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Ecosystem management based on natural disturbances: hierarchical context and non-equilibrium paradigm

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Summary

1. Maintenance of ecological integrity and biodiversity must be based on well-grounded principles of disturbance ecology. However, non-equilibrium aspects of ecosystems, such as unpredictability, instability and stochasticity due to various natural disturbances, have not been satisfactorily integrated into practical application. Failure to acknowledge the dynamic nature of systems will inevitably lead to unexpected changes and unachieved conservation goals.
2. This review discusses non-equilibrium ecology in terms of natural disturbances and the conservation and management of terrestrial ecosystems and landscapes.
3. Several key components, which require further ecological consideration, are specifically discussed. These include the hierarchical disturbance regime, disturbance legacy, multiple post-disturbance pathways, climate instability, spatial and temporal variability, and resilience.
4. Natural disturbance regimes are complex and difficult to define. This is because some disturbances can be nested, and they interact with other qualitatively and quantitatively different disturbances, constituting a hierarchy of natural disturbances. Large temporal and spatial perspectives are therefore required to incorporate the hierarchical context of natural disturbance regimes into regional management plans.
5. Conservation managers may often seek some kind of dynamic equilibrium based on protection of species and seral stages from extinction. However, because climate instability interrupts any shift toward an equilibrium, most terrestrial vegetation systems are inherently prone to large environmental changes and diverse disturbances, and thus, are dynamic and non-equilibrating.
6. *Synthesis and applications.* Resiliency is the key to conserving ecological integrity via the ability to cope with inevitable changes. As long as ecosystems are resilient and disturbances are natural, we should not impede natural shifts in disturbance regimes and resultant ecosystem changes, even if changes are abrupt and unpredictable and thus have large consequences. If ecological resilience has already been eroded by humans, it is important that resilience should be enhanced by restoring keystone features of vegetation systems to prevent disturbance-induced undesirable ecosystem degradation.

Key-words: climate instability, disturbance legacy, hierarchical disturbance regime, multiple post-disturbance pathways, resilience, spatial and temporal variability

Introduction

Ecology has been undergoing a significant paradigm shift that emphasizes the role of disturbance, dynamics and disequilibrium concepts over 'balance of nature' or 'equilibrium' concepts for predicting complexity, instability and inevitable changes in ecosystems (White & Pickett 1985; Wu & Loucks 1995; Levin 1999; Phillips 2004; Appendices S1 & S2, Supporting Information). Many scientists have recognized that classical equilibrium theories are generally inadequate (Levin 1999), leading to the acceptance of a 'non-equilibrium' view of terrestrial ecology. In many regions, ecosystems are open and heterogeneous and are thus in a non-equilibrium state (Phillips 2004; Wallington, Hobbs & Moore 2005). In these non-equilibrating dynamic systems, disturbances play inherent and central roles (Phillips 2004; Moore *et al.* 2009). Pickett (1980)

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noted that the persistence of certain species in plant communities requires disturbance. After earlier studies by Pickett & White (1985), disturbances have been recognized in various plant populations and communities as agents of primary vegetation dynamics (Sprugel 1991; Laska 2001). Disturbances, especially natural disturbance regimes, have been gradually taken into consideration in the management of natural resources and land areas.

Despite gradual scientific acceptance of the non-equilibrium concept in ecology, simply integrating the non-equilibrium ecological paradigm into actual practical application is inadequate (Phillips 2004; Wallington, Hobbs & Moore 2005; Table 1; Appendix S2, Supporting Information). A possible reason is that unplanned and unexpected disturbances may adversely affect humans, and therefore, disturbances are often considered disastrous and detrimental in resource management (Holling & Meffe 1996; Noss *et al.* 2006), and the concept itself still lacks scientific consensus (Moore *et al.* 2009). However, for the ongoing development of ecosystem management (Grumbine 1994; Christensen *et al.* 1996) or ecosystem-based management (Lertzman *et al.* 2002) concepts, accumulating knowledge on naturally recurring disturbances, which profoundly regulate the function, structure, and dynamics of ecosystems, is of fundamental importance (Perry 1998; White *et al.* 1999; Appendix S2, Supporting Information). Thus, comprehensive concepts are required to understand the roles of natural disturbances in ecosystems and landscapes and promote non-equilibrium ecology.

Efforts to maintain ecological integrity and conserve biodiversity in dynamic ecosystems must be based on well-grounded principles of disturbance ecology (White & Jentsch 2001; Wallington, Hobbs & Moore 2005; Noss *et al.* 2006; Appendix S2, Supporting Information). In an ecosystem approach, natural disturbance regimes are one of the most significant ecological processes and should be conserved or restored to maintain species composition and diversity (Yaffee 1999). Failure to acknowledge dynamic nature of systems will inevitably result in unexpected changes and unachieved conservation goals (Wallington, Hobbs & Moore 2005). This review discusses the ecological context of non-equilibrium ecology based on natural disturbances in the context of the conservation and management of vegetation ecosystems and landscapes. In particular, on the basis of studies that have inferred the instability, dynamics, and unpredictability of ecosystems, this review discusses several key components (Appendix S1, Supporting information) that require further investigation and ecological consideration in the management and conservation of ecological processes in terrestrial systems from the viewpoint of non-equilibrium ecology.

Definition of disturbance and natural disturbance regimes

This review uses White & Pickett's (1985) definition of disturbance in plant ecology. They noted that disturbances are relatively discrete events in time that disrupt the ecosystem, community, or population structure and bring about a change in resources, substrate availability, or the physical environment. On the basis of previous studies (e.g. Runkle 1985; White & Pickett 1985), White *et al.* (1999) noted that the 'disturbance regime' of a vegetation system, which is the sum of all disturbances affecting the system, can be characterized by several parameters: kind, spatial characteristics, temporal characteristics, specificity, magnitude and synergisms. Kind refers to the type of disturbances, which vary with climate, topography, substrate and biota. Spatial characteristics are the area, shape and spatial distribution of patches created by disturbances. Temporal characteristics are the frequency, return interval, cycle and rotation period of disturbances. Specificity is the correlations between a type of disturbance and specific characteristics of disturbed sites, such as species, size class, seral stage and location. Magnitude includes the intensity (the physical force per event per area per time) and severity (the impact on organisms and ecosystem structure and composition) of disturbances, and generates patch variations, internal heterogeneity and biological legacies. Synergisms are the interactions among different kinds of disturbances.

