Operations, Smithers, British Columbia V0J 2N0 Canada*
[6]*Forest Sciences Center of Catalonia (CTFC), Solsona 25280 Spain*
[7]*Centre for Ecological Research and Forestry Applications (CREAF), Autonomous University of Barcelona, Bellaterra 08193 Spain*
[8]*Bulkley Valley Research Centre, Smithers, British Columbia V0J 2N0 Canada*
[9]*Department of Forest and Conservation Sciences, University of British Columbia, Vancouver, British Columbia V6T 1Z4 Canada*
[10]*Department of Agricultural, Food and Forest Systems (GeSAAF), University of Florence, Florence 50145 Italy*
[11]*Department of Forest Ecosystems and Society, Oregon State University, Corvallis, Oregon 97331 USA*
[12]*Department of Biology, University of Florida, Gainesville, Florida 32611-8526 USA*
[13]*Institute of Temperate Forest Science (ISFORT), University of Québec in Outaouais, Ripon, Québec J0V 1V0 Canada*

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Abstract. Complex systems science provides a transdisciplinary framework to study systems characterized by (1) heterogeneity, (2) hierarchy, (3) self-organization, (4) openness, (5) adaptation, (6) memory, (7) non-linearity, and (8) uncertainty. Complex systems thinking has inspired both theory and applied strategies for improving ecosystem resilience and adaptability, but applications in forest ecology and management are just beginning to emerge. We review the properties of complex systems using four well-studied forest biomes (temperate, boreal, tropical and Mediterranean) as examples. The lens of complex systems science yields insights into facets of forest structure and dynamics that facilitate comparisons among ecosystems. These biomes share the main properties of complex systems but differ in specific ecological properties, disturbance regimes, and human uses. We show how this approach can help forest scientists and managers to conceptualize forests as integrated social-ecological systems and provide concrete examples of how to manage forests as complex adaptive systems.

Key words: adaptation; complex systems; forests; resilience; social-ecological systems.

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[14] Present address: Téluq, Université du Québec, Montréal, Québec H2S 3L5 Canada.
† **E-mail:** elise.filotas@gmail.com

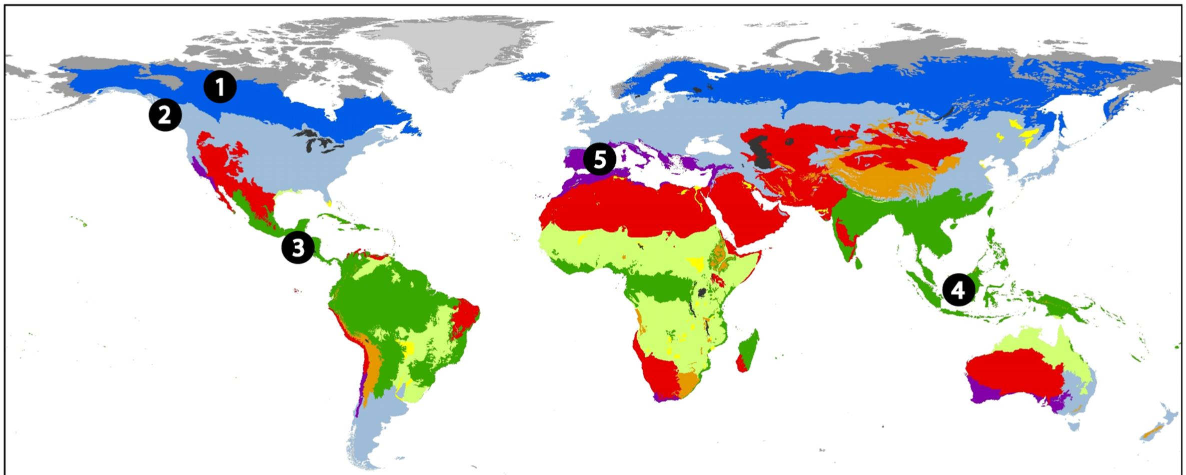
INTRODUCTION

Complex systems science (CSS) provides a transdisciplinary framework to study a variety of biological, social, and physical systems (Mitchell 2009). With roots in non-linear physics and information theory, CSS has applications in systems of all scales, sizes, and functions, from epidemiology (Ferguson et al. 2003) to economics (Haldane and May 2011). Underpinning these broad applications is the idea that locally interacting entities produce global dynamics that cannot readily be predicted from their individual behaviors (Newman 2011). Irrespective of the nature of their constituents, complex systems share the properties of heterogeneity, hierarchy, self-organization, openness, adaptation, memory, non-linearity, and uncertainty (Solé and Goodwin 2000, Boccara 2004, Mitchell 2009). A unified understanding of the spatiotemporal dynamics of complex systems has emerged over the past 20 years; here we review how CSS can be applied to forest ecology and management.

Although forests are prime examples of complex systems (Perry 1994), CSS is rarely invoked in forest ecology or forestry. In other areas of ecology, contributions of CSS are many and varied (Anand et al. 2010). Important advances have been achieved in understanding and modeling population fluctuations (Inchausti and Halley 2002), spatial dynamics (Blasius et al. 1999), animal movements (Couzin et al. 2005), the structure of interspecific networks (Dunne et al. 2002), ecological indicators (Parrott 2010), and detecting ecosystem regime shifts (Scheffer et al. 2012). CSS applications are also found in conservation biogeography (Cumming et al. 2010), social-ecological system management (Walker et al. 2002), evolution of land-use (White and Engelen 1993), and meteorology (Peters and Neelin 2006). Ecologists (Levin 1999, Gunderson and Holling 2002, Liu et al. 2007) and some foresters (Puettmann et al. 2009, Haeussler 2011, Messier et al. 2013) maintain that CSS can contribute to holistic management approaches for enhancing the adaptive capacity of forests, and ecosystems in general, and their resilience to global changes.

In this paper, we review eight attributes of four well-studied forest biomes: temperate, boreal, tropical and Mediterranean (Fig. 1) to show how CSS can unify the study of global forests and provide new insights into their management. These focal forests differ in species diversity, structure, disturbance regimes, histories, and contributions to local economies. In Mediterranean Spain and Italy, the forest sector contributes little to the national economy and employment, whereas in Canada the forest industry is a principal employer, providing the economic foundation for many rural communities (Natural Resources Canada 2012). Market forces and social pressure to conserve biodiversity have caused governmental institutions in Canada's temperate and boreal forests to formulate sustainable forest management regulations. In tropical Borneo, by contrast, deforestation and forest degradation are enduring problems caused by legal and illegal logging and large-scale conversion of native forests to oil palm plantations (Tacconi 2007, Palmer and Bulkan 2010). Despite these differences, viewing forests through the shared properties of complex systems improves our understanding of how they may respond to environmental, biological, and social changes.

The properties reviewed below are largely recognized as key features of forest systems, but are seldom studied together. It is this integrated view of systems that distinguishes the CSS approach. CSS links properties previously studied in isolation, for example, ecological hypotheses are typically tested at a single "appropriate" scale, ignoring cross-scale interactions. Moreover, human (social) and non-human (ecological) components of forest dynamics continue to be interpreted as inhabiting fundamentally separate domains. CSS is particularly relevant for forest management because the number of elements and processes at play increases with inclusion of the human dimension. The application of CSS to forest management builds on existing concepts, such as ecosystem-based management, and is another step in the continuous refinement of practices in forestry. We envision this next stage of management as explicitly linking the properties of CSS within forests, and integrating the social and ecological dimensions of forestry into a single framework (Messier et al. 2013).



