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Early efforts in wildlife management focused on reducing population variability and maximizing yields of selected species. Later, Aldo Leopold proposed the concept of habitat management as superior to population management, and more recently, ecosystem management, whereby ecological processes are conserved or mimicked, has come into favour. Managing for resilience builds upon these roots, and focuses on maintaining key processes and relationships in social-ecological systems so that they are robust to a great variety of external or internal perturbations at a range of ecological and social scales. Managing for resilience focuses on system-level characteristics and processes, and the endurance of system properties in the face of social or ecological surprise. Managing for resilience consists of actively maintaining a diversity of functions and homeostatic feedbacks, steering systems away from thresholds of potential concern, increasing the ability of the system to maintain structuring processes and feedbacks under a wide range of conditions, and increasing the capacity of a system to cope with change through learning and adaptation. The critical aspect of managing for resilience, and therefore ecosystem management, is undertaking adaptive management to reduce uncertainty and actively managing to avoid thresholds in situations where maintaining resilience is desired. Managing adaptively for resilience is the approach best suited for coping with external shocks and surprises given the non-linear complex dynamics arising from linked social-ecological systems.

Key words: adaptive management, complex systems, ecosystem management, maximum sustained yield, resilience, scale, social-ecological systems, sustainability, wildlife management

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It is important that wildlife management goals are carefully developed and clearly stated, and that they continually evolve in the face of new challenges, ideas and theory. Over the more than 70 years that wildlife management has been a recognized discipline, its goals have changed substantially. Wildlife management has evolved in response to changing societal views of nature, advances in science and technology and an increasing recognition of the uncertainty that is inherent in the dynamics of both ecological and social systems (Groom et al. 2006).

From its inception until the 1960s, wildlife management in many nations focused primarily on the management of game species. Game management included such activities as the control of predators, the establishment of hunting regulations and the direct manipulation and creation of habitat considered suitable for target species. Since the 1960s, this focus has gradually broadened. In particular, during the last two decades, a convergence of the formerly discrete fields of wildlife biology, ecology and conservation biology has occurred, reflecting a shift in dominant stakeholder groups from hunters to non-consumptive users (van Heezik & Seddon 2005). Wildlife biology, which in fact was 'game biology' for much of its history, has started to embrace a broader view of wildlife that includes non-game species, and wildlife management is no longer exclusively focused on providing harvestable game resources, but increasingly deals with conservation of threatened species, invasive species control and the regulation of populations that are perceived as overabundant. Globally, wildlife management has followed similar patterns in different countries over the last few decades as international boundaries have become more open and communication and travel easier and faster. However, attitudes toward 'management' and 'conservation' still bear the stamp of historical contingency and reflect the norms of the cultures and governments of the countries within which managers reside.

A relatively recent trend in wildlife biology is a more explicit focus on biodiversity conservation, monitoring and the protection of endangered species and their critical habitat (Biddle et al. 1995, Baxter et al. 1999). During the 1980s and 1990s, there was a concomitant increase in awareness of the social issues and uncertainties surrounding wildlife management (Cutler 1982). Increasingly, wildlife managers have implicitly or explicitly recognized that "managing wildlife includes managing people" (Baxter et al. 1999, Mascia et al. 2003). Often, however, people are dealt with through programs in human dimensions of wildlife management (Jacobson & McDuff 1998), and the management of people and wildlife occurs in parallel but separate domains.

In this paper, we provide an overview of what we consider some of the central issues in wildlife management and outline the essential elements of an approach to the management of wildlife, wildlife habitats and biological diversity that embraces emerging theories of resilience in social-ecological systems. We discuss some of the strengths and weaknesses of these alternative management strategies and outline an approach that emphasizes managing adaptively for resilience, an approach we argue is best suited for coping with external shocks, including global change, climate change and the complex dynamics of linked social-ecological systems.

Changes in wildlife management in the 21st century

Although wildlife management has moved beyond its original goal of providing for the consumptive use of game species, often for maximum