It has been suggested that it is impossible to define natural vegetative disturbance regimes in a strict sense, given a changing climate and resultant shifts in disturbance regimes over the past several centuries (Sprugel 1991). Non-equilibrium ecological views are largely based on inevitable ecosystem changes linked with climate instability (Sprugel 1991). Landres, Morgan & Swanson (1999) also stated that no *a priori* time period or spatial range should be used to define 'natural variability,' which is spatio-temporal ecosystem variability driven by disturbances. However, with respect to conservation practices, the term 'natural' often means 'without human influence' (Hunter 1996). In restoration ecology, resource management and ecosystem approaches, the term generally refers to ecological variations after excluding anthropogenic effects. Thereby, although climate instability significantly alters vegetation structures and disturbance regimes, it should be embedded in disturbance-based management issues. In this review, natural disturbance regimes are thus referred to in a broader sense by accepting climatic effects on disturbance regimes as a natural driver.

Equilibrium vs. non-equilibrium in ecosystem management

SCALE DEPENDENCY: ECOSYSTEM- AND LANDSCAPE-LEVEL VIEWPOINTS

In classical ecological theory, disturbances are treated as periodic factors that contribute to maintaining equilibrium, rather than as sources of non-equilibrium (Phillips 2004). In this regard, the term 'equilibrium' is used to refer to a steady state, where disturbances at a smaller scale (fluctuation) may occur around a constant mean condition. Many definitions and interpretations of equilibrium vs. non-equilibrium ecology are summarized in the studies of White *et al.* (1999) and White & Jentsch (2001). The spatial and temporal scales required for a system to be in dynamic equilibrium or non-equilibrium

Table 1. The panel shows examples of actual management issues that may be improved once the non-equilibrium ecology is acknowledged

(a) **Grazing** (examples from dry rangelands in Mongolia and USA)

1. Some current management focuses on preventing the disturbance of vegetation. In rangeland ecosystems, the classical equilibrium view emphasizes that livestock strongly influences vegetation and leads to severe anthropogenic degradation (Wesche *et al.* 2010), promoting a need for grazing exclusion.

2. However, in the case of dry rangelands, where climate factors are overwhelming, grazing exclusion has little effect on the composition and diversity of vegetation (Wesche *et al.* 2010) and sometimes promotes the invasion of exotic species (Loeser, Sisk & Crews 2007). On some rangelands, an intermediate level of grazing primarily contributes to maintaining and enhancing native plant diversity (Loeser, Sisk & Crews 2007; Sasaki *et al.* 2009).

3. Notably, other disturbances such as wind erosion and episodic droughts interact with cattle grazing, resulting in complex disturbance-diversity relationships (Sasaki *et al.* 2009) and infrequent but significant shifts in plant communities (Loeser, Sisk & Crews 2007).

4. The non-equilibrium perspective is thus needed for rangeland management, through consideration of the interactive effects of disturbances that are a source of diverse ecosystem states, rather than simple grazing exclusion that mainly aims to restore a specific vegetation structure.

(b) **Winds** (examples from secondary cool temperate forests in northern Japan)

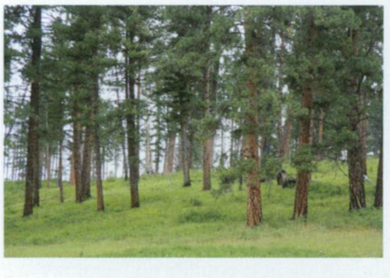
1. Some current management focuses on the avoidance of all large disturbances. In the northern forests of Japan, regional management primarily aims to reduce the susceptibility of forests to large-scale wind damage (mainly by typhoons) (Hokkaido Forest Administration Bureau 2005). In the plan, wind-throws that occurred in 2004 were regarded as a disaster.

2. However, this event is not necessarily a disaster, although it may be partly attributed to intense plantations following a severe typhoon in 1954. Because naturally regenerating mixed forests, which comprise trees of various size and species, are more tolerant than conifer plantations to wind damage, the plan recommended transition from uniform plantations to forests resembling natural regeneration (Hokkaido Forest Administration Bureau 2005). This is based not on disturbance-based management acknowledging natural dynamics but the simply reduction of future wind-throws.

3. Notably, the plan introduced active salvage logging to reduce a risk of further events (i.e. insect outbreaks were mentioned as a 'disaster' in the plan) (Hokkaido Forest Administration Bureau 2005). This management might collide with synergisms of the forest ecosystems and extinguish disturbance legacies that various ecological processes and diverse species depend on. Lindenmayer & Noss (2006) stated such salvage as an 'ad hoc and crisis-mode decision'.

4. The non-equilibrium perspective is thus needed to manage northern secondary forests by recognizing the potential of episodic large changes caused by typhoons and other natural disturbances, rather than management grounded on the equilibrium view that is trying to completely exclude the possibilities and outcomes of large disturbances. In this manner, disturbance legacies and interactions between different disturbances can contribute to enhance diversity and heterogeneity at both coarser and finer spatial scales.

(c) **Fires** (examples from open, park-like pine forests in southwestern USA)



1. Some current management focuses on the conservation of a specific ecosystem state that is maintained by the current predictable disturbance regime. One clearer example is the open forests of ponderosa pines in the southwestern United States. Arguments about too much emphasis on the equilibrium view in current fire management, which was criticized by Shinneman & Baker (1997) and Baker (2006), are described in the main text.

2. However, this is still an unclear and challenging issue (Baker 2006; Fulé, Heinlein & Covington 2006).

3. Notably, arguments made by Baker (2006) and Fulé, Heinlein & Covington (2006) imply that palaeoecological evidence is useful in determining the historical disturbance regime and natural variability in ecosystems but has some limitations.

4. The non-equilibrium perspective is one of the important approaches in the case of such incomplete knowledge because seemingly stable ecosystems may unexpectedly and abruptly change in the current situation of interactive effects of human activities, climate change and disturbances. Managers and scientists can then adaptively cope with inevitable changes found in natural terrestrial ecosystems (i.e. adaptive management).

greatly differ among systems and regions. White & Jentsch (2001) proposed that disturbance effects on biodiversity in a dynamic equilibrium or non-equilibrium should be evaluated according to the multiple-patch scale. Such an evaluation focuses on scales across all patches, including both disturbed and undisturbed patches, to infer how disturbances correspond to the absence or presence of equilibrium and variance in ecosystems. Because disturbance regimes are an important consideration in the ecosystem approach (Yaffee 1999), careful consideration should be given to dependency of the equilibrium on the scale of disturbances. This is important for the conservation of pre- and post-disturbance ecological processes in systems prone to various disturbances (White *et al.* 1999).

