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Can forest management based on natural disturbances maintain ecological resilience?

C. Ronnie Drever, Garry Peterson, Christian Messier, Yves Bergeron, and Mike Flannigan

Abstract: Given the increasingly global stresses on forests, many ecologists argue that managers must maintain ecological resilience: the capacity of ecosystems to absorb disturbances without undergoing fundamental change. In this review we ask: Can the emerging paradigm of natural-disturbance-based management (NDBM) maintain ecological resilience in managed forests? Applying resilience theory requires careful articulation of the ecosystem state under consideration, the disturbances and stresses that affect the persistence of possible alternative states, and the spatial and temporal scales of management relevance. Implementing NDBM while maintaining resilience means recognizing that (*i*) biodiversity is important for long-term ecosystem persistence, (*ii*) natural disturbances play a critical role as a generator of structural and compositional heterogeneity at multiple scales, and (*iii*) traditional management tends to produce forests more homogeneous than those disturbed naturally and increases the likelihood of unexpected catastrophic change by constraining variation of key environmental processes. NDBM may maintain resilience if silvicultural strategies retain the structures and processes that perpetuate desired states while reducing those that enhance resilience of undesirable states. Such strategies require an understanding of harvesting impacts on slow ecosystem processes, such as seed-bank or nutrient dynamics, which in the long term can lead to ecological surprises by altering the forest's capacity to reorganize after disturbance.

Résumé : Étant donné l'augmentation globale des stress dans les forêts, plusieurs écologistes croient que les gestionnaires doivent maintenir la résilience écologique, c'est-à-dire la capacité des écosystèmes à absorber les perturbations sans subir de changements importants. Dans cette revue, nous nous demandons si le nouveau paradigme de l'aménagement basé sur les perturbations naturelles peut maintenir la résilience écologique dans les forêts aménagées? L'application de la théorie de la résilience exige une articulation minutieuse de l'état de l'écosystème considéré, des perturbations et des stress qui affectent la persistance d'états alternatifs potentiels ainsi que les échelles spatiales et temporelles de la pertinence de l'aménagement. L'application de l'aménagement basé sur les perturbations naturelles, tout en maintenant la résilience, oblige à reconnaître que (*i*) la biodiversité est importante pour la persistance à long terme de l'écosystème, (*ii*) les perturbations naturelles jouent un rôle crucial dans la genèse de l'hétérogénéité de la structure et de la composition à de multiples échelles et (*iii*) l'aménagement traditionnel tend à rendre les forêts plus homogènes que celles qui sont naturellement perturbées et à augmenter les chances de changements catastrophiques inattendus en réduisant la variation de processus environnementaux clés. L'aménagement basé sur les perturbations naturelles peut maintenir la résilience si les stratégies sylvicoles permettent de conserver les structures et les processus qui perpétuent les états désirés tout en réduisant ceux qui favorisent la résilience d'états indésirables. De telles stratégies exigent de comprendre les impacts de la récolte sur les processus écosystémiques lents, tels que la banque de graines ou la dynamique des nutriments, qui peuvent causer des surprises à long terme en modifiant la capacité de la forêt à se réorganiser après une perturbation.

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Introduction

The structure and composition of forests are increasingly influenced by global phenomena such as the presence of introduced species, climate change, and anthropogenic alterations of biogeochemical cycles (Newman 1995; Vitousek et al. 1997; Simberloff 2000; Dale et al. 2001; Honnay et al. 2002). Major transformations of forest ecosystems have occurred or are underway, in many cases resulting in substantial losses of timber values or commercial extinction of valuable tree species, along with a reduction in native biodiversity (Liebhold et al. 1995; Laurance 1999; Simberloff 2000; Hoekstra et al. 2005). In addition to these global influences, forests are also being shaped by regional and local forces. In Canada, for example, the area logged per year doubled between 1960 (~500 000 ha·year^{-1}) and 1995 (~1 Mha·year^{-1}) and, in many years, harvesting has replaced fire as the dominant disturbance in productive forests (World Resources Institute 2000). Moreover, forests often experience the cumulative and often fragmentary impacts of development pressures such as road-building, oil and gas development, urban and suburban encroachment, and agriculture (Forman 2000; Trombulak and Frissell 2000; World Resources Institute 2000; Schneider et al. 2003). This combination of disturbance and developmental pressures can reduce biodiversity and diminish the capacity of forests to continue providing ecological goods and services of the same quantity and quality in perpetuity (Toman and Ashton 1996; Costanza et al. 2000).

In response to these concerns, many ecologists have argued that resource managers should focus on maintaining ecological resilience, defined here as the capacity of natural systems to absorb disturbances without undergoing change to a fundamentally different state (e.g., Holling 1973; Holling 1986; Peterson et al. 1998). These authors propose that rather than setting specific and sustained targets, such as allowable annual cuts or a minimum amount of wildlife habitat, managers should seek to enhance the resilience of ecosystem states deemed essential to the provision of ecological goods and services while at the same time decreasing the resilience of states that do not provide these or that do so at low levels (Gunderson and Holling 2002). Here we ask: Can natural-disturbance-based management (NDBM) maintain or confer ecological resilience in managed forests? We review the concepts inherent in such a question, drawing principally from examples in North American forests, and present ideas on how to anticipate and avoid potential ecological surprises that can arise when goods and services are extracted from forest ecosystems on a sustained basis. We then recommend how forest managers can integrate resilience into their silvicultural regimes in the context of NDBM. While our recommendations are most applicable to large tracts of forest managed for traditional forest values such as timber or wildlife habitat, we believe that they also apply to other types of tenure such as wood lots or community forests.

Review of concepts

Ecological resilience

Ecological resilience is the capacity of an ecosystem to absorb disturbance and undergo change while maintaining its essential functions, structures, identity, and feedbacks (Holling 1973; Peterson et al. 1998; Walker et al. 2004). Resilience is often synonymous with adaptive capacity, i.e., the ability of a system to reconfigure itself in the face of disturbance or stresses without significant decreases in critical aspects such as productivity or composition (Gunderson 2000; Carpenter et al. 2001). Resilience is an emergent property of ecosystems that may be estimated from the magnitude of disturbance a system can absorb without undergoing significant transformational change (Gunderson 2000; Walker et al. 2004). For example, resilience of aspen parkland can be estimated from the maximum frequency of intense fires or drought that it can experience before converting to grassland. This definition of resilience therefore assumes the existence of alternative system states (e.g., parkland vs. grassland) and is primarily concerned with (*i*) how changes in the structure of an ecosystem can alter its behaviour, and (*ii*) how a given state persists over time (Holling 1973; Gunderson 2000; Walker et al. 2004). Alternatively, resilience may be measured as the probability that a given state will persist over the time period of interest (Peterson 2002*b*). Whether resilience is desirable or not depends both on the values desired from the system and on its current state (Carpenter et al. 2001). For instance, a fragmented patch of forest composed principally of exotic species with low social utility may be an undesirable but highly resilient state; alternatively, a productive monoculture of trees may be an economically desirable state with low resilience to root disease or other pathogens.