Forest biomes Region	**boreal** ❶ Canada	**temperate** ❷ British Columbia Canada	**tropical** ❸ Mesoamerica	**tropical** ❹ Borneo	**Mediterranean** ❺ Spain
					
Forest composition	Evergreen gymnosperms (*Picea* , *Pinus* , *Abies* , *Larix*) and seral angiosperms (*Populus* , *Betula*)	Dominantly evergreen gymnosperms	Tropical moist broadleaf forest (lowland through montane), tropical dry broadleaf forests, tropical coniferous forest	Dominated by species in the Dipterocarpaceae	Evergreen gymnosperms (mainly *Pinus*) and angiopserms (mainly *Quercus*)
Major disturbance agents	Lightning-caused fire, outbreaks of defoliating insects.	Lightning and human-caused fire, native fungi and insect outbreak, and some windthrow.	Hurricanes and storms, fires (in dry forest regions), deforestation for cultivation and pastures.	Lightning and human-caused fire, small windthrows, selective logging, and deforestation.	Forest fires (mainly human-caused), drought, some wind and snowthrow.
Land-use history	Subsistence hunting-gathering pre-1700, fur trade 1700-1940, commercial forestry and hydroelectric development 1900-present, extensive petroleum and mineral exploration and development 1950-present.	Aboriginal use of cedar poles (3,000 y BP - 1900s), railway tie cutting 1910, 1910-present commercial forestry and <3% of total forest area cleared for farming.	Extensive deforestation during Mayan Pre- and Late-Classic period (4000-1100 BP). In 1900s, >40% of native forests converted for farming. 2001-present, forest is expanding due to reduced deforestation and growing rates of secondary regeneration.	Harvesting of non-timber forest products in most forests away from rivers until commercial logging started in the 1960s. At present, approx. half of the forests has been converted into African oil palm plantations.	Intensive deforestation from the Neolithic to the Middle Ages. Forest cover at a minimum in 1800s. Active reforestation programs in the 1900s. At present forest is expanding due to rural abandonment.
Approximate human population density (hab/km2)	1	12	60	22	94

Fig. 1. Description of the forest biomes presented in this paper. Photo credits: Mélanie Desrochers (1), Jean Mather (2), Matthew Clark (3), Francis E. Putz (4), and Pere Casals Tortras (5).

A Tour through Some General Properties of Complex Systems

Heterogeneity

CSS takes a holistic perspective that fosters understanding of systems with interacting components whose global dynamics cannot be calculated by summing the dynamics of individual components (Box 1 and Fig. 2). Foremost, complex systems are systems of interacting components (Green and Sadedin 2005). Generally, these components are heterogeneous. This heterogeneity is expressed by the nature of the components and their behaviors, structural organization, spatial location, and extent or history. Linear and non-linear interactions among these

Box 1

Conceptual representation of a complex system

In Fig. 2, at the base of the hierarchy (left), heterogeneous entities interact locally, giving rise to higher-level entities that affect lower-level entities through feedback loops. Entities at every level are open to external forces. When forests (right) are viewed as complex systems, lower level entities include individual trees, fungi, mammals or birds (bottom right) that compete for resources. They can also represent forest stakeholders with divergent behaviors and goals (forest harvesters, residents, recreational visitors). When these entities interact locally, they form forest ecosystems at the stand scale (center right). Forest ecosystems are linked to other systems essential to community well-being, including sawmills, farms and district transportation systems. At the landscape scale (top right), forest stands, cut blocks, residential areas, and agricultural fields are networked by roads, rivers, or vegetation corridors. The pattern of land use is the emergent result of lower-level processes and interactions. Forest disturbances at the landscape scale reverberate down the hierarchy: large disturbances alter local attributes such as stand age and composition, population dynamics, and rural economies. These alterations in turn change the survival, food preferences, or leisure activities of forest inhabitants.

heterogeneous components give rise to a variety of responses that drive system dynamics. Heterogeneity is thus an essential attribute of the dynamics of complex systems and is also necessary for maintenance of their responsiveness and resilience.

Ecosystems such as forests, have multiple and diverse components. Even boreal forests, which are less species-rich aboveground than tropical or temperate forests, are highly heterogeneous ecosystems (Zasada et al. 1997). Phenotypic differences associated with growth stages within tree species are common throughout the boreal biome, and even monospecific stands may have substantial genetic variability. Many boreal forests include hybrids (e.g., between *Pinus contorta* and *P. banksiana* in Canada) and interclonal variations are widespread within and among forest stands (e.g., *Populus tremuloides*; Burton 2013).

Typically, components of complex systems interact over a range of spatiotemporal scales (Levin 1992). In forest systems, heterogeneity encompasses the vertical, horizontal and temporal dimensions of stand composition and structure (i.e., soil horizons and canopy layers, spatial patchiness, and age classes or successional stages). Each vertical stratum has a unique microclimate and provides a different set of resources to sustain plant, animal, and fungal biodiversity (Brokaw and Lent 1999). Age differences among trees contribute to forest heterogeneity, with variation in mortality rates influencing tree size and age, canopy gap formation, and the presence of snags and fallen logs. Long-lived trees represent biological legacies that determine how forest heterogeneity changes over time (Lindenmayer et al. 2012).

In the horizontal dimension, vegetation cover and composition vary with elevation, soil quality, and hydrology and in response to disturbances. The patchy occurrence and severity of wildfires, insect outbreaks, cutovers, and their interactions generate habitat diversity in boreal landscapes. In moist tropical forests, canopy gaps created naturally or by selective logging vary greatly in size and in the extent of soil and understory disturbance. For example, half of the gaps in a 44-ha Costa Rican tropical forest were <25 m^2 (Kellner et al. 2009), but tropical forest disturbances can also be large and internally heterogeneous, such as >30 ha blowdowns in Amazonia (Nelson 1994).

Human use often substantially modifies forest heterogeneity. At the extreme, human activities create ecological patterns and interactions without historical equivalents for which traditional management practices are inappropriate (Seastedt et al. 2008). Timber, energy and mineral extraction, as well as agriculture, fires, urbanization, and road construction fragment and shape

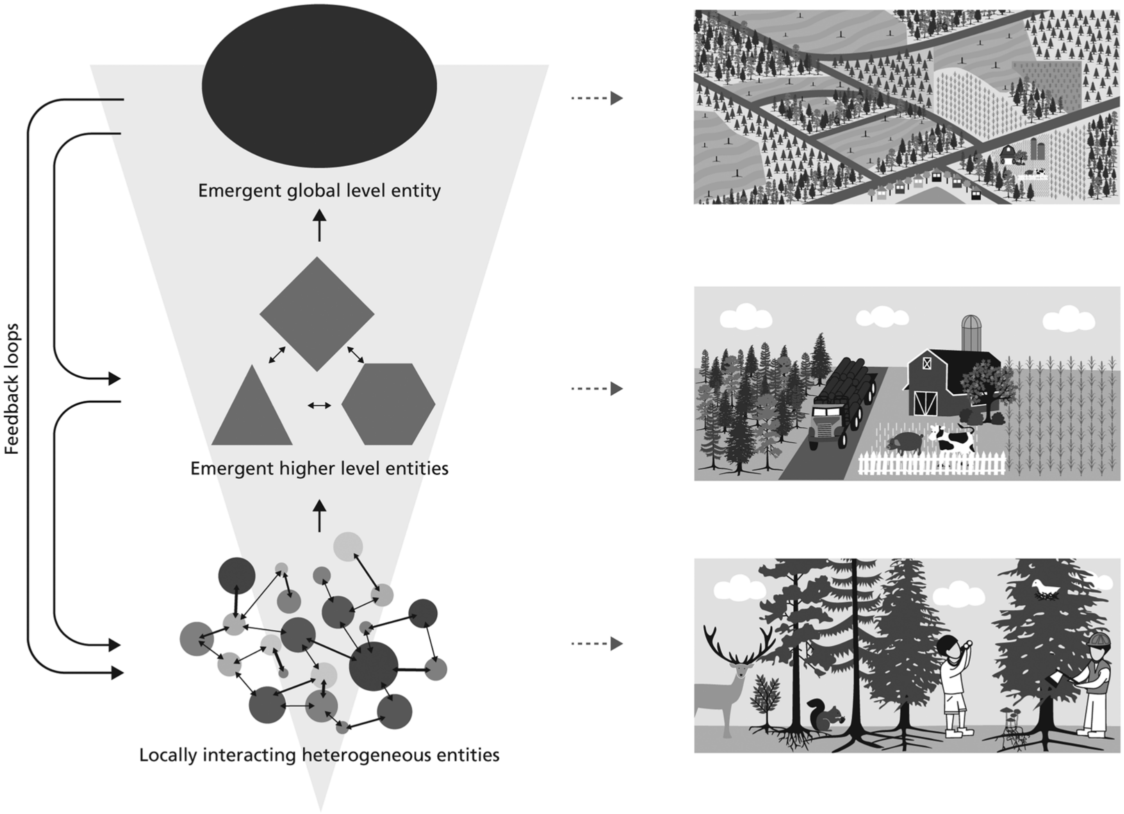


Fig. 2. Conceptual representation of a complex system (see Box 1).