Differences between equilibrium and non-equilibrium views, which are highly dependent on the spatial and temporal scales of focal ecosystems, can be seen by focusing on the concept of the shifting-mosaic steady state of Bormann & Likens (1979). According to this concept, vegetation changes at individual points in a landscape; however, if the vegetation distribution is averaged over a sufficiently long time or large area, the proportion of the landscape in each successional stage is relatively constant; i.e. the landscape is in equilibrium. Early evidence of a steady-state mosaic was presented for the northern hardwood forests of New England in the US (Bormann & Likens 1979), wave-generated balsam fir *Abies balsamea* forests of the north-eastern US (Sprugel 1976; Sprugel & Bormann 1981), and northern Swedish boreal forests (Zackrisson 1977). However, it has been suggested that the shifting-mosaic concept seems to be applicable only when disturbances are small and frequent in a large area of homogeneous habitat (White & Pickett 1985). Therefore, landscapes characterized by infrequent large disturbances, such as extensive wildfires, are considered to be in non-equilibrium and never reach the steady-state mosaic (Romme & Despain 1989; Turner & Romme 1994). Turner *et al.* (1993) re-evaluated the concept of landscape equilibrium and concluded that because equilibrium is predicted when the disturbance magnitude and extent are smaller than the fluctuation and size of the landscape, it is highly scale dependant. Furthermore, Sprugel (1991) stated that forests in a shifting-mosaic steady state, such as eastern hardwood and wave-regenerated forests, are in equilibrium or quasi-equilibrium when disturbance is sufficiently frequent and of a small scale relative to the landscape and most processes are fairly constant over the whole area. He also noted that achieving an equilibrium state is usually unlikely because individual disturbances, such as hurricanes, disease outbreaks, and wildfires, are large or infrequent and ephemeral events have long-lasting disruptive effects on vegetation (Sprugel 1991).

Although understanding the natural vegetation, disturbance regimes and reference conditions are important, their precise definitions are almost impossible because of climatic and vegetation instability and attempting to do so may sometimes lead to undesirable and misguided management (Sprugel 1991; Landres, Morgan & Swanson 1999). Land managers and conservationists sometimes tend to think of 'pristine wilderness' (Gillson & Willis 2004), which emphasizes a specific period and area as the conservation goal. Vegetation changes caused by climatic shifts, destructive events due to infrequent extensive disturbances and human impacts are often inevitable in most ecosystems and landscapes; hence, the struggle to achieve an equilibrium state may lead to undesirable consequences in ecosystem-based management. Therefore, instead of attempting to define natural disturbance regimes and identify the scales required to attain quasi steady state, acceptance of large variations and inevitable natural changes in ecosystems and landscapes would be beneficial in the adaptive management of terrestrial systems prone to various natural disturbances.

DISTURBANCE VS. FLUCTUATION: POPULATION- AND COMMUNITY-LEVEL VIEWPOINTS

White & Jentsch (2001) mentioned that, in disturbance ecology, ecosystem responses to disturbances should be evaluated at the patch scale as well as at the multiple-patch scale. This involves consideration of disturbances and responses on a small spatial scale. In this regard, gap dynamics and associated population/community processes have been considered for many decades. The dynamics on this scale are sometimes referred to as fluctuations rather than disturbances (Laska 2001; Phillips 2004). Laska (2001) introduced conceptual differences between fluctuations and disturbances and noted that fluctuations are sometimes considered as a dynamic process involved in stabilizing, and not disturbing, a given community. The assumption that fluctuations contribute to the maintenance of the stability of populations and community processes implies the presence of a kind of equilibrium (Laska 2001). Therefore, how should we treat fine-scale ecological phenomena such as the death of a single tree due to senescence? Can it be regarded as a fluctuation or disturbance? At a larger scale (ecosystem or landscape level), it may be just a part of the steady-state mosaic and considered as a fine-scale fluctuation. However, at a smaller scale (community or population level), it cannot be treated as a fluctuation. Laska (2001) stated that the death of a single tree can also be treated as a disturbance because the tree itself and the gap created by its death can disturb the surrounding physical environment, and thus, affect resource availability for the plants growing there. This implies that even a standing dead tree at the single-tree scale may lead to some kind of non-equilibrium.

Old-growth forests characterized by minimum-scale dynamics at the scale of single-tree standing mortality have been reported occasionally (e.g. Antos & Parish 2002; Mori & Takeda 2004b). The ecosystem is often expressed as 'stable' and/or 'undisturbed,' reflecting the fact that along a succession gradient, old-growth stands are generally close to the end point and far from stand-initiating disturbances (Aplet, Laven & Smith 1988; Kneeshaw & Gauthier 2003). Single-tree death and resulting creation of a small gap are also considered to be at the far end of a continuum of disturbance scale, size, extent, and severity in forest ecosystems. Nevertheless, several studies have failed to detect structural, compositional or demographic steady states in a tree community in these forests (Woods 2000; Mori, Mizumachi & Komiyama 2007). This indicates that even the death of a single tree, which seems to be a fluctuation, does not lead to the stabilization of community processes. Even in these very old-growth forests, often called climax forests, major catastrophic events, which occur on centurial and millennium scales, are essential for the persistence of the dominating tree species (Woods 2000; Antos & Parish 2002; Mori, Mizumachi & Komiyama 2007). Therefore, it may be a profound mistake to generally regard old growths as stable and independent of major disturbances. It may be better to more broadly recognize inherent disturbances than to struggle to define differences between fluctuations and disturbances.

Key components for managing ecosystems from the non-equilibrium viewpoint

HIERARCHICAL DISTURBANCE REGIME

Disturbances naturally occur at multiple spatiotemporal scales. Focusing on multi- and cross-scale linkages of natural disturbances and understanding pre- and post-disturbance phenomena are important in conserving habitat diversity at multiple scales including microhabitats, stands, ecosystems and landscapes. Here, a key approach to understanding how naturally recurring disturbances should be regarded as a significant component of ecosystem management is the 'hierarchical context of natural disturbances' (Appendix S1, Supporting Information). Spies & Franklin (1989) proposed a simplified hierarchy that divides disturbance regimes into coarse- and fine-scale dynamics. Wu & Loucks (1995) emphasized hierarchical patch dynamics, which explicitly incorporates environmental stochasticity and biotic feedback interactions that can cause ecosystem instability and contribute to dynamics at various scales. Recently several studies have further emphasized that perspectives of cross-scale interactions, which refer to processes at one spatial or temporal scale interacting with processes at another scale, are increasingly important in considering ecosystem dynamics (Peters *et al.* 2004; Falk *et al.* 2007). Many scientists now recognize that most ecosystems are shaped by several different types of disturbances that have interacted sometimes strongly and sometimes weakly with anthropogenic activities and climatic influences. However, less attention has been paid to the potential importance of management based on the cumulative and hierarchical nature of multiple natural disturbances.