Unfortunately, the multiple meanings given to ecological resilience in the literature have created confusion and hindered application of a concept that is inherently somewhat inexact (Beisner et al. 2003; Walker et al. 2004). To estimate resilience, it is necessary to specify several qualitative characteristics. These include the state(s) and spatial scale of the system being considered (resilience *of* what), the perturbations of interest that affect the persistence of system states (resilience *to* what), and the temporal scale of interest (Carpenter et al. 2001; Walker et al. 2004). The temporal scale depends on relevant aspects of the system of interest, such as turnover rates of dominant species; for example, it will be considerably shorter in studies of microcosms than in those of forests (Connell and Sousa 1983). Temporal scale is also important for classifying the system processes as either fast or slow, i.e., as either variables or parameters in a model of the system (Ludwig et al. 1978; Beisner et al. 2003).

In a forest context, it is important to clarify the relationship of succession to the system states of interest. A forest that changes as it ages is not necessarily changing states; rather it may be considered to be undergoing compositional and structural change internal to the system without switching to an alternative state, e.g., when a forest changes into a grassland, tundra, or sphagnum bog. However, there are some circumstances when succession may give rise to an alternative and less desired state, such as when a forest undergoes gradual paludification to a bog-like state (Banner et al.1983; Fenton et al. 2005), or when a shade-intolerant deciduous stand senesces into a permanently shrub-dominated condition (Shields and Bockheim 1981; Nierenberg and Hibbs 2000). In essence, the role played by succession depends on how research questions or management issues are

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Table 1. Alternative stables states in forest ecosystems.

Location	Alternative states	Reference(s)
Boreal forest of New Brunswick, Canada	Outbreak vs. endemic abundance of spruce budworm	Jones 1975; Ludwig et al. 1978
Deciduous old-growth stands in Minnesota, USA	High vs. low abundance of a forest forb relative to high abundance of an ungulate herbivore	Augustine et al. 1998
Serengeti Mara woodlands, Tanzania	Wooded vs. grassland states resulting from fire and elephant disturbance	Dublin et al. 1990;
Northern boreal forest, Sweden	Birch–spruce succession vs. pine dominance as a function of ungulate browsing	Danell et al. 2003
Southern boreal forest of Quebec, Canada	Dense spruce–moss stands vs. lichen woodlands as a function of compounded disturbance	Payette et al. 2000; Dussart and Payette 2002
Pinelands in New Jersey, USA	Open, sparsely vegetated areas dominated by lichen mats vs. moss-dominated areas that foster pitch pine (*Pinus rigida* Mill.) forests	Sedia and Ehrenfeld 2003
Sandhill forests, Florida, USA	Hardwood vs. longleaf pine (*Pinus palustris* Mill) as a function of fire frequency	Peterson 2002*b*
Tropical rain forests	Mesic, fire-inhibiting vs. xeric fire-susceptible forests mediated by opening of roads and agriculture	Cochrane 2003

formulated, the time scales involved, and their relationship to relevant system states (Carpenter et al. 2001).

Alternative stable states

"Alternative stable state" can have one of two, not necessarily mutually exclusive, meanings (Beisner et al. 2003). In population or community ecology, stable state is a relatively constant configuration or assemblage of individuals or species (Lewontin 1969; Sutherland 1974; Law and Morton 1993). In ecosystem ecology, a stable state is a set of self-perpetuating and mutually reinforcing structures and processes (Holling 1973; Peterson et al. 1998); this is the definition used in this paper. Within a "stable" state, ecosystem attributes such as species composition can fluctuate, but these fluctuations occur within certain relatively constant limits maintained by internal ecosystem structures or external constraints (Connell and Sousa 1983; Scheffer et al. 2001). Moreover, stable states always show slow trends, such as paludification (Scheffer and Carpenter 2003). When resilience is diminished and an ecosystem reorganizes, control of ecosystem behaviour shifts from one set of interacting physical and biological structures and processes to another (Peterson et al. 1998).

A great variety of ecosystems can exist in alternative stable states (Walker and Meyers 2004). Alternative stable states have been documented for lakes, coral reefs, marine fisheries, benthic systems, wetlands, forests, savannas, and rangelands (Carpenter et al. 2001; Scheffer et al. 2001). Examples of alternative stable states in forest ecosystems are presented in Table 1.

As with resilience, whether a specific stable state is desirable depends on its social or economic utility and the management context. In unmanaged ecosystems, evolution has led to dominant states that have high resilience as a function of how prevailing natural disturbances influence the structures and processes that provide this resilience. Human intervention beyond the historical range of variability can cause novel pressures on ecosystems and alter the natural dynamics between disturbances and stable states, thereby changing the "stability landscape" (Scheffer et al. 2001) in the managed ecosystem. Often, this change is manifested as an increase in the number of stable states.

Typically, shifts among states can occur in one of two ways: (1) changes in slow processes that trigger responses in a fast process, and (2) compounding of disturbances. A classic example of changes in slow variables triggering rapid change in forests is the control of spruce budworm (*Choristoneura fumiferana* Clem.) by birds and its relationship to the density of the spruce budworm's primary prey, balsam fir (*Abies balsamea* (L.) Mill.) in spruce–fir forests of eastern Canada (Holling 1973; Ludwig et al. 1978). Between outbreaks, the density and size of balsam fir and spruces (*Picea* spp.) increase gradually (slow process), reducing the efficiency with which predatory birds forage (fast process). Once foraging efficiency drops below a certain threshold, avian predation can no longer play an important role in maintaining low spruce budworm abundance and, in combination with other controlling factors, this leads to budworm outbreaks (Holling 1988).