forest landscapes. As demands for ecosystem goods and services shift and intensify, so do their imprint on the landscape (Robson and Berkes 2011). Mediterranean forests have been severely altered by interactions among humans, climate and geomorphology for three millennia (Anderson et al. 2011). At landscape scales, a spatiotemporally patchy mosaic of woodlots, scrublands, pastoral grasslands, and farmlands has emerged (Blondel 2006, Nocentini and Coll 2013). Intensification and standardization of cultivation practices within and among woodlots have homogenized forest cover and resident biota. Afforestation programs and farm abandonment in the 20th century further modified the landscape structure. CSS emphasizes the importance of interactions between landscape stressors and patterns of heterogeneity. Altering these patterns may greatly affect the landscape's ability to sustain function, leading to less diverse human communities (e.g., Clavero and Brotons 2010) and loss of resilience.

Enhanced forest heterogeneity is a primary goal of most new silvicultural systems. Heterogeneity is promoted through a greater diversity of cuts that: (1) emulate natural disturbances (Kuuluvainen and Grenfell 2012); (2) leave behind varied structures and organisms, including live and dead trees and intact forest patches (Gustafsson et al. 2012); and (3) encourage tree species mixtures (Scherer-Lorenzen et al. 2007). These practices are linked to the relatively new approach of using biodiversity to increase yield and resilience in natural and managed ecosystems (Mori et al. 2013).

Hierarchy

A second property of complex systems is that their components are organized hierarchically (Box 1 and Fig. 2). Elements at different levels interact to form an architecture that characterizes the system. CSS asserts that a phenomenon occurring at one scale cannot be understood without considering cross-scale interactions (Simon 1962, Li 2000). Grasping the dynamics of a complex system therefore begins by investigating how it is organized. The notion of cross-scale interactions, as used here, may relate to the ranking structure within food webs or social webs of interacting stakeholders. It may also refer to spatial dimensions, including the size structure of disturbances and management prescriptions. Additionally, it may denote temporal dimensions, such as species longevity or length of planning horizons.

Many complex systems are networks in which the structures formed by connected components span several levels (Strogatz 2001). In ecosystems, interspecific webs follow a hierarchical structure from producers through multiple levels of consumers, often including humans. For example, investigation of the relationship between the spruce budworm (*Choristoneura fumiferana*) and balsam fir (*Abies balsamea*) in boreal forests reveals a rich foodweb of intricate connections spanning five hierarchical levels (Fig. 3). The hierarchy of forest ecosystems should be viewed as a meta-network spanning several spatiotemporal scales (Simard et al. 2013; Box 2 and Fig. 4).

Forest hierarchies include the social and economic dimensions of industries, governments, local communities, and other users of forest products and ecosystem services. The scope of influence of these actors and their interdependencies vary with their authority, social and commercial objectives, economic conditions, and cultural backgrounds. In Borneo, for example, forest colonists may hold a few hectares and some communities have rights over thousands of hectares, but concessionaires with government-granted usufruct rights control hundreds of thousands of hectares (Putz 2013). The interests of these stakeholders vary widely: ambitious corporations may be driven by international timber markets, while communities harvest logs for their own use or to sell logs in local markets. When international development projects and other donors are involved, communities may participate more to secure land title or to capture available subsidies than to profit from selling timber (McDaniel 2003).

CSS teaches us that ecosystems are not simple systems that can be managed top-down. Management must acknowledge that forests encompass multiple components (not simply trees) and functions, and must explicitly consider the interactions linking hierarchical scales (Puettmann et al. 2009). Policies that support sustainable forests also require an understanding of the social-ecological systems in which decision-makers are embedded.

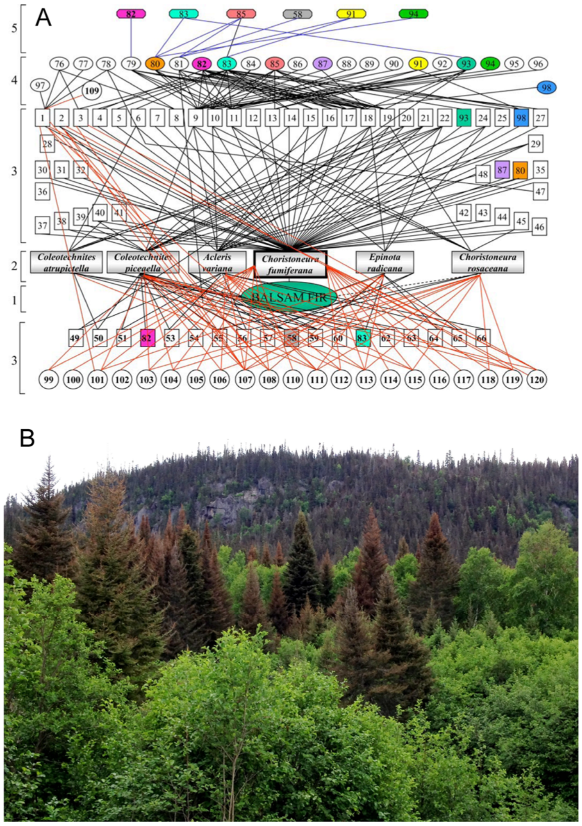


Fig. 3. (A) Food web of consumers associated with balsam fir (*Abies balsamea*) in northeastern North America. The spruce budworm (*Choristoneura fumiferana*) and five other herbivores feed on balsam fir and are themselves hosts to 66 primary parasitoids (squares), 21 primary entomopathogens (circles), 23 secondary parasitoids (ovals), 1 secondary entomopathogen, and 6 tertiary parasitoids (octagons). From Eveleigh et al. (2007); used with permission. (B) Spruce budworm outbreak in balsam fir forest, eastern Canada. Photo credit: Patrick James.

Robust modelling frameworks and other quantitative approaches from CSS contribute novel methods to the forest manager's toolbox that recognize the hierarchical structure of ecosystems and produce better management