In the spruce–fir forests of the eastern US, Worrall, Lee & Harrington (2005) proposed a 'nested bicycle' for disturbance dynamics, emphasizing that a cycle of gap-phase stand dynamics is nested within a long-term cycle of infrequent, episodic but regular intervals of insect outbreaks at the landscape level. The interactions and nested structures of various natural disturbances imply that focusing on any one hierarchy level of ecological dynamics should be avoided when describing a natural disturbance regime. Furthermore, Falk *et al.* (2007) theoretically demonstrated that measures of fire frequency are area-dependent and that the fire return interval cannot be described by a single number independent of spatial scale. Thus, approaches considering interactions and feedbacks at multiple spatial and temporal scales are essential in managing ecosystems prone to various natural disturbances. Reflecting the specificity, magnitude and synergisms of disturbance regimes, hierarchical disturbance regimes are a fundamental component of non-equilibrating ecosystems. Although the concept of the steady-state mosaic recognizes within-landscape spatiotemporal variations of a single or specific type of disturbance, it ignores the inherent complexity of multiple disturbances, which vary spatially and temporally, resulting in different successional trajectories. Failure to recognize the possible hierarchical context of disturbance regimes may result in misguided management and undesired consequences of post-disturbance ecosystem processes, leading to a reduction in ecological variability and resilience.

A clear example that requires further focus on the hierarchical context of disturbances is observed in ponderosa pine *Pinus ponderosa* forests in the western US. In these forests, frequently recurring low-intensity surface fires maintain open, park-like forests of large old trees by thinning trees in the understorey (Spies *et al.* 2006). However, after Euro-American settlement, human-induced modification of disturbance regimes, such as fire exclusion and livestock grazing, have profoundly changed the tree density and age structure of pine stands (Swetnam, Allen & Betancourt 1999; Spies *et al.* 2006), which is believed to have built up fuel throughout the landscape, resulting in a higher risk of catastrophic high-intensity crown fires and disease outbreaks and insect attacks (Fulé, Covington & Moore 1997; Shinneman & Baker 1997). It has been commonly suggested that thinning and prescribed fires in these forest landscapes are required to reduce excess fuel-loads and to restore historical disturbance regimes. According to Shinneman & Baker (1997), this management process places too great an emphasis on the equilibrium view of ecosystems, in which a dynamic balance exists between low-intensity fires and stable old-growth climax conditions. Recent studies have further demonstrated that because unpredictable crown fires are an essential element of historical landscape structures, application of only equilibrium-based management may lead to further deviation from the natural range of variability (Shinneman & Baker 1997; Baker 2006; Appendix S2, Supporting Information). These studies recommend the re-consideration of natural disturbance regimes at a different scale in regional management plans.

Evidence for non-equilibrium ecosystems, resulting from interactive or nested occurrences of multiple disturbances, has also been provided at the stand level. In late-successional forests, which are seemingly in a steady state and unaffected by major disturbances, the population structure and dynamics of shade-tolerant trees – so-called climax species – have been traditionally regarded as fairly stable. In such old systems, the population structure of trees is often evaluated on the basis of the size distribution, and the inverse J-shaped size distribution is a typical structural characteristic of late-successional species (e.g. Mori & Takeda 2004b), which implies that although lifetime mortality increases with size (implying age), recruitment occurs constantly in smaller size classes (i.e. younger classes) so that the entire population structure is relatively unchanged.

However, in an old-growth mixedwood forest in central Japan, Mori, Mizumachi & Komiyama (2007) demonstrated that the inverse-J structure of dominant firs (*A. mariesii* and *A. veitchii*) do not necessarily guarantee continuous recruitment without a major disturbance because canopy dynamics of the studied forest, characterized by single-tree standing deaths, hardly increase the availability of understorey light. Moreover, fir juveniles cannot be recruited into the shady forest despite their high shade tolerance; therefore, the size distribution changes greatly during a 25-year dynamic process and the fir populations are demographically in non-equilibrium. Because fir recruitments in this forest are closely associated with the presence of light-demanding birch *Betula ermanii* trees, which provide favourable microsites for advance regeneration of these firs (Mori & Takeda 2004a), population persistence of the two fir species is indirectly dependant on major episodic disturbance events, such as canopy blowdowns by typhoons, which favour birch regeneration. Mori, Mizumachi & Komiyama (2007) thus concluded that tree populations and communities fluctuate on a template shaped by both ancient and recent disturbances, and thus, they are in non-equilibrium, both demographically and compositionally, even in a seemingly stable, late-successional old forest.

The non-equilibrating plant community and population dynamics within old-growth stands emphasize that ecological management of vegetation systems needs further careful consideration because of the complexity of the role of and variability in multiple natural disturbances. Old-growth forests are undoubtedly important cradles of biodiversity (Spies 2004; Spies *et al.* 2006) and are a typical 'icon' used to generate support for conservation projects through the implication of the 'eternalness' of such ancient systems. However, populations and communities even in these old systems not only fluctuate but are also regulated by underlying catastrophic disturbances that leave long-lasting diverse legacies. Therefore, we need to accept inevitable natural changes and not interfere with them, particularly unpredictable sudden shifts in plant population and community dynamics, in the management of various terrestrial ecosystems and landscapes in the future.

DISTURBANCE LEGACY

Recent studies have demonstrated that even in ecosystems that have developed through long-term ecological processes, diverse legacies left by disturbances that took place several decades, centuries, and sometimes more than a millennium ago remain and have long-lasting effects on ecosystem dynamics (Foster, Knight & Franklin 1998; Wimberly & Spies 2002; Kulakowski & Veblen 2007; Appendix S1 & S2, Supporting Information). Disturbance legacy is roughly distinguishable in terms of physical structures, such as sediments, mounds and lavas, and biological remnants, such as seeds, seedlings, standing dead trees and logs (Foster, Knight & Franklin 1998). After a large-scale disturbance, systems diverge from the pre-disturbance phase according to biological and/or physical legacies.