In addition to slow changes in environmental variables, shifts between ecosystem states depend on the frequency, intensity, and compounding of disturbances. Typically, disturbances at the larger end of their range of intensity and size do not cause a lasting change in the fundamental character of a system (Paine et al. 1998). Large infrequent disturbances usually do not undermine the mechanisms that determine species composition, as composition before and after such disturbances is typically similar (Turner et al. 1997). Exceptions include very severe events, such as lava flows or intense and soil-destroying fire, which eliminate key ecosystem components. Wholesale transition to fundamentally different states — "regime shifts" — is most frequent when multiple disturbances occur within the normal recovery time of the system (Paine et al. 1998). When either the spatial extent or, more commonly, the frequency of a given severe disturbance is at or beyond the extreme end of its historical

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range of variability, the regenerative capacity of a ecosystem may be overwhelmed (Paine et al. 1998). One example of such a regime shift is the abrupt change from closed-canopy spruce–moss forest to open-canopy woodland that can occur following consecutive disturbances in eastern North America (Payette et al. 2000). When insect outbreaks, fire, and harvesting occur in rapid succession, their combined impact can dramatically reduce the spruce seed pool, not only immediately after disturbance but for a prolonged period, thereby engendering a shift from closed forest to sparse trees with thick lichen mats that inhibit further tree establishment in a positive feedback loop (Payette et al. 2000; Payette and Delwaide 2003). Wind and fire can similarly occur as cascading catastrophic perturbations in northern hemlock–hardwood forests, causing a shift in dominance from shade-tolerant trees to sustained aspen–birch dominance (Lorimer 1977; Frelich and Reich 1999). Likewise, in the near-boreal forests of Minnesota, USA, when two severe fires occur within 10 years, a shift in species dominance from jack pine (*Pinus banksiana* Lamb.) to trembling aspen (*Populus tremuloides* Michx.) can occur as the result of the second fire consuming surviving jack pine propagules (Heinselman 1973).

Panarchy: an integrative theory of change and ecosystem dynamics

A general theory of change in complex adaptive systems, termed panarchy, integrates resilience and ecosystem dynamics at multiple scales (Gunderson et al. 1995; Holling 2001; Gunderson and Holling 2002). It combines the notion of an adaptive cycle with the hierarchical structure of ecosystem structures and processes. Briefly, panarchy considers ecosystems as a set of interacting adaptive cycles that occur at different spatial and temporal scales. It is a way of looking at natural systems rather than being itself a specific testable hypothesis (Carpenter et al. 2001; Gunderson and Holling 2002).

The adaptive cycle

Resilience theory states that complex systems such as forests do not simply tend towards an equilibrium condition, but rather cycle dynamically, based on the tension between forces that select for efficiency and those that select for novelty (Gunderson and Holling 2002). This adaptive cycle can be divided into four phases: rapid growth and exploitation (r) and conservation (K) — the front loop — followed by release or collapse (Ω) and, subsequently, renewal or reorganization (α) — the back loop (Holling 1986; Fig. 1). The growth and conservation phases usually occur slowly as a system organizes. Collapse and renewal are usually rapid as a system reorganizes. The two complementary and sequential loops foster both conservation and change (Holling 1986; Holling 2001). The front loop maximizes production, efficiency, and accumulation of capital, while the back loop maximizes invention, variety, and re-assortment. The lags between these periods of stability and bouts of strong selection and innovative rearrangement mean that diversity is perpetually created, thereby providing the elements for resilience over time across a large range of environmental conditions (Holling and Gunderson 2002).

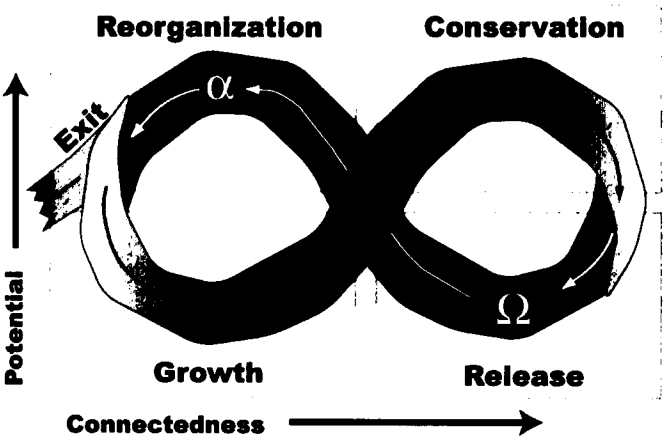

Fig. 1. Adaptive cycle of a complex adaptive system. The arrows indicate the speed of change in the cycle: short, narrowly spaced arrows indicate slow change, while long arrows indicate rapid change. The exit from the adaptive cycle at the left suggests where in the cycle the potential of a system can leak away and where a switch into a system with lower productivity and organization is most likely to occur.

The front loop of the adaptive cycle is essentially ecological succession. The system slowly builds biomass, connectedness, and potential for change. Gradual change in the front loop increases a system's vulnerability to disruption and reorganization. For example, as a stand ages and its dominant trees ascend beyond the canopy, windthrow hazard gradually increases for the entire stand (Everham and Brokaw 1996). During the front loop, resilience is initially high during the exploitation phase — the system is capable of absorbing a wide range of disturbances without shifting into an alternative stable state — but gradually decreases through the K phase as the system reaches its limits of mature growth (Fig. 2). Rigidity and internal control of processes (connectedness) increase, as do the system's stored energy and biomass (potential). At the end of the K phase the system has low resilience, so even small perturbations can initiate a cascade of rapid structural changes throughout the highly connected system. In the K phase the system may actually be very stable, e.g., a forest will rebound quickly from a small disturbance such as localized windthrow. However, this stability is narrow and local (Gunderson 2000), highlighting the possible trade-off between resilience and stability (Holling 1973).

Rapid change and reorganization characterize the back loop. As the system collapses (Ω) and begins to reorganize (α), attributes or components of the ecosystem can be lost or dramatically changed before a new system begins to organize itself. Moreover, external forces or variability can exert a strong influence on the system, e.g., seeds from veteran trees or trees outside the disturbed area can exert a lasting influence on the composition of a regenerating stand. As the α phase unfolds, many experimental and innovative combinations of system components are "tried" locally and most fail, as is observed, for example, in the many distinct assemblages of trees and shrubs that established following the eruption of Mount St. Helens (Franklin and MacMahon 2000). It is during these periods of collapse and reorganization that the future development of the system can most inti-

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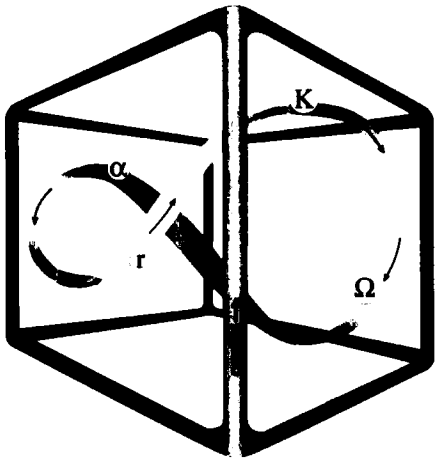
Fig. 2. Resilience as a third dimension in the adaptive cycle. Resilience changes throughout the cycle, gradually decreasing as the cycle moves from the *r* to the K phase and increasing as the system rapidly shifts in the back loop.