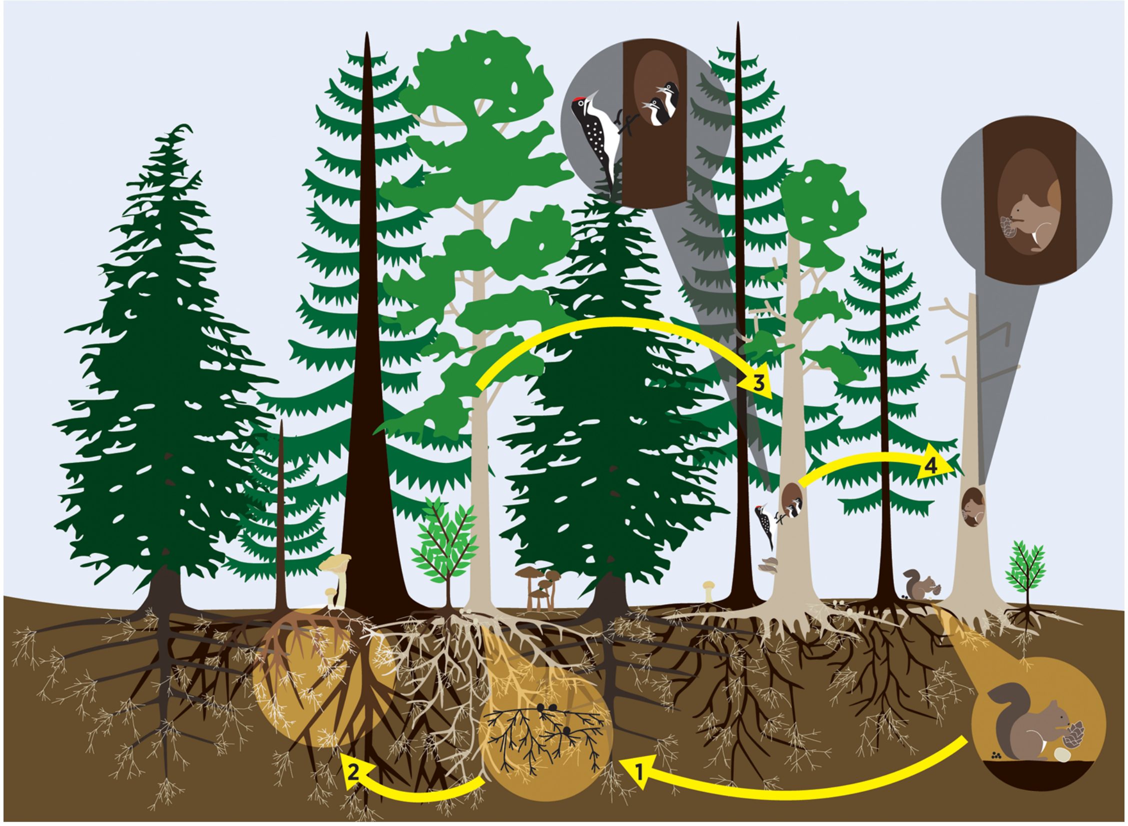


Fig. 4. Interior Douglas-fir forests of south central British Columbia as a self-organizing meta-network (see Box 2).

Box 2

Interior Douglas-fir forests of south central British Columbia as a self-organizing meta-network

A red squirrel emerges from an abandoned woodpecker cavity in a senescent aspen tree, peels Douglas-fir cones, eating most of the seeds, but leaving some seeds behind that germinate the following spring (Fig. 4). Squirrels and mice also forage for *Rhizopogon* truffles, the subterranean mushrooms of mycorrhizal fungi associated with Douglas-fir. A mycorrhiza, literally "fungus root", is a mutualism whereby fungi supply trees with soil nutrients and trees supply the fungi with sugar. Some fungal spores dispersed by rodents in their feces germinate in spring when they receive chemical signals from germinating Douglas-fir to colonize their roots (arrow 1). The new fungal mycelia join established mycorrhizal networks of older Douglas-fir trees (arrow 2). Mycorrhizal networks, ubiquitous in forests globally, link almost all trees in a forest. The root systems of large old trees serve as network hubs into which the new germinants link and receive larger pools of nutrients than the seedlings could access on their own. Conifer seedlings in the understorey depend on carbon and nutrients from overstory trees through these networks—the more shaded the seedling, the more of its resources it receives from neighbors. When the aging trees become softened by decay fungi, woodpeckers excavate cavities for nesting and roosting (arrow 3) that are later used by cavity using species such as squirrels, owls and ducks (arrow 4). Mature and old trees thus support a nest-web network of over 40 cavity using birds and mammals, which in turn disperse seeds and spores for future generations of trees.

decisions. Bottom-up modeling provides one way of exploring cross-scale interactions (Durrett and Levin 1994, Parrott et al. 2012) that improves our understanding of how ecosystem dynamics emerge from lower-scale components such as interacting trees, wildlife, harvesters and managers (Judson 1994, Grimm et al. 2005, Parrott 2011). Bottom-up models such as SORTIE (Coates et al. 2003) could be combined with existing top-down approaches to investigate, for example, the long-term consequences of novel silvicultural treatments for managing insect outbreaks at various spatiotemporal scales. Models developed for different purposes can be linked into a meta-model to analyze cross-scale interactions as was done for boreal forests of Labrador, Canada (Sturtevant et al. 2007). Network theory has produced numerous tools for examining interactions across scales and subsystems (Strogatz 2001, Proulx et al. 2005, Barabasi 2009) that can be applied to social-ecological interactions (Janssen et al. 2006, Gonzalès and Parrott 2012), including the interdependencies in natural resource governance. Network models have recently been applied to conservation planning (Cumming et al. 2010, Galpern et al. 2011) and forest fragmentation studies (Saura et al. 2011), where they serve to restore the connectivity of forest patches.

Self-organization and emergence

Self-organization is the process whereby local interactions among a system's components cause coherent patterns, entities, or behaviors to emerge at higher scales of the hierarchy, which in turn affect the original components through feedbacks (Perry 1995, Levin 2005; Box 1 and Fig. 2). Self-organization occurs spontaneously and is widespread in ecosystems. The meta-network constituting Douglas-fir (*Pseudotsuga menziesii*) forests (Box 2 and Fig. 4) is one example of a self-organizing unit (Simard et al. 2013).

Regulating mechanisms that enhance species coexistence serve as self-organizing processes in forest ecosystems. Density-, distance-, and frequency-dependent processes all regulate plant populations in tropical and temperate forests (Webb and Peart 1999, Haeussler et al. 2013). The Janzen-Connell hypothesis (Janzen 1970, Connell 1971), for example, endeavors to explain the high species diversity of tropical forests by proposing that local negative feedback between parent trees and the density of their seedlings generates spacing patterns between trees and limits domination by any one species.

Some disturbances play a self-organizing role essential for forest maintenance. In fire-prone Mediterranean, boreal and temperate forests, pines often bear serotinous cones (e.g., *Pinus halopensis, P. pinaster, P. banksiana, P. contorta*). Serotiny is correlated with dead branch retention, which renders these trees flammable (Bond and Keeley 2005). A positive feedback between fire occurrence and pine regeneration results when seeds released by heat from fires germinate to produce trees that are highly susceptible to fire. Likewise, gap dynamics can be viewed as a self-organizing process in wetter tropical, temperate, and boreal forests (Fig. 5A). Canopy gaps created by tree-falls release advanced regeneration and stimulate seedling recruitment of tree species with structural traits (e.g., susceptibility to uprooting) that perpetuate the gap disturbance-succession loop (Chazdon and Arroyo-Mora 2013).

A CSS view of the socio-economic components of forest ecosystems also reveals self-organizing mechanisms. Forest management is typically the outcome of collective actions among government officials, ecologists, managers, forest workers, and concerned citizens. Self-organization is not necessarily optimal for forest persistence, as it may sustain feedbacks with detrimental consequences. For instance, illegal logging in Borneo can be seen as a self-organizing phenomenon supported by interactions among all levels in the stakeholder hierarchy (Putz 2013). The lowest level often involves pit sawyers eking out livings and pirate loggers taking advantage of governance failures. Higher in the chain, unscrupulous timber buyers and corrupt governmental officials launder the illegal wood. Finally, savvy international traders provide lucrative outlets for ill-gotten goods. Where illegal logging occurs, wood markets are flooded, wood prices are depressed, and standing trees are undervalued. Under such conditions, community forest managers are not motivated to implement sustainable forest management practices, which often involves short-term investments for only long-term returns (Cerutti et al. 2011). These conditions result in a positive feedback that sustains illegal logging.