Infrequent large disturbances are known to result in diversity and heterogeneity in ecological features within a given landscape (Turner *et al.* 1998; Kashian *et al.* 2005; Mori & Lertzman 2011; Appendix S2, Supporting Information). A clear example of such a disturbance is the 1988 Yellowstone fires that burned over 320 000 ha. Large fires ($>10{,}000$ ha) are often believed to be an ecological 'disaster' rather than a disturbance because they are perceived to devastate vast areas (Keane *et al.* 2008). The 1988 fires surprised managers, scientists and the public. Although it was feared that the fires would leave a desolate area of uniform devastation (Turner, Romme & Tinker 2003), post-fire studies revealed that important features of the Yellowstone landscape were not destroyed but rather long-persisting ecological variations were generated (Schoennagel, Smithwick & Turner 2008). For example, the 1988 fires created a complex mosaic of lodgepole pine *P. contorta* var. *latifolia* densities ranging from <100 to more than 500 000 seedlings ha^{-1} across the landscape (Kashian *et al.* 2004; Turner *et al.* 2004). Kashian *et al.* (2005) demonstrated that these initial patterns may persist for more than two centuries, indicating that the 1988 fires indeed left a long-lasting imprint on stand structural variations. Because large wildfires leave various kinds of legacies, such as patches with different fire severities, various densities of unburned trees, and different forms of dead trees within a vast landscape, they are not treated as a factor contributing to the homogenization of the landscape but rather as a diverse template for ecological processes. Although sudden, large-scale, severe disturbances in a landscape may be perceived as socially and ecologically disastrous, the heterogeneity and long-term ecological consequences introduced following large disturbances are greatly beneficial to ecological integrity and biodiversity (Williams & Bradstock 2008).

In addition to the landscape-level evidence of disturbance legacies, long-lasting influences of historically large disturbances on ecological dynamics can also be observed at the stand level. In late-successional conifer–northern hardwood forests in the US Great Lakes region, Woods (2000) showed that population dynamics are still influenced by historical catastrophic blowdowns with return times exceeding one millennium. As mentioned earlier, in an old-growth subalpine forest, Mori, Mizumachi & Komiyama (2007) demonstrated that remnant canopy trees of pioneer species, which regenerated at the time of a past large episodic disturbance, function as a long-lasting legacy and still largely affect tree population dynamics of late-successional species. Furthermore, in late-successional forests of the US Pacific Northwest, Wimberly & Spies (2002) clarified that the abundance of western hemlock *Tsuga heterophylla* – a fire-susceptible, late-successional species – is largely determined by legacies of cumulative fire effects (number of burns in a stand) in the past and less controlled by current gap-dynamics regimes. These studies emphasize the importance of long-lasting effects of past disturbances in understanding the persistence of tree species in later successional stages, again questioning the conservation concept, which is based on the eternalness of old-growth forests and trying to maintain these developed ecosystems in some steady state.

Disturbance legacy studies are useful in ecosystem management because the present-day vegetation ecosystems and landscapes in most regions have been largely shaped by human activities for centuries and sometimes millennia. Therefore, knowledge of non-equilibrium dynamics in terms of the broader context from population to landscape level is applicable in evaluating possible legacy impacts of historical anthropogenic disturbances on ecological processes. For instance, in the tropical rain forests in southern Cameroon, van Gemerden *et al.* (2003) clarified that the present-day compositional characteristics of tree community are largely associated with three- to four-century-old human land-use disturbances, invalidating the common belief that species-rich old forests in central Africa are pristine and undisturbed by humans. Furthermore, in the northern boreal forests of Fennoscandia, which have no signs of modern exploitation, Josefsson, Hörnberg & Östlund (2009) found persisting legacies derived from past human land-use, indicating that even supposedly pristine forests cannot be indiscriminately used as reference conditions for conservation activities. Thus, the validity of many current biodiversity conservation strategies based on the principle that all old-growth forests are equally important is questioned. It is challenging to extract the natural variability in systems that have been shaped by long-term human activities because even natural forcing is complex and contributes to natural perturbations in many ecosystems. In some systems, anthropogenic effects have been of long duration and interacted with natural factors so that they now cannot be completely separated from natural variability (Josefsson, Hörnberg & Östlund 2009; Appendix S2, Supporting Information). The likelihood of regime shifts may increase when humans reduce resilience by altering disturbance regimes (Folke *et al.* 2004). Therefore, it is important to evaluate the anthropogenic disturbance effects on ecological processes. Because ecosystem restoration and forest practices now respect natural disturbance processes (Franklin *et al.* 1997; Lindenmayer & Franklin 2002; Kuuluvainen 2009; Appendix S2, Supporting Information), further evaluations of legacy features and the impacts of anthropogenic and natural disturbances are beneficial to future forest management with the aim of conserving ecological integrity.

MULTIPLE POST-DISTURBANCE PATHWAYS

Disturbance legacy studies have revealed that post-disturbance ecosystem development is largely controlled by quality, quantity and spatial arrangement of physical and biological elements left at disturbed sites (Lindenmayer & Franklin 2002; Lindenmayer, Franklin & Fischer 2006; Lindenmayer & Noss 2006). Therefore, the post-disturbance pathway of ecosystem development is variable and multidirectional (Foster, Knight & Franklin 1998; Wimberly & Spies 2002; Appendix S1, Supporting Information). In the case of the Yellowstone forests, Kashian *et al.* (2005) showed that stand structures largely diverge depending on legacy conditions in the early phases of succession, and then gradually converge through long-term developmental processes lasting more than two centuries. This indicates that the ecological roles of disturbances are not only to introduce heterogeneity during the early successional phase but also to imprint diversity during the long-term ecosystem development.

The importance of heterogeneity, which can be confirmed on a coarse scale, such as the spatial configuration of various habitats and patches in a given disturbed landscape, is profound in the early successional phase. Therefore, within-landscape structural variations, such as variations in stand density, seemingly homogenize with progressing succession. However, fine-scale heterogeneity and variability are seen in later successional stages because fine-scale disturbances, such as gap formations, contribute to within-stand structural variations (Kashian *et al.* 2005; Lindenmayer, Franklin & Fischer 2006). Thus, past and present disturbances interact to maintain structural and compositional diversity from an entire-landscape scale to within-stand scale. Furthermore, it is notable that because forest stands are inherently prone to fine-scale disturbances nested within large events (e.g. Worrall, Lee & Harrington 2005), re-disturbed stands may show further divergence even in the middle of a stand developmental process following a large disturbance, thus further generating instability and complexity in the developmental pathways of ecosystems.