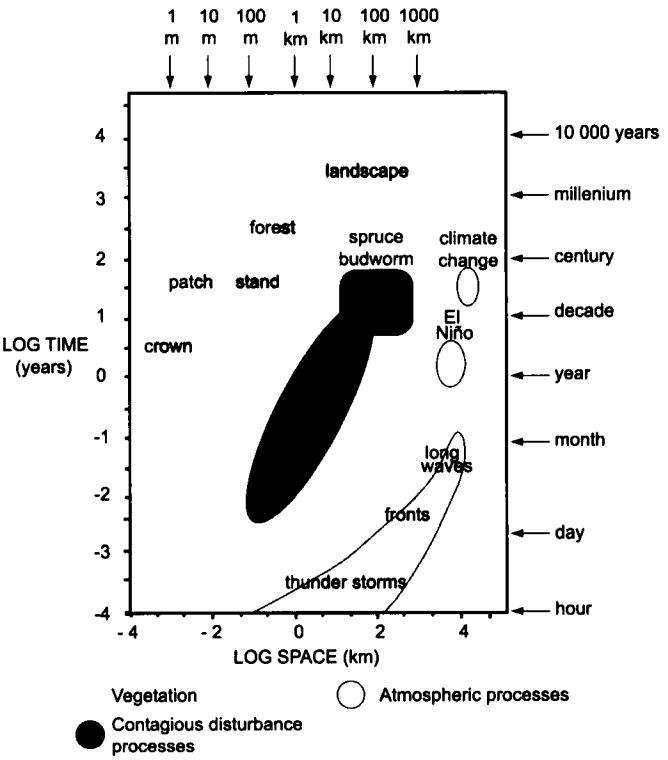
mately depend on small, fast processes, i.e., as it reorganizes around "seeds" of order emerging from lower levels of organization (Peterson 2000). During the back loop, connectedness and potential are low and internal controls of system processes are weak; resilience to another similar disturbance is high because change in one component of the system has few consequences for other components (Fig. 2). Following the back loop, if sufficient system components remain, the system may then reenter the *r* phase and begin anew to build complexity, connectedness, and resilience. Alternatively, the system may reorganize into a new configuration based on the arrival of novel species or components.

Cross-scale structure and connections

The processes and structures that control ecosystem behaviour can be understood as a cross-scale, nested set of adaptive cycles (Holling and Gunderson 2002). In the boreal forest, for instance, Holling (1986) recognizes the following scales and their associated processes (Fig. 3). At fine scales, pattern and process are dictated by biophysical forces that control plant physiology and morphology. At the coarser and slower scale of patch dynamics, competition among plants for nutrients, light, and water determines local species composition and regeneration. The next coarser and slower scale is set by mesoscale contagious processes such as fire, insect outbreaks, and large-mammal herbivory that together determine the structure and successional dynamics of stands at scales ranging from tens of metres to kilometres, and from years to decades. At the landscape scale, climate, along with geomorphological and biogeographical processes, alters ecological structure over hundreds of kilometres and millennia.

The hierarchical structure contributes to resilience because it performs two important functions: (1) conserving and stabilizing conditions for the smaller and faster levels, i.e., interactions across scales in a hierarchy are asymmetrical, so larger, slower levels constrain the behaviour of smaller, faster levels, and (2) generating and "testing" innovations such as mutations or new species assemblages by means of experiments occurring within each level (Simon

Fig. 3. Time and space scales in the boreal forest (Holling 1986) and atmosphere (Clark 1985) illustrating relationships among processes that structure the forest. The interactions among the slow vegetation processes and faster atmospheric processes are mediated by mesoscale contagious processes like fire or spruce budworm outbreaks.



1974; Levin 1981; O'Neill et al. 1986). In other words, finer scale positive feedback creates heterogeneity, while coarser scale negative feedback stabilizes it (Levin 2000).

Two types of cross-scale connections or feedbacks among adaptive cycles affect resilience: "revolt" and "remember" (Holling and Gunderson 2002; Fig. 4). These connections are important during times of rapid change in adaptive cycles. Revolt refers to what occurs when a level in the hierarchy enters the collapse (Ω) phase and triggers a crisis in the next larger, slower cycle because the larger, slower cycle is itself in its *K* phase, a phase of low resilience. In the western boreal forest, for example, this occurs when fuel loads and climatic conditions allow a locally ignited ground fire to spread to a tree crown, then to a patch of trees, and eventually an entire stand. If revolt leads to another crisis in higher cycles undergoing a phase of low resilience, then change to an alternative state can be caused by an abrupt positive-feedback chain of collapse (Holling 1996; Carpenter et al. 2001).

Remember refers to the cross-scale connection that occurs when collapse occurs at one level and its development is shaped by the accumulated biomass or potential of a slower and larger level in its *K* phase (Fig. 4). A forest "remembers" its predisturbance composition and structure by the presence of at least three interacting parts (Nystrom and Folke 2001; Lundberg and Moberg 2003; Folke et al. 2004): biological legacies, mobile links, and support areas. Biological legacies are species, patterns, or structures that persist