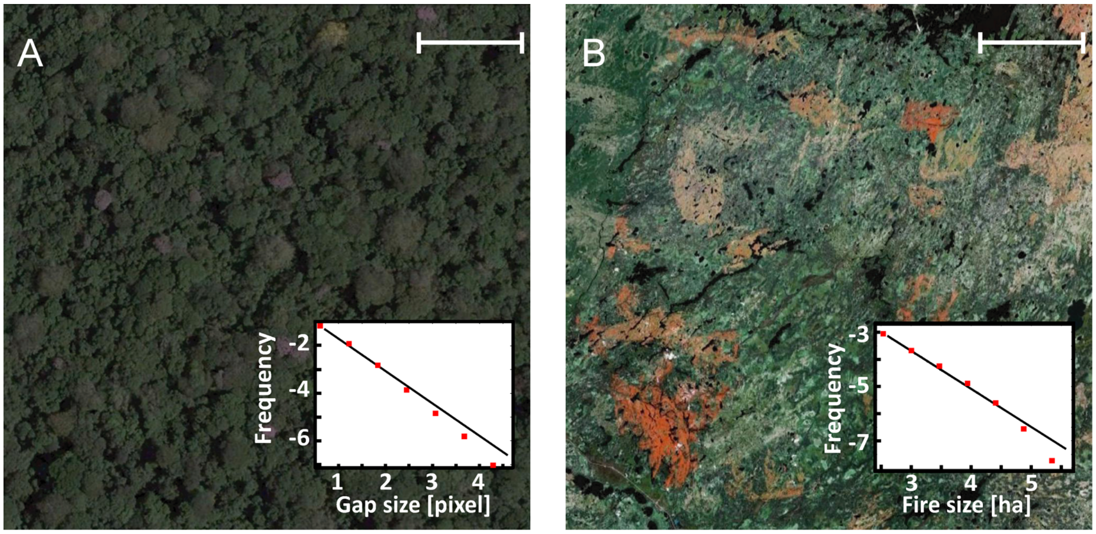


Fig. 5. (A) Canopy gaps in a tropical forest plot of Barro Colorado Island (Panama), scale = 75 m, © 2012 Google Earth, © 2012 DigitalGlobe. Inset denotes the frequency distribution of gap sizes on a double logarithmic scale and is approximated by a power-law. Neighboring pixels with values <0.5 following a conversion to digital image (1 pixel = 0.23 m^2) were amalgamated. (B) Emergence of patches of burned forest in the boreal shield, Ontario, Canada, scale = 20 km, ©2012 Google Earth, ©2012 TerraMetrics, ©2012 Cnes/Spot Image. Inset denotes the frequency distribution of fire sizes on a double logarithmic scale and follows approximately a power-law. Fires (>200 ha, 1959–1999) are from the Canadian Large Fire Database (Canadian Forest Service 1999). Frequency distributions were calculated using logarithmic binning with bin frequency normalized by its size.

Self-organization is often associated with the emergence of striking spatiotemporal patterns. One example is the power-law that describes the global size distribution of burned forest patches (Perry et al. 2011, Zinck et al. 2011) (Fig. 5B). Although individual fire behavior is stochastic, a statistical signature of fire regimes nevertheless emerges at regional scales. Individual burning trees form patches with characteristic size distributions and impact severities whose structure, in turn, influences light and nutrient availability and hence tree regeneration at local scales. As succession proceeds, clusters of forest fuel emerge that later affect how fires spread. Interactions among fire occurrence, fire propagation, and forest recovery generate region-wide patterns.

The prior examples show that self-organization and emergence are pervasive phenomena in forests. Ecologists and foresters should be alert to the presence of both amplifying and dampening cross-scale feedback loops in their forest systems and consider how they could be strengthened or weakened through management interventions. Tree species selection policies, for example, could be less prescriptive and instead encourage managers to consider future ecosystem stressors and to promote tree species mixture with diverse functional traits (e.g., shade tolerance, regeneration biology, nitrogen use, climate tolerance) that will allow the ecosystem to either resist or adapt to those stressors. In plantation forestry, planting a mix of tree species should increase resilience and enable future stands to regenerate naturally. In extensively-managed forests, foresters can facilitate seed migration, employ diverse cutting regimes, and carry out enrichment planting, where needed, to ensure representation of a range of functional traits.

Openness

In complex systems, openness means that energy, matter and, information are exchanged with the external environment through porous system boundaries (Box 1 and Fig. 2). Unlike closed systems, the dynamics of a complex system—including all ecosystems—are influenced by outside factors. Such systems remain far from equilibrium because their components are rarely maintained in space or time. Moreover, because of cross-scale interactions and emergent phenomena, complex system dynamics are not bounded. Determining what is internal and external to the system (i.e., its identity) is challenging (Cumming and Collier 2005).

In forest management, openness is rarely explicitly considered. The spatiotemporal extent of forest dynamics is often simplified, for example, by managing at stand scales over time horizons of decades rather than centuries. Climatic and socio-economic equilibria are also assumed. But ecosystems are continuously shaped by external influences, which transform their soils, species composition, and geophysical patterns over long and short time scales. Climate strongly affects tree demography, from fecundity and germination to tree growth, survival, and mortality. These couplings also cause forest diversity, function, and structure to be sensitive to fluctuations in regional and global climates (Thomas et al. 2010, Haeussler et al. 2013).

Through a CSS lens, forests are characterized by exchanges through open boundaries; the boundary definitions vary with the scales of study (i.e., at the stand, landscape or biome scale, or over single or multiple cycles of harvests or disturbances). Management plans should acknowledge that important drivers of ecosystem sustainability or change are external to the boundaries at which these plans are applied. For example, fire suppression policies in ponderosa pine forests in the southwestern United States were based on interpretation of understory fire as an undesirable external element that did not contribute to forest dynamics. Ignoring fire as an essential component of the forest system contributed to changes in forest composition and increased tree densities and surface fuel loads (Larson et al. 2013) that now contribute to the incidence of huge crown fires that endanger human and ecological communities (Allen et al. 2002).

A CSS view of forests as open systems with porous boundaries acknowledges the degree to which anthropogenic influences interact with other ecological factors to shape forest dynamics. In Mediterranean landscapes, where forests have co-evolved with rural societies over millennia, clear distinction between forest and non-forest systems is often impossible. Landscapes form irregular checkerboards of forest patches, agricultural lands, degraded areas and human settlements (Nocentini and Coll 2013). Similarly, the extensive northern boreal forests of the world need to be viewed as coupled social-ecological systems strongly affected by timber, energy and mineral extraction (Asikainen et al. 2010). These human impacts fluctuate with exogenous economic demand, technological advances, and social tastes. For example, trends in demands for wood products in British Columbia (Fig. 6) have modified forestry practices to include tree species that formerly had no commercial value (Burton et al. 1992). Because external fluctuations are generally not predictable, the openness property creates great uncertainty about future states and values of forests.

Adaptation

Adaptation, as used here, refers to adjustments in the behavior and attributes of a complex system in response to changes in external inputs. Adaptation is similar to self-organization in that it depends on cross-scale interactions, but differs in that it is externally driven. Ecosystems continually adapt because changes in the external environment (nutrient availability, temperature, exotic species arrivals, rules governing land use), are the norm rather than the exception.

The adaptive capacity of many complex systems is related to the concept of ecosystem resilience (Gunderson and Holling 2002) but with an important difference. Ecological resilience can be characterized by the amount of change that an ecosystem can absorb before it loses its ability to maintain its original function and structure, i.e., its identity. Following a disturbance, a resilient system has the potential to recover its original structure, functions and feedbacks. In contrast, adaptation enables an ecosystem to modify its structure and composition so it can sustain major functions or develop new ones. It enables the ecosystem to reorganize in a manner that avoids maladaptation to the new environmental conditions (Parrott and Lange 2013).