It has been demonstrated that heterogeneous patterns of disturbance legacies greatly determine ecosystem productivity (Turner *et al.* 2004), carbon dynamics (Litton, Ryan & Knight 2004), biological diversity (Spies & Turner 1999; Lindenmayer & Noss 2006) and disturbance regimes (Kulakowski & Veblen 2007) in stands and patches that have developed following major disturbances (Appendix S2, Supporting Information). The fact that all stands are susceptible to multiple perturbations in the hierarchical structure of natural disturbances implies that the diversity of these ecological properties is assured by acknowledging multiple post-disturbance pathways. In particular, disturbances can significantly enhance ecological heterogeneity at multiple scales (White & Jentsch 2001; Schoennagel, Smithwick & Turner 2008; Mori & Lertzman 2011), so that the multidirectional post-disturbance pathways further contribute to altering this heterogeneity. Recent studies have demonstrated that landscape-level spatial heterogeneity plays an important role in determining plant species richness (Kumar, Stohlgren & Chong 2006), butterfly species richness (Kumar, Stohlgren & Chong 2009), butterfly population stability (Oliver *et al.* 2010) and soil faunal diversity (Vanbergen *et al.* 2007). Positive relationships between habitat heterogeneity and species diversity do not occur only on a coarse scale. Finer-scale heterogeneity such as the stand-level structural complexity is also an essential component in conserving biological diversity (Tews *et al.* 2004; Lindenmayer, Franklin & Fischer 2006; Janssen, Fortin & Hebert 2009). In maritime pine plantation forests in southwestern France, Barbaro *et al.* (2005) showed that bird, carabid and spider species richness were well explained by stand-level structural diversity. Thus, biodiversity in a given ecosystem, landscape or region can be conserved by acknowledging multiple post-disturbance pathways, which sustain diverse ecological processes and functions found in each developmental phase from early to late-successional stages. Although simply acknowledging natural disturbances does not necessarily ensure that ecological diversity is maintained, it should be integrated into decision making and management to ensure this.

CLIMATE INSTABILITY

Climate instability is a significant component of non-equilibrium dynamics (Appendix S1, Supporting Information). Palaeoenvironmental data, such as data derived from fossil pollen, charcoal, stable isotopes and tree rings, indicate that ecosystems have historically co-varied with climate variability (Jackson 2006). For example, in Kootenay National Park in western Canada, Hallett & Walker (2000) demonstrated that according to the lake sediment record, there was a return to the current wet–closed forest vegetation *c.* 700 years ago. Although the present-day dominant vegetation type in this mountain landscape is mesic, late-successional spruce–fir (*Picea engelmannii* and *A. lasiocarpa*) forests, the ongoing global warming trend and Holocene climate variability suggest an increase in the fire-prone conditions in the future, resulting in a drier and more open structure with increased *Pseudotsuga/Larix* cover, which is very different from the current disturbance and vegetation type (Hallett & Walker 2000). If we consider this disturbance regime shift and ecosystem change with climatic shifts as natural variability, the common management strategies that aim to maintain and arrange all seral stages within a given protected area or in a landscape, which are based on a directional succession trajectory to the current climax vegetation type, might be inappropriate.

Climate affects the vegetation structure by altering abiotic conditions suitable for each population, such as growth season and resource availability. In addition, a regional climatic shift can alter disturbance regimes by changing the regional temperature and hydrology. Simultaneously, climatic shifts alter biotic interactions in a community, such as competition, facilitation and symbiosis, leading to large compositional and structural ecosystem shifts. Thus, ecosystem change associated with climate instability is a complex outcome of both environmental and biological changes. Furthermore, given that humans have influenced most terrestrial ecosystems on the planet, past climatic and anthropogenic factors may have interacted to shape present-day ecosystems and landscapes (Swetnam, Allen & Betancourt 1999; White *et al.* 1999). The concept of ecosystem management proposed by Grumbine (1994) recognizes that humans cannot be completely separated from nature; thus, respecting natural disturbance regimes in an ecosystem approach should be based on the minimization of human impact, reduction of land-use legacy, and restoration of natural disturbance regimes. As noted before, it is challenging to separate anthropogenic variations from natural environmental variations. How should we deal with this confounding problem? Gillson & Willis (2004) noted that palaeoecological evidence is helpful in conservation planning and practice because it is an outcome of interactions of various confounding factors, including human activities, climate variability and disturbances. Taking this long-term perspective and elucidating how ecosystems respond to environmental changes is the key rather than mimicking past reference conditions (Gillson & Willis 2004). Simply emulating past conditions may be conceptually similar to the equilibrium approach, which focuses less on the complexity and perturbations of ecological processes. In the non-equilibrium approach, further efforts to understand biotic and abiotic interactions are required for future ecosystem restoration, conservation and management under a changing climate.

TEMPORAL AND SPATIAL VARIABILITY

The problems that we must solve in ecological management are inherently related to the application of our understanding of the temporal and spatial variability of ecosystems and landscapes (Freckleton 2004; Appendix S1, Supporting Information). Should we consider stochastic catastrophic events such as volcanic eruptions and earthquakes with return intervals exceeding thousands of years? Is it realistic to conduct ecological management that assumes large temporal variations in environmental conditions, such as climatic conditions of the Last Glacial Maximum?

We must first consider possible ecosystem changes caused by environmental shifts such as climate change (Hulme 2005). We face the problem that it is difficult to choose an *a priori* point in time as a reference for restoration and conservation (Sprugel 1991). In terrestrial regions, current vegetation might have been established because of the climatic conditions that occurred several centuries ago because trees older than 150 years of age germinated in colder and/or wetter conditions during the Little Ice Age (Gillson & Willis 2004). Therefore, this time scale at least should be taken into consideration in ecosystem restoration and management. Gillson & Willis (2004) indicated that a longer perspective is needed because many conservation activities ignore a temporal perspective greater than the past 50 years. In the case of North America, people are concerned about the human impact on ecosystems after Euro-American settlement. Therefore, people are generally interested in restoring natural disturbance regimes by focusing on the past 200–300 years. Given the effects of climate variability, Jackson (2006) stated that this temporal perspective is too narrow to assess the historical variability of ecosystems and that consideration of this narrow time span may result in underestimation of the range of variation within which an ecosystem is sustainable. Temporal variability is a difficult problem in ecosystem management according to the non-equilibrium view. Because temporal variability in ecological phenomena is tightly linked with climate variability, the first step is to elucidate possible climatic effects on disturbance regimes, multiple post-disturbance pathways, and resultant diverse ecosystem responses.