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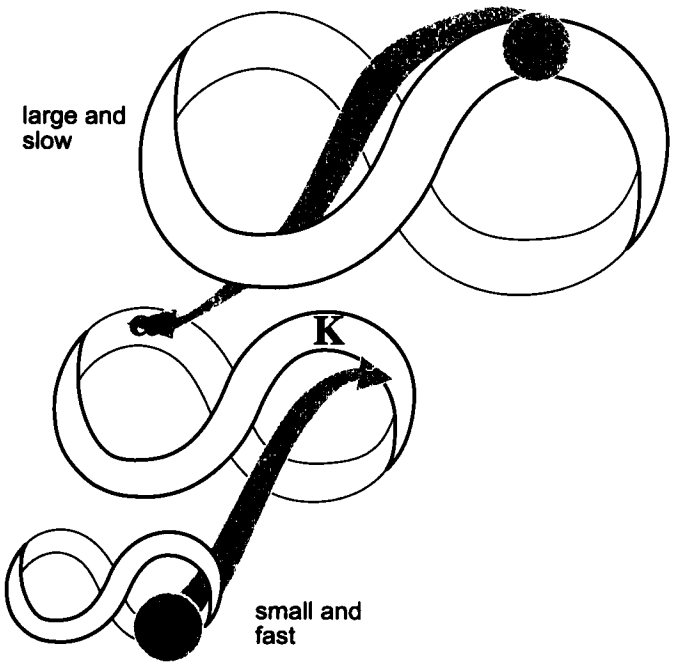
Fig. 4. Connections among adaptive cycles in panarchy. "Revolt" refers to how a critical change in one adaptive cycle can cascade upwards to a vulnerable stage in a larger, slower cycle, e.g., when forest conditions are such that a locally ignited ground fire can spread to a tree crown, then to a patch of trees, and eventually to the entire stand. "Remember" refers to how renewal is facilitated at scale by drawing on the accumulated potential in a larger, slower cycle, e.g., by the presence of veteran trees that can be refugia from fire or provide seeds and nutrients to a regenerating stand.



within a disturbed area and act as sources of ecosystem recovery, such as large living and dead trees or tree clusters that provide seeds, buried rhizomes or roots, and nutrients to the regenerating stand (Franklin and MacMahon 2000). In some cases these legacies may be biased towards structures or patches that are more likely to survive the disturbance, such as wet or low-lying sites during forest fires. Mobile links are "keystone" organisms that move between habitats and ecosystems after a disturbance to provide essential ecosystem processes that are lacking, such as pollination, seed dispersal, or nutrient translocation, by connecting areas that may be widely separated spatially or temporally (Lundberg and Moberg 2003). Support areas refer to landscape patches or habitats that maintain viable populations of mobile links (Lundberg and Moberg 2003). Together these interacting parts play a pivotal role in renewal and reorganization of a disturbed system.

Natural-disturbance-based management

NDBM refers to silvicultural practices and strategic-planning approaches that emulate natural-disturbance regimes (Hansen et al. 1991; Hunter 1993; Attiwill 1994; Bergeron and Harvey 1997; Angelstam 1998). The underlying rationale is that management approaches based on the dominant natural-disturbance regime will restore or maintain biodiversity and essential ecosystem functions by restoring or maintaining the full historical range of habitat heterogeneity observed at multiple scales in unmanaged forests (Franklin and Forman 1987; Pickett et al. 1997). It is essentially a coarse-filter approach to biodiversity conservation that recognizes that (*i*) humans tend to homogenize or constrain the type, frequency, severity, and size of disturbed patches to the mesoscale (Bergeron et al. 2002; Kuuluvainen 2002), and (*ii*) spatial and temporal variability in disturbances, both human and natural, is essential to maintaining the habitat heterogeneity on which all component species of an ecosystem depend (Hunter et al. 1988; Kuuluvainen 2002). Typically, NDBM approaches seek to maintain biodiversity relative to present or reference (pre-industrial or pre-European settlement) forest ecosystems (Bergeron et al. 2002).

NDBM approaches have been articulated for landscape and stand scales. At the landscape or strategic-planning scale, NBDM entails creating or maintaining, as closely as possible to that observed in "natural" forests, the abundance and distribution of different age classes, the diversity of size classes of disturbed areas, and the spatial arrangement of different stand types over time (Angelstam 1998; Bergeron et al. 1999). These objectives may be attained by varying rotation length (Burton et al. 1999; Seymour and Hunter 1999) or diversifying silvicultural practices in different cohorts (Bergeron et al. 2002). At the stand scale, NDBM focuses on silvicultural systems, such as variable retention, that preserve elements of forest structure within the historical range of variability retained by dominant disturbances (e.g., large woody debris, trees of various sizes and species, including large-canopy dominants, snags of various sizes and stages of decay, and gaps in the canopy) (Franklin 1993; Franklin et al. 1997; Mitchell and Beese 2002; Aubry et al. 2004). Retaining structure can maintain associated ecological functions and processes; preserve genetic information of trees, shrubs, and associated biota; maintain structural complexity; improve connectivity between cutting units and forested areas; and serve as "lifeboat" habitat for organisms that might otherwise be lost temporarily or permanently (Franklin et al. 1997; Haeussler and Kneeshaw 2003). At both scales, NDBM schemes include a myriad other components that are beyond the scope of this article (e.g., frequency of landscape-scale disturbances, strategies for managing the abundance and distribution of various structural types in time and space, process restoration such as by prescribed fire).

Traditional forest management, biodiversity, and resilience

Typically, at the onset of a given management regime, managers do well at achieving a narrow set of well-defined objectives by controlling a target variable such an allowable annual cut or a given rotation period (Holling and Meffe 1996; Gunderson 2000). This success is typically the result of a "command and control" strategy that seeks to standardize or minimize the natural variability of key ecosystem processes such as fire or regeneration (Pastor et al. 1998). Unfortunately, initial management successes have the simultaneous consequences of (*i*) encouraging people to become dependent on the continuation of the management regime and (*ii*) eroding the ecological resilience of the desired ecosystem state by slowly changing other parts of the ecosystem

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and reducing ecosystem variability in time and space (Holling 1986). This leads to a condition in which ecological change becomes increasingly undesirable yet more difficult to avoid. When dramatic change does arrive, it is typically a surprise and a policy crisis ensues (Gunderson et al. 1995). Such is the "pathology of resource management" — any system of practices, institutions, and regulations that manages an ecosystem for the consistent and predictable flow of goods or services results in reduced resilience, dependent societies, and inflexible management agencies (Holling and Meffe 1996). For example, elevated harvesting rates and intensive management for sustained timber yields from the 1950s to the 1980s greatly reduced compositional, structural, and age-class diversity across the spruce–fir forests of New Brunswick, Canada. This shift had several unexpected consequences, including a long-term decline in diversity (though not volume) of wood products, elevated harvesting costs, widespread failures of advance regeneration, the commercial extinction of eastern white pine (*Pinus strobus* L.), a long period of chronic spruce budworm infestations, and sustained shortages of high-quality timber (Baskerville 1985, 1988; Regier and Baskerville 1986).