Mycorrhizal networks play substantial roles in forest recovery and adaptation following disturbances. Trees in mixed Douglas-fir/paper birch (*Betula papyrifera*) stands of British Columbia's interior forests, for example, are connected by

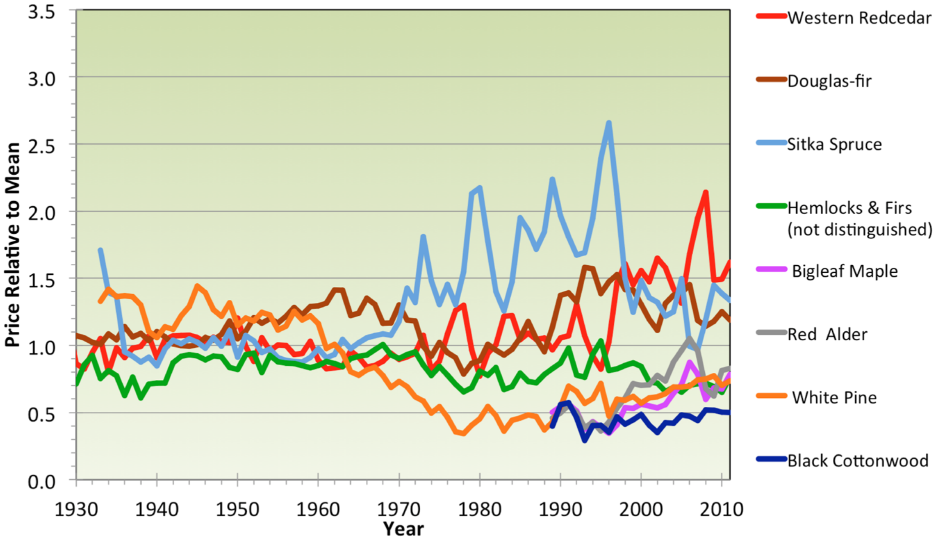


Fig. 6. Fluctuations in the relative price of logs for coastal tree species in British Columbia, Canada. Bigleaf maple, red alder and black cottonwood did not have marketable values prior to 1990. British Columbia Ministry of Forests, Lands and Natural Resource Operations, Timber Pricing Branch, *unpublished data*.

mycorrhizal networks that transfer nutrients among individuals and species (Simard et al. 2002). Following a disturbance, Douglas-fir seedlings establish more vigorously when linked mycorrhizally to older firs (Simard et al. 1997*b*) or to paper birch (Simard et al. 1997*a*). Mycorrhizal networks also facilitate adaptation to climate stress, ease native plant migration, inhibit weed invasion, and mitigate tree mortality in all forest biomes (Simard et al. 2013).

Heterogeneity and biodiversity are key determinants of ecosystem adaptation and resilience (Levin 1998). External changes do not affect all species identically and a diversity of responses may exist among species accomplishing the same ecological function (Elmqvist et al. 2003). For example, most trees in the tropical forests of the island of Samoa (Western Polynesia) rely on five frugivorous species for seed dispersal. Following cyclones in the 1990s, populations of the previously dominant species (*P. tonganus* and *D. pacifica*) decreased by more than 90%, while the impact on other subdominant species (e.g., *P. samoensis*) was less than 10%. Seed dispersal in the forest was thus maintained by the differences in species response (Pierson et al. 1996). Functional diversity facilitates the adaptation of forest ecosystems to biodiversity loss caused by natural or anthropogenic forces.

Spatial heterogeneity in forest landscapes also fosters adaptive capacity. *Dehesa-montado,* a classical form of Mediterranean landscape management, creates mosaic-like landscapes by combining three rural activities, forest product harvesting, livestock husbandry, and agriculture (Fig. 7; Blondel 2006). Forage grasses grow beside scattered oak trees that mitigate hydrological stress for the herbaceous layer, improve grass nutrition, and shelter livestock. Livestock, in turn, reduce woody shrub ingrowth and limit the propagation of fire. Spatial heterogeneity diversifies the local ecological role of each landscape element, thereby increasing resistance to drought and fire (González-Bernáldez 1991). This coupled human-ecological system has been maintained for centuries in the Iberian Peninsula.

A CSS view suggests that management guidelines that preserve the capacity of forest ecosystems to respond to a range of perturbations while providing desired ecosystem goods and services are key to surviving the expected future increases in climatic variability and uncertainty. Management programs must acknowledge that spatiotemporal variability is an inherent attribute that allows ecosystems to adapt.

Examples of harvest operations that incorporate cross-scale redundancy of ecosystem functions and processes (Peterson et al. 1998) include

Fig. 7. *Dehesa-montado* landscape in Mediterranean Spain. Oak trees for acorn and fuelwood production grow sparsely alongside forage grass needed for raising livestock. Spatial heterogeneity maintained by this management system promotes adaptation to fire and drought. Photo credit: Pere Casals Tortras.

adopting a range of harvest openings and reserve tree densities and arrangements that encourage a diversity of plant species with different habitat needs. Silvicultural prescriptions should also seek to increase the diversity of palatable or insect pollinated plants and insectivores to support richer food and nest webs. These practices may protect against increases in temperature, drought, frost or pest damage.

Adaptation can be fostered at the stand scale by frequent low-intensity harvests that accelerate changes in species composition, followed by planting of tree species with key functional traits (Nolet et al. 2013). New research suggests that many organisms can evolve to adapt to new environments within reasonable ecological time scales (Schoener 2011). At the landscape scale, well-positioned multi-species plantations can reduce fragmentation by fostering seed dispersal among neighboring stands following disturbance, allowing a larger pool of species to colonize newly available microsites.

Memory

Complex systems accumulate information from the past that influences future trajectories through persistent change in the system's structure and composition (Anand et al. 2010, Parrott and Lange 2013). This *memory* may derive from past events, some minor or random, that are reinforced through feedbacks in the system and constrain its future trajectory. In forests, early recruitment of pioneer species following a disturbance modifies the habitat and influences prospective colonists (Levin 1998, De Grandpre et al. 2009; see also Fig. 8). Forest management

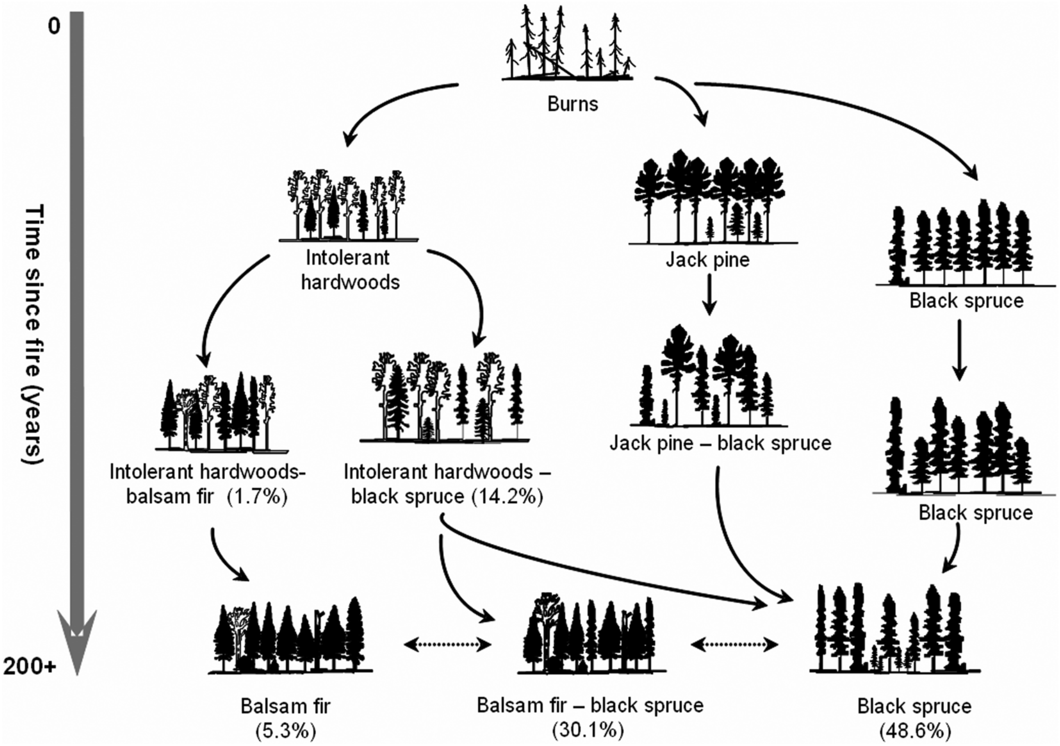


Fig. 8. An example of multiple post-fire successional trajectories in Quebec boreal forest. From De Grandpré et al. (2009); used with permission.

practices may also create path dependency, as for example in Canada, where an emphasis on stand-level silvicultural planning still drives current management practices. This emphasis persists despite new technologies (such as GIS and GPS) that readily permit management at larger scales that may be more ecologically and economically relevant.