Secondly, spatial variability is also a great concern. Odion & Sarr (2007) stated that functional heterogeneity in ecosystems is maintained by retaining variations in disturbances, habitat types, age classes and legacy features. It may be easier to achieve all of these in a system that is relatively predictable and stable such that frequent, continuous low-intensity disturbance results in a forest at equilibrium, with certain parts of the landscape at various stages and in various pathways of development remaining constant throughout time, as seen in the shifting-mosaic steady-state system. However, at the other extreme, infrequent, large and severe disturbances can greatly affect the entire landscape for hundreds and sometimes thousands of years. The hierarchical context of disturbances tells us that many ecosystems are inherently shaped by multiple natural disturbances with differing severity, extent and consequences. This complexity often results in disagreement between equilibrium and non-equilibrium viewpoints. There is sometimes evidence of past disturbances that are completely different from the currently predominating disturbance. In the temperate rain forests on the Pacific coast of Canada, which are currently characterized by plentiful precipitation (more than 3000 mm year^{-1}) and a lack of wildfires, Lertzman *et al.* (2002) found scars indicating severe fires for the period from several centuries to over 6000 years ago. In addition, in Grand Canyon National Park of the US, Baker (2006) suggested the past common occurrences of stand-replacing fires in ponderosa pine forests, where management now aims to lower the probability of large fires for the purpose of restoration to the pre-settlement fire regime. This resulted in debate (e.g. Fulé, Heinlein & Covington 2006) and it is unclear whether historical variability should include infrequent large fires in these open forests characterized by frequent surface fires; nevertheless, the argument of Baker (2006) may influence the conservation of natural dynamic processes from a broader ecological viewpoint. The possibility of infrequent but widespread, catastrophic disturbances in ecosystems that are seemingly extraneous to these events may further reinforce one of the general principles of Lindenmayer, Franklin & Fischer (2006), who stated that at the regional scale, management should establish large ecological reserves to conserve forest biodiversity. However, if people try to impede the occurrence and spread of large-scale natural disturbances within reserves because they are seemingly social, economic and/or ecological disasters or hazards, the intentions behind having large reserves would be partially or completely defeated through the obstruction of natural disturbance processes.

RESILIENCE

In considering ecosystem management under the influences of various natural and anthropogenic disturbances, the concept of resilience should be discussed because it is useful to evaluate the ability of an ecosystem to cope with disturbance-driven changes (Gunderson 2000; Folke *et al.* 2004; Appendices S1 & S2, Supporting Information). The first comprehensive description of resilience was given by Holling (1973), who defined ecological resilience as the amount of disturbance that a system can absorb without shifting into a different state. Definitions of resilience and its conceptual significance have often been controversial, mainly because of assumptions about the presence of either a single equilibrium or multiple states in ecological systems (Gunderson 2000). This results in different views of resilience; i.e. ecological resilience vs. engineering resilience. Engineering resilience is the measure of the rate at which a system returns to a specific equilibrium state after temporal disturbance or perturbation (Holling 1973; Folke *et al.* 2004). Gunderson (2000) criticized the suggestions that engineering resilience makes the implicit assumption of global stability, which means that there is only one equilibrium or steady state, and, most notably, if other operating states exist, it is considered that they should be avoided by applying safeguards. This implies that management is oriented toward an equilibrium approach. In the present view of non-equilibrium ecology, acknowledging multiple pathways following disturbances, which contributes to maintaining and enhancing diversity and heterogeneity, the concept of ecological resilience, which recognizes the presence of various ecosystem states, would be more applicable in managing terrestrial ecosystems.

All ecosystems are inherently prone to the influences of natural (e.g. climate instability, glaciation, fires, wind-throws and herbivory) and anthropogenic (e.g. harvesting, biotic exploitation, nutrient loading, pollution and habitat fragmentation) forces. When external disturbing forces exceed resilience, ecosystems are forced to change to a state with different functions and structures (Thrush *et al.* 2009). If an ecosystem changes linearly with a predominant environmental condition, it is relatively easy to predict and manage its future state. However, abrupt nonlinear changes in ecosystems occasionally occur, and they are recognized as regime shifts (Scheffer & Carpenter 2003) or threshold changes (Sasaki *et al.* 2008) (Appendix S2, Supporting Information).

Sudden shifts/changes to an undesirable ecosystem state are increasingly common as a result of human activities that erode ecological resilience, such as land-use change and alteration of disturbance regimes (Folke *et al.* 2004), leading to considerable degradation of ecosystem services (Guttal & Jayaprakash 2008; Thrush *et al.* 2009). For instance, in the southern Illinois forests of the US, Nelson *et al.* (2009) showed that a period of drainage and conversion to agriculture, beginning in *c.* 1900, changed site hydrologic conditions, resulting in a disturbance regime shift. In the case of Mongolian rangelands, Sasaki *et al.* (2008) showed a threshold change in the floristic composition along a grazing gradient. Human activity and resultant anthropogenic disturbances have left certain legacy effects on present ecosystems and landscapes, leading to the loss of resilience. If resilience has been lowered by the cumulative effects of human activities, even a lower magnitude of disturbance (whether anthropogenic or natural) that an ecosystem used to tolerate to retain its current state might cause unexpected sudden change (Holling 1973; Folke *et al.* 2004). Thus, managers should be careful about not only the (natural or anthropogenic) causality of disturbances and their control but also the resilience of ecosystem prior to future disturbances; otherwise, ecosystems that have been considerably affected by humans have the possibility of easily dropping into an undesirable state that never appears under only natural forces. Such ecosystem shifts should be clearly distinguished from inherent ecosystem changes found along diverse multiple pathways following natural disturbances occurring at various spatio-temporal scales.