The resilience theory summarized above suggests that homogenization of landscape structure and composition through reductions in the variability of disturbance regimes can entrain faster major cycles of adaptive change because normalized forests are more connected and less diverse across both time and space. This suggestion is consistent with general concerns that increased forest homogenization can increase overall landscape susceptibility to fires, insects, and diseases (Franklin and Forman 1987; Turner and Romme 1994; Bergeron et al. 1998) or that disturbances initiated in one part of the landscape are more easily transmitted to other parts in a well-connected landscape (Peterson 2002*a*). In the long term, reducing the diversity in type, frequency, or size of disturbance means that fewer selective forces are at work, owing to the harmonization of disturbance cycles; this harmonization would lead to less renewal and, eventually, less diversity. Evidence of this process at work comes from documentation of extensive losses of biodiversity in intensively managed Scandinavian forests due to the combined effects of fire suppression and long-term intensive forest management (Berg et al. 1994; Berg et al. 1995; Hansson 1997; Angelstam 1998).

Given the homogenizing potential of traditional management on forest diversity, ecologists and managers are increasingly emphasizing that biodiversity should be maintained to sustain desirable system states as environmental conditions change over time (Peterson et al. 1998; Kuuluvainen 2002; Bengtsson et al. 2003). It is established in the literature that (*i*) heterogeneous natural systems like forests are more stable than simpler artificial systems like crops and laboratory populations (Murdoch 1975; McCann 2000), (*ii*) adequate performance of ecosystems depends on having diverse species in all necessary functional groups (pollinators, primary producers, herbivores, etc.) (Schindler 1990), and (*iii*) the persistence of ecological function over time depends on the diversity of response by different species within a functional group to changing environmental conditions (i.e., response diversity) (Naeem et al. 1994; Walker et al. 1999; Elmqvist et al. 2003). In other words, resilient ecosystems depend on functional diversity and response diversity at multiple scales (Peterson et al. 1998).

In forests, evidence that diversity and complexity afford increased resilience comes from studies of both natural and managed areas. These studies show that forests with greater structural and compositional diversity more easily resist disturbance, more quickly regain predisturbance composition, and in some cases, are more productive than less diverse forests. At the landscape scale, increasing complexity may decrease the spread rate and extent of diseases and disturbances (Turner et al. 1989; Rodriguez and Torres-Sorando 2001), decrease survival and reproductive rates of introduced species (Simberloff 1988; Cantrell and Cosner 1991; Saunders et al. 1991; Andren 1994; Bender et al. 1998; Hiebeler 2000), and globally stabilize locally unstable population dynamics (Hastings 1977; May 1978; Reeve 1990; Taylor 1990). At the stand scale, species composition has been shown to be more stable and to recover more quickly from disturbance in sites with a high diversity of understory plants than in less species-rich sites (De Grandpre and Bergeron 1997; Turner et al. 1999). Plantations are typically less resilient to disturbances such as fire and often experience more pest outbreaks than natural forests (Schowalter 1988; Perry 1998; Coyle et al. 2005). In terms of productivity, Caspersen and Pacala (2001) analyzed a large set of US forest inventory data and found that rates of stand growth increase monotonically with canopy species richness, irrespective of successional status. In other words, stands with high tree diversity, of either early- or late-successional status, had higher annual growth rates than respective low-diversity early- or late-successional stands (Caspersen and Pacala 2001).

In practice, whether enhanced connectedness due to homogenizing management activity is beneficial or detrimental depends on the exchange process, patch types, stresses or disturbances, desired states, and management objectives for the forest in question. For example, if maintaining viable grizzly bear populations in managed areas is an objective, retaining connectedness among habitat types required by grizzlies for foraging and reproduction is critical (Weaver et al. 1996). Conversely, if management objectives include the maintenance of viable populations of endemic herbs, the enhanced connectedness provided by forest roads that augment the dispersal of introduced plant species is clearly detrimental (Trombulak and Frissell 2000).

Can forest management based on natural disturbances maintain ecological resilience?

In a forestry context, resilience-based management refers to a set of planning and silvicultural practices aimed at building an ecosystem's capacity to persist in a desired state and to reorganize in the face of severe disturbances (Walker et al. 2002). In cases where the ecosystem is already in an undesirable state or configuration, resilience-based management means reducing the resilience of the present state and enhancing that of more desirable states. Any such practices or planning approaches must consider the present system state in relationship to its adaptive cycle, its likely trajectories given ongoing stresses, or other likely influences on system change (i.e., climate change, the presence of introduced

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species, development pressures from urbanization, etc.) and how the present state compares with desired system states.

The principal foci for a NDBM approach that can maintain ecological resilience are, clearly, disturbances and their retained biological legacies. Both NDBM and a resilience perspective recognize the importance of maintaining structural and compositional heterogeneity at multiple scales, as well as the role that disturbances play in generating heterogeneity. Integrating the two perspectives requires an understanding not only of the dynamics of disturbance to allow emulation of disturbance at relevant scales, but also of the impacts of such an approach on the processes and structures that perpetuate desired system states. Moreover, it requires an understanding of how management can affect slow system processes, such as long-term seed-bank or nutrient dynamics, that may in the long term lead to ecological surprises by altering the capacity of a forest to reorganize and reestablish following a disturbance. For instance, tree removal in northern forests can alter the competitive balance on the soil towards cryptogram mats that inhibit the germination and establishment of regenerating trees (Dussart and Payette 2002).

At a strategic or landscape level, implementing NDBM while maintaining resilience means that forest managers must make several decisions regarding the role of disturbances within their jurisdiction, in particular whether harvesting will be a substitute for or additive to the frequency of intense natural disturbances. If the former, the role of large-scale disturbance suppression and its impacts on the slow variables that can, in the long term, diminish the resilience of certain states needs to be addressed. If the latter, a decision needs to made about the implications of compounded impacts on the resilience of any desired states put at risk by the additive disturbances, especially if present harvesting rates are deemed to be outside the historical range of variability or if harvesting has become the dominant disturbance across the landscape. A further landscape-level consideration is that the potential for homogenization makes it important to avoid implementing the same silvicultural system everywhere. Given the infeasibility of truly replicating natural disturbance by harvesting, preventing homogenization also depends on a network of reserves and protected zones to maintain heterogeneity throughout the managed area as well as support areas for important mobile-link species (Bengtsson et al. 2003).