Memory often arises from long-lived system components whose influence extends over lengthy time periods. In ecological systems, such memories are referred to as biological legacies (Franklin 1990). Ancient trees, for example, retain the memory of past forest environments in their wood properties and canopy structure (Briffa 2000). At larger scales, fires in boreal forests, influence tree species composition for hundreds to thousands of years by changing soil nutrient conditions, seed- and bud banks and the resulting spatial pattern of regeneration (Bergeron 2000). Anthropogenic forest disturbances also create legacies. Overharvest of silver fir (*Abies alba*) for ship and building construction during medieval times, has caused changes in species composition in the Apennines of Italy that still persist (Nocentini and Coll 2013).

In complex adaptive systems, memory may act as an important agent of resilience. Following forest disturbances, biological legacies provide continuity of ecological functions and facilitate forest regeneration. Internal sources of memory include seed banks, nurse logs, tree stumps, snags or coarse woody debris, mycorrhizal networks, and old or dying trees. Following disturbances, dying trees maintain partial shade for germinants, provide mycorrhizal networks into which new germinants can link, and harbor fungi and animals, including seed dispersers, that are essential for regeneration (Simard et al. 2013). The surrounding landscape supplies important external sources of memory including adjacent and remnant patches of vegetation, often vectored by mobile linkages (e.g., seed-dispersing mammals and migratory birds). In the tropics, forests recover more quickly after cyclones when located near remnant forest patches that serve as sources of new recruits and propagules (Chazdon 2003).

The frequent presence of old oak stumps and oak seedlings in understories of large forest areas now dominated by natural and planted *Pinus* spp. in many Mediterranean countries can be interpreted as evidence of memory (Nocentini and Coll 2013). The oak stumps reflect past coppice management for charcoal and firewood. The European jay (*Garrulus glandarius*) disperses acorns into pine stands from old isolated trees growing in nearby fields (Puerta-Pinero et al. 2012). The presence of these oaks increases the present adaptability of these forests to fire, because unlike pines, oaks are able to resprout and rapidly establish ground cover and a tree overstory after fires (Rodrigo et al. 2004).

Management programs based on a CSS view of forests should preserve biological legacies as a way to enhance forests' adaptive capacity. For example, they should reduce the harvest of old-growth forests and increase rotation ages. Old and large trees have wide mycorrhizal networks and they conserve a genetic diversity that may become valuable under changing climatic conditions (Martin et al. 2004, Whitham et al. 2006, Drever et al. 2008). Where soils are degraded, or coarse woody debris were removed, silvicultural treatments that restore native soil fungal inoculum are recommended. Regeneration plans that protect advance regeneration during and after harvest help to conserve the genetic memory of forest stands. Post-disturbance salvage operations should be limited in scope and modified to ensure that legacies such as residual trees, snags and coarse woody debris are effectively distributed and that sites are reforested rapidly enough to retain the memory of the previous forest (Lindenmayer et al. 2009).

Non-linearity and thresholds

Non-linearity, a defining feature of complex system behavior, occurs when the outputs from a system are disproportional to associated inputs. This feature creates sensitivity to initial conditions so that small differences are amplified and lead to divergent trajectories (Strogatz 1994). Forest recovery following a disturbance could, for example, follow many different successional trajectories due to such minor differences as the proximity of surviving mature trees, seed banks, seed crop size, or weather conditions (De Grandpré et al. 2009, Johnstone et al. 2010). Sensitivity to initial conditions and contingencies means that the tree species community that develops following a fire in a Quebec boreal forest (Fig. 8) could vary from pure balsam fir, to pure black spruce (*Picea mariana*), to stands with both species.

Non-linear processes and feedbacks play a key role in the regulation, spatial synchrony and chaotic dynamics of plant and animal populations in all ecosystems (Costantino et al. 1997, Blasius et al. 1999). Examples from forest systems include density-dependence in mammalian reproductive and mortality rates (Hanski et al. 1993) and density-dependence in plant fecundity and seedling survival (Stone and Ezrati 1996).

Non-linearity implies that the dynamics of complex systems may show unexpectedly large or small responses to slow acting variables. Many ecosystem processes may be surprisingly fragile or unexpectedly robust to gradual changes in temperature (Anderson-Teixeira et al. 2013), rainfall (Staver et al. 2011), grazing pressure (Kefi et al. 2007), landscape fragmentation or connectivity (Fahrig 2003). The spatial magnitude of the 1980s western spruce budworm (*Choristoneura occidentalis*) outbreak in interior Douglas-fir forests of British Columbia can be seen as a non-linear response to forest management practices. The budworm and Douglas-fir show a long-term pattern of coexistence marked by outbreaks of intermediate size (Campbell et al. 2006). Historically, frequent ground fires removed Douglas-fir regeneration, favoring non-host tree species. Harvesting and fire suppression created dense, multi-layered Douglas-fir- canopies ideal for spruce budworm (Maclauchlan and Brooks 2009). These gradual alterations in forest structure and composition progressively homogenized the landscape, making it possible for spruce budworm to propagate over large spatial scales. Non-linearity also means that ecosystem responses may depend on whether changes occur in isolation, together, or sequentially. Management practices, together with climate changes are implicated as drivers of the exceptional landscape-scale eruption of the mountain pine beetle (*Dendroctonus ponderosae*) in western North America (Raffa et al. 2008).

Non-linear responses can lead to regime shifts in forest ecosystems where the dominant vege-

Box 3

Bornean forest conversion: a threshold phenomenon with unforeseen outcomes

In Borneo, the process of forest conversion into commercial pulpwood or oil palm plantations often happens quickly and over spatial scales of >10,000 ha. The timeframe for these transitions depends upon whether the starting point is taken to be when the area is first opened by loggers, when loggers re-enter for final felling of all marketable timber, or when the plantation bulldozers start clearing unmarketable trees.

Passage and implementation of a 2009 forest regulation (SILIN) in Indonesia provides a good example of the unpredictability of many complex systems (Putz 2013). SILIN requires increased logging intensities followed by line-planting along clearcut strips of nursery-grown seedlings or cuttings of 5-6 species of commercial timber species of Dipterocarpaceae. Implementation of this regulation means that forests that escape conversion into oil palm or pulpwood plantations, instead of undergoing steady and slow degradation by repeated-entry logging, are now slated for sudden and rapid degradation followed by establishment of even-aged stands with few species and a limited range of genotypes. Perhaps at some level in the Indonesian forestry hierarchy the transition to silvicultural intensification was gradual, but for many researchers and advocates of natural forest management as a conservation strategy, the policy came as an unwelcome surprise. That so much published research demonstrating the sustainability benefits of low-intensity or reduced-impact logging could be disregarded by policy-makers in favor of enrichment planting can in part be attributed to failure of the researchers to effectively communicate their recommendations.

tation type is replaced (Johnstone et al. 2010). Successive disturbances erode the resilience of the original forest, which becomes unable to regenerate. Such threshold-like dynamics may lead to new persistent (alternative stable) states (Scheffer et al. 2012). Following years of logging on British Columbia's Skeena River floodplain, the original Sitka spruce (*Picea sitchensis*) forest was replaced by deciduous forest of red alder (*Alnus rubra*) and cottonwood (*Populus balsamifera* ssp. *trichocarpa*) which are lower in both biodiversity and commercial value (Haeussler et al. 2013). The cumulative effects that led to a regime shift in this system were a loss of large conifer logs that created stable platforms for spruce regeneration coupled with a nutrient enrichment by invasive alders and earthworms that led to unprecedented booms in small mammal populations and competing vegetation. Repeated silvicultural efforts to re-establish Sitka spruce exacerbated the nutrient feedback while further reducing supplies of coniferous woody debris. As a result, Sitka spruce failed to re-establish.

Threshold phenomena seem more the rule than the exception in many social-ecological systems, particularly those in which the fates of large portions of landscapes can be determined by enactment of single land-use or economic policies (Walker and Salt 2006, Messier et al. 2013). In Borneo, for example, forest conversion into commercial pulpwood or oil palm plantations can be seen as a threshold phenomenon with unpredicted outcomes (Box 3).