Carpenter & Gunderson (2001) noted that changes in the state of an ecosystem provide surprises to scientists and great uncertainties to stakeholders and policy makers. Climate change is presently an important issue that has the potential to abruptly alter disturbance regimes. For instance, the wildfire regime in the boreal forests of western North America, which

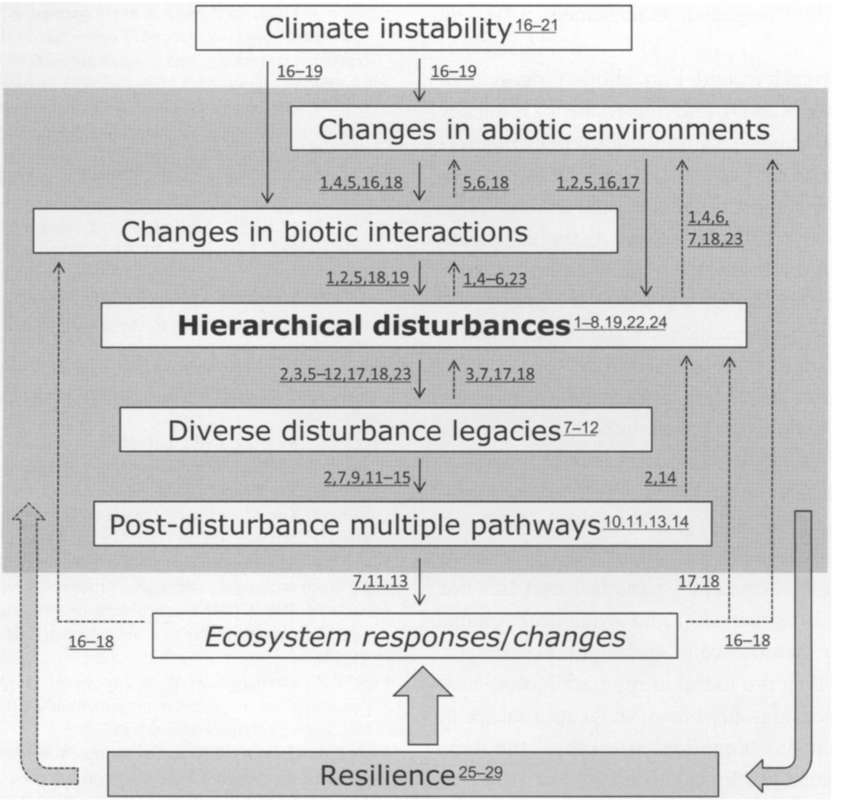


Fig. 1. A simple conceptual diagram emphasizing hierarchical disturbances as mediators of ecosystem changes in non-equilibrating systems. Solid and dotted arrows indicate effects and possible major feedbacks respectively. The grey area affects ecological resilience. The resilience determines ecosystem change. Numbers indicate corresponding ecological literature as a scientific basis given in Appendix S1 (Supporting information).

is tightly linked with the mode of the northern Pacific climate (i.e. the Pacific decadal oscillation), had an abrupt shift around 1976/77 (Macias Fauria & Johnson 2008). Some ecosystems are not resilient enough to cope with shifts in disturbance regimes under a changing climate. For instance, in the case of a pinyon–juniper (*Pinus edulis* and *Juniperus monosperma*) woodland of the southwestern US, Mueller *et al.* (2005) clarified that global climate change (increased levels of carbon dioxide, elevated temperatures and resultant increases in the frequency and severity of drought) caused higher mortality of adult pinyons than junipers, resulting in increased dominance of junipers. About 1000 species are associated with pinyons, and thus, the extreme mortality of pinyons significantly reduced the habitat available to them, leading to a remarkable shift in community structure and diversity (Mueller *et al.* 2005). Notably, the loss of mature pinyon pines significantly reduced the abundance of avian seed dispersers, ectomycorrhizal fungi and conspecific nurse plants, all of which are essential for pinyon recruitment and establishment, suggesting that the return to the pre-drought vegetation state is difficult (Mueller *et al.* 2005). This example implies that shifts in a disturbance regime under the current situation of global climate change can cause irreversible shifts in ecosystems.

Conclusions

Ecosystem management, which recognizes the non-equilibrium nature of ecosystems and landscapes, should take into consideration unpredictability, instability and stochasticity as these can lead to inevitable ecosystem changes. Climate instability might be an important factor for unforeseen ecosystem changes. This process is mediated by interactions between various pre-/post-disturbance processes described in this article (Fig. 1). Natural disturbance regimes are complex and difficult to define. This is because some disturbances can be nested within the interactions of other infrequent large-scale disturbances, constituting a hierarchy of disturbance regimes. Conservation managers may often seek some kind of dynamic equilibrium, which is based on protection of species and seral stages from extinction but permits fluctuation (White & Jentsch 2001). However, as Sprugel (1991) stated, climate change interrupts any kind of shift toward an equilibrium state. Therefore, almost all vegetation systems, from old-growth stands characterized by ongoing small-scale dynamics to landscapes shaped by infrequent large disturbances, are inherently prone to large environmental changes and diverse disturbances, and thus are dynamic and non-equilibrating. Fraterrigo & Rusak (2008) also emphasized that not only changes in mean responses of ecosystems to disturbance but also the variability of ecological processes can be greatly altered following disturbance, making the ecosystem response to disturbance enormously diverse. Acceptance of inevitable natural changes in ecological systems is more important than attempting to define absolute disturbance regimes. Therefore, non-equilibrium perspectives at various temporal and spatial scales are required to incorporate the hierarchical context of natural disturbance regimes into regional management planning (Table 1).

Disturbances can trigger a shift into another permanent state (Scheffer & Carpenter 2003), and thus resiliency is the key to conserving ecological integrity without interfering with inevitable change. As long as ecosystems are resilient and disturbances are natural, we should not impede natural shifts in disturbance regimes and resultant changes in the ecosystem state, even if changes are abrupt and unpredictable and thus have large impacts. In this regard, it is necessary to evaluate the resilience that each ecosystem ought to have under the situation of no major human intervention. To do this, palaeoecological evidence contains important information because it provides scientists and managers with information on the inherent 'keystone features' of each system such as foundation species (reviewed by Ellison *et al.* 2005) and keystone structures (reviewed by Tews *et al.* 2004) at various hierarchical levels. On the basis of such references, it may be possible to determine the historic environmental variation that has not caused an irreversible ecosystem shift and dynamically maintains an ecosystem. In the absence of such data, experiment, observation and modelling are useful in estimating ecological resilience; however, adopting only one of these approaches in vegetation management has limitations because of the scale dependency of each system (see Freckleton 2004; Hooper *et al.* 2005). As a consequence of such evaluations, if it is judged that the ecological resilience has already been eroded by humans, it is important to enhance the resilience by restoring structural, compositional and functional keystone characteristics of vegetational systems to minimize disturbance-induced undesirable ecosystem degradation.

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Supporting Information

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

Appendix S1. Several key sentences from the earlier publications.

Appendix S2. Additional supportive references for each concept.

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