At the stand scale, the retention of ecological structures during harvest as prescribed by a NDBM approach fits well with managing for resilience. Retaining structure allows for the harvested stand to "remember" its preharvest condition — genetically, compositionally, structurally, and otherwise. In this respect, a NDBM approach that maintains resilience involves paying close attention to management impacts on "neighbourhood effects", i.e., any feedback processes mediated by canopy trees that alter the probability of replacement by the same or other species following the death of the canopy trees (Frelich and Reich 1995, 1999). Neighbourhood effects may act as positive feedback (self-replacement) or negative feedback (replacement by another species). Examples of positive neighbourhood effects include stump sprouting, seed rain, or the deep shade cast by shade-tolerant species (Wilson and Agnew 1992; Frelich and Reich 1999). Examples of negative neighbourhood effects include alterations of soil physical and chemical properties or changes in mycorrhizal characteristics that favour the growth of species other than those presently on site (Frelich and Reich 1999; Frelich 2002). Tailoring prescriptions of stand-level retention to the species and structures that have positive neighbourhood effects can help maintain the resilience of desired states. In doing this, it is important to keep in mind that although management may seek to emulate disturbance by retaining structure, fundamental differences exist between harvesting and fire, windthrow, insect outbreaks, and pathogens (Quine et al. 1999; McRae et al. 2001). These differences mean that maintaining diversity through harvesting may be insufficient to maintain resilience unless the process, not only the pattern, of disturbance is emulated (Haeussler and Kneeshaw 2003). For example, in the boreal forest of Quebec, a form of clear-cutting that protects regeneration and soils may produce stands with the same even-aged structure as severely burned stands, but these stands may be less productive that postfire stands because of enhanced biomass partitioning into the forest floor rather than living trees (Fenton et al. 2005; Lecomte et al. 2005).

An important consideration is the compounding of severe disturbances resulting from salvage operations. Salvage logging of burned, insect-attacked, or blowdown areas can reduce biological legacies during a critical phase of system recovery, diminish capacity for reestablishment of predisturbance communities, and alter biogeochemical and hydrological processes (Beschta et al. 2004; Lindenmayer et al. 2004). For example, large-scale salvage operations following the 1938 hurricane in central New England, USA, entrained a regional-scale shift in hydrology and, compared with nonsalvaged areas, delayed or prevented the recovery of predisturbance composition and ecosystem processes (Foster et al. 1997). Moreover, removal of burned logs and other woody structure can have long-term consequences on forest diversity and productivity. In the eastern Canadian boreal zone, for example, thin, postfire soils are particularly sensitive to compaction and alteration by harvesting equipment (Brais et al. 2000), and salvage logging simplifies the biodiversity in ground vegetation (Purdon et al. 2004). Other important salvage impacts include the recruitment dynamics of trees that require nurse logs for regeneration and habitat for cavity-nesting birds and other keystone taxa (Harmon et al. 1986; Imbeau et al. 2001; Nappi et al. 2004; Fisher and Wilkinson 2005). In many cases, it may not be economically or socially desirable to entirely forgo timber supply lost through fire or other disturbances, making trade-offs necessary in terms of biological legacies and salvaged timber. In these cases, resilience theory can be especially helpful in identifying key structural legacies, such as seed trees or coarse woody debris, that are of paramount importance in maintaining ecosystem functions and processes.

To return to our title question, can NDBM maintain resilience? The answer is probably yes, if silvicultural strategies implemented on the basis of natural disturbances retain the patterns, structures, and processes that perpetuate desired states while reducing those that enhance the resilience of undesirable states. Essentially, forest managers should view harvesting and regeneration treatments as the back loop of the managed forest. In this context, we make several recom-

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Table 2. Management recommendations at ecosystem, landscape and stand scales to maintain ecological resilience of desired forest states while implementing natural-disturbance-based management.

Scale	Recommendation	Example	Reference(s)
Ecosystem	Know your ecosystem — determine its possible alternative system states, understand how disturbance affects transitions among these states, and investigate how slow processes such as seed-pool or nutrient dynamics affect long-term persistence of desired states	Closed-canopy spruce–moss forest or open-canopy lichen woodland in eastern boreal of North America	Payette et al. 2000
	Contextualize management area within relevant hierarchy of scales and understand how disturbances maintain habitat heterogeneity across time and space	Time and space scales of the boreal forest	Holling 1986
	Understand how type, frequency, and intensity of silvicultural interventions affect the persistence of structures and processes that sustain desired states; ensure that compounded management actions do not diminish or fundamentally alter these structures and processes	Deleterious effects of compounded logging and fire on spruce regeneration	Payette and Delwaide 2003
Landscape	Understand how dominant disturbances create or maintain heterogeneity in landscape age-class structure and composition; seek to emulate these *processes* with harvesting, rather than an arbitrary characteristic such as disturbance size	Role played by fire in eastern Canadian boreal zone and its impacts on abundance and distribution of old-growth forest or bird species assemblages	Bergeron et al. 2001; Drapeau et al. 2000
	Characterize, map, and model how different disturbance regimes affect age-class composition and structure across landscape	Delineation of different management zones according to historical fire frequency in an Oregon, USA	Cissel et al. 1998; Cissel et al. 1999
	Diversify forest practices — do not implement the same silvicultural system everywhere	"Triad" zoning approach for intensive, extensive, and emphasis-on-biodiversity management	Seymour and Hunter 1999; D'Eon et al. 2004
	Maintain landscape heterogeneity by allocating permanent and temporary reserve networks; these networks should (*i*) provide support areas and allow connectivity for mobile-link species important for desired states, and (*ii*) act as reference areas to facilitate understanding of slow ecosystem changes and characterize range of variability of key processes such as disturbance	Riparian reserves to maintain mobile-link role of salmon–bear interactions for the transfer of marine nutrients into temperate rain forests	Hilderbrand et al. 1999; Wilkinson et al. 2005; Nappi et al. 2004
	Understand and minimize impacts of salvage harvesting on biodiversity	Reduction of woodpecker habitat and subsequent impacts on secondary cavity-nesters	
Stand	Understand how harvesting intensity and frequency affect diversity and abundance of component species and structural heterogeneity	Impacts on plant and structural diversity of harvesting, in combination with other disturbances, in eastern boreal forest	De Grandpre et al. 1993; De Grandpre and Bergeron 1997; Reich et al. 2001; Haeussler et al. 2002
	Retain biological legacies in harvested areas that enhance "neighbourhood effects" for desired states	Retention of patches of large veteran pine trees as seed sources in fire-dependent ecosystems	Palik and Pregitzer 1994; Weyenberg et al. 2004
	Tailor the amount, type, and pattern of retention to maintain representation of species in all functional, e.g., pollination or nutrient cycling, groups	Retention of white birch (*Betula papyrifera* Marsh.) in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stands to maintain ectomycorhizzal linkages	Simard et al. 1997
	Maintain habitat of mobile-link species	Retention of snags as habitat to maintain mobile-link role of woodpeckers and secondary cavity-nesters for endemic pest control	Parry et al. 1997; Fayt et al. 2005

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Table 3. Examples of management actions aimed at maintaining ecological resilience of pine-dominated forests to a catastrophic outbreak of mountain pine beetle at each phase of the adaptive cycle.