Uncertainty

The dynamics of complex systems are riddled with uncertainty, which challenges predictions about future states. Uncertainty arises from many sources. First, it is caused by the stochasticity inherent to most internal processes driving the dynamics of social-ecological systems. Forest ecosystems are subject to stochastic variation in the physical environment and in the occurrence and outcome of biotic events such as seed survival and predator-prey encounters. Another source of uncertainty is non-linearity, especially unforeseen regime shifts, as in the case of Bornean forest replacement by *Imperata cylindrica* grasslands after repeated fires that were fostered by this very flammable grass (Putz 2013).

Openness creates a third source of uncertainty. The CSS viewpoint stresses that forests are vulnerable to changes in peripheral systems to which they are coupled (e.g., economic, political, demographic, climatic). In Mediterranean Spain, for example, landscape homogenization expanded due to 21st century changes in the economy marked by agricultural land abandonment and decreased forest utilization. In Borneo, rates of illegal logging rise with political instability and when corrupt elected or appointed governmental officials come to power (Putz 2013). Uncertainty is reinforced by the unpredictable events that punctuate natural and human history (tsunamis, epidemics, wars, market crashes; Taleb 2007). Strong linkages between social and ecological systems can enhance the consequences of unpredictable fluctuations, such as the global economic crisis of 2008–2009.

A final source of uncertainty emerges from the adaptiveness of complex systems. When an ecosystem experiences unprecedented events, how can we predict how it will respond? How can we predict how forest ecosystems will respond to management practices under altered conditions (Puettmann 2011)? Given the heterogeneity of their components and interactions, the sources of innovation in complex systems are innumerable. Compositional, structural, or behavioral changes at the bottom of the system's hierarchy can drive, through self-organizing processes, massive rearrangements such that little remains of the original system's dynamics or functions (Mascaro et al. 2012). As temperatures rise in the Northern Hemisphere, for example, shifts in tree species distributions will profoundly affect the composition of boreal forests (Gustafson et al. 2010). New communities that reflect species' dispersal and survival abilities under warmer conditions will emerge. Specific ecosystem responses to changes across organizational scales are inherently unpredictable and imply that uncertainty will prevail.

Flexible and adaptive management programs are needed to prepare for unpredictable ecosystem behavior (Walters 1986). Currently, uncertainties about future events are addressed as they arise rather than formally incorporated into plans. In much of Canada's boreal forest, for example, the annual allowable cut does not explicitly consider fire or recurrent insect epidemic risks and is only revised a posteriori following a large disturbance (Dhital et al. 2013). Rather than focusing on a single, optimal vision of the future, forest managers should use adaptive management or scenario building models to explore an envelope of probable futures that becomes wider the further forward one projects (Lempert 2002, Peterson et al. 2003, Parrott and Meyer 2012). Planners quantify the likelihood of each scenario, and address the ranges of uncertainties in ecological, social, and economic dimensions. Success of management operations should be measured at multiple spatiotemporal scales rather than at the stand scale (Puettmann and Tappeiner, *unpublished manuscript*).

Recent research has emphasized incorporating into forest management decisions the uncertainty about climate change, the price of timber vs. carbon, the risk of losing rare species, and other such factors into forest management (Yousefpour et al. 2012). Techniques for such analyses exist but have rarely been operationalized, due in part to their intricacy. A recent example evaluated how the risk of losing endangered woodland caribou in Labrador, Canada depends on the level of logging (Ben Abdallah and Lasserre 2012).

Promoting variability in stand and tree species characteristics may require less management inputs while increasing the likelihood that unknown future conditions will affect the trajectory of each stand differently. Silvicultural treatments may need to abandon the goal of recreating historic variability in forest conditions and processes, to instead promote novel response-type diversities that enable ecosystems to adapt to unprecedented future conditions (Hobbs et al. 2006). Mixed species stands have more possible "pathways" to react to changes than dense monocultures. Indeed, differential responses to disturbances should emerge in stands with heterogeneity in tree spacing, size, ages and reproductive strategies and varied understory vegetation. For example, harvest prescriptions could encourage species with nitrogen fixing abilities (Ares et al. 2010), contrasting regeneration modes (e.g., resprouting, seedbanking, serotinous cones) and resistances to fires, drought, wind or pest damage (Neill and

Puettmann 2013).

A key in managing for uncertainty is to promote greater heterogeneity in stand composition, structure and services. Forest management could be optimized for wood production as well as other (non-monetized) services such as hydrologic regulation, carbon sequestration, nutrient cycling, biodiversity conservation, pollination and, pest control. Managing now for multiple services may ensure that the future forest retains elements necessary to supply services that could become increasing valuable. Moreover, it seems likely that economic prospects will be enhanced by adopting more flexible standards of acceptability for the next rotation (30 to 100 years). Forest managers should recall costly silvicultural interventions that did not meet expectations or were counterproductive when market value for some tree species changed. Some examples include, growth and yield of many intensive plantations being much lower than expected due to unexpected biotic disturbance (Woods and Coates 2013), tropical silvicultural interventions that did not succeed in maintaining yield (Dawkins and Philip 1998), and temporarily low wood prices for one tree species that promoted its replacement by another higher-valued tree species (Fig. 6). More realistic cost/benefit analyses that incorporate diverse ecosystem services and levels of uncertainties are likely to generate very different management strategies.

CONCLUSIONS

We employed the lens of CSS to review various attributes of global forest biomes. While the forest ecology literature abounds with examples of non-linear phenomena, self-organizing mechanisms or long-term legacies, much can be gained from viewing all these as interacting facets of an integrated dynamic system. CSS provide a unifying framework that offer new perspectives on known phenomena in forest ecology and forestry. CSS can change how we understand, study, and thus manage forests and provides a strong scientific platform from which to develop novel management practices that explicitly recognize forest complexity (Messier et al. 2013). CSS can be seen as a logical progression and refinement of earlier concepts and practices in forestry. Notably, CSS conceptualizes forests as open systems with functions driven by social as well as ecological factors, and reduces the dichotomy between economic and ecological perspectives. CSS thus creates an integrative view of widely different forests within which human impacts vary substantially.

Complex systems science fosters understanding of seemingly unrelated issues by identifying common patterns in the structural organization and spatiotemporal dynamics of a diversity of systems. Studying forests, and ecosystems in general, as complex systems therefore facilitates the sharing of insights and applications among different fields.

Finally, CSS views forests as dynamic systems that constantly adapt to new conditions and thereby emphasize that precise predictions of future states are impossible. This perspective provides a basis for the development of holistic management approaches that improve the resilience and adaptive capacity of forests in uncertain times. Forests are experiencing unprecedented rates of abiotic (climate change, landscape fragmentation, pollution, increased nitrogen deposition), biotic (exotic species, biodiversity loss, loss of predator control), and socio-economic (human population growth, resource consumption, urbanization, market globalization) change—with unpredictable direct or indirect outcomes. Climate-induced alterations in the frequency and severity of disturbances coupled with exotic species invasions, affect the composition and successional trajectory of tree communities to the extent that novel forest ecosystems are emerging. Growing food and fiber demands increase pressure on old-growth forests. These drivers, and many others, will have largely unknowable consequences on forests. Uncertainty, especially in developing countries with political instability, is amplified by international to local initiatives, under pressure from multiple stakeholders and policy-makers, to improve forest management. The forests of tomorrow will be profoundly different from those of today. Guidelines for management must acknowledge that variability and uncertainty are the norm in ecosystem conditions and dynamics.

Viewing forests as complex systems highlights the fact that principles based on maintaining stable forest composition and structure cannot continue to guide management strategies. If nothing else, an appreciation of non-linearities and system openness should instill a sense of humility among forest managers, a recognition that we cannot precisely control the future of any tract of forest. Finding ways to manage forests that facilitate desirable outcomes and avoid undesirable ones, despite uncertainty, needs to be a prime goal of forest research. Modern pressures and uncertain futures mean resilience and adaptive potential are replacing productivity (in commercial forests) and stability (in protection forests) as primary goals of forest management. Scenario building that explores a range of possible futures will replace predictive expectations. Complex systems science can help facilitate these important and necessary paradigm shifts.

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