	Phase of adaptive cycle			
Scale	Exploitation (*r*): "enhance"	Conservation (*K*): "resist"	Collapse (Ω): "minimize damage"	Renewal (α): "direct"
Tree-level responses	Investment in belowground resources	Development of thick bark	"Pitching out"	Seed dispersal to mineral soil
		Enhancement of cone production		
Stand-level treatments	Mixed-species planting	Variable-density thinning	"Green-tree" group-selection harvesting	Retention of non-host and unaffected trees during salvage
	Promotion or maintenance of stand complexity	Creation or protection of snags	Prescribed fire following harvesting	Retention of habitat for beetle predators and pathogens
			Maintenance of stand complexity during salvage	
Landscape-level tactics	Maintenance of heterogeneous age-class structure	Reduction of beetle dispersal (e.g., pheromone baiting, habitat management)	"Leading-edge" sanitation harvesting	Retention of entire killed stands
	Retention of resistant stands			Maintenance of dead-fuel continuity

mendations to managers who want to implement NDBM while seeking to maintain the resilience of desired ecosystem states (Table 2). The recommendations assume that (*i*) resilience to changing environmental conditions depends on maintaining both adequate membership in all functional groups as well as diversity and redundancy within and across scales for all functional groups (Peterson et al. 1998; Walker et al. 1999; Elmqvist et al. 2003), (*ii*) patterns of retention at stand and landscape scales should maintain elements of ecological "memory" of desired system states such as support areas, and (*iii*) retained biological legacies at stand and landscape scales should maintain specific ecological functions or habitats of mobile-link taxa. Examples of structural features that allow stands to reorganize after disturbance include seed trees, advance regeneration, coarse woody debris, snags, and sources of inocula for mycorrhizae.

To illustrate the above recommendations, we provide an example of how they may be applied in the context of western North America's pine forests (Table 3). The largest recorded outbreak of a native insect, the mountain pine beetle (*Dendroctonus ponderosae* Hopkins), is currently underway. These insects caused significant mortality of pines across over four million hectares in British Columbia, Canada, in 2003 alone (Taylor and Carroll 2004). The pine forests of this region are connected at multiple scales — the last seven winters of above-normal temperatures have greatly increased the climatically suitable habitat for mountain pine beetles while freeing these insects from the overwintering mortality that typically keeps them at low abundances (Carroll et al. 2004). Moreover, in recent decades central interior British Columbia has experienced a tripling of susceptible mature pine forest as a result of reduced fire frequency, providing an unprecedented connectedness of the beetles' preferred habitat type: mature pine forest (Logan and Powell 2001; Taylor and Carroll 2004). Unless cold winters return, this outbreak could continue to spread until the supply of susceptible pine trees is exhausted. Such a scenario entails significant and sustained long-term decreases in timber supply (British Columbia Ministry of Forests 2003) and widespread ecosystem changes. The combination of climatic conditions and landscape age-class structure suggests that this forest landscape is "resetting" itself and that a collapse (α) phase is unfolding. Understanding this historical development and its possible future consequences (e.g., the potential for catastrophic fires resulting from a large "pulse" of dead forests across the landscape combined with forecast increases in the severity of fire weather; Flannigan et al. 2001) provides essential context for designing a strategic management approach that may sustain resilience during times of rapid change (Table 3). Moreover, since outbreaks are at different stages in different parts of the landscape, different practices will be simultaneously useful for enhancing resilience.

Conclusion

Understanding resilience may hold the key to overcoming the challenges inherent in applying NDBM for the sustainable use of forest resources. Moreover, this understanding can resolve the fundamental mismatch between the dynamics of unmanaged systems and human-dominated systems (Levin 2000), such as disturbance cycles that create a diver-

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sity of forest types vis-à-vis economic forest rotations that reduce much of this diversity. The mismatch makes it difficult (*i*) to see the signs of possible irreversible change until that change is underway (Scheffer et al. 2001), (*ii*) to understand the effects of individual management decisions on coarse scales, and (*iii*) for individuals to feel that their actions can influence sustainability, since it is the actions of billions of people that dictate the dynamics of the global commons (Levin 2000). Resolution of this mismatch in the context of forest management may come from developing policies and practices concerning resource use that recognize the following.

(1) Traditional forms of harvesting are fundamentally different from fire, windthrow, or other disturbances in our forests. The relevant question, from a scientific perspective, is not whether traditional logging or other severe silvicultural interventions fit within the range of historical natural variability, but rather how far management can deviate from this range before compromising ecosystem integrity and resilience (Perry 1998). That said, NDBM should not only emulate structure and pattern but also process, as ecological processes and functions are a fundamental component of resilience.
(2) Ecosystems are prone to catastrophic change when managed by command-and-control strategies that minimize variation of key environmental variables such as disturbance regime or when subjected to long-term anthropogenic pressures that simplify the forest landscape (Holling and Meffe 1996; Carpenter et al. 2001). This potential means that management approaches and policies based on maximum sustained yield are appropriate only in the rare situations when certainty and controllability of the managed system are high (Peterson et al. 2003).
(3) The globalization and intensification of anthropogenic stresses such as those caused by introduced species and climate change are expected to increase the frequency and intensity of compounded perturbations and thereby the frequency of both adaptive and catastrophic shifts within ecosystems, including forests (Paine et al. 1998; Regier and Kay 2002). This increase implies that "revolt" may become more common and puts the onus on managers to build or maintain resilience.

Implementing these elements in a management regime that maintains resilience may be easier for forests than for other resources such as fisheries or grazing grounds because forest inventories are easily tractable, there is ample knowledge about ecosystem function and dynamics, and social willingness to preserve their goods and services for future generations is increasing (Ostrom et al. 1999; Scheffer et al. 2000). At the very least, understanding resilience can better contextualize NBDM within its broader goal of sustainability, focus management attention on process rather than principally on pattern, and help managers escape their preoccupation with the likely unattainable goal of unfaltering stability (Carpenter et al. 2001; Johnson et al. 2003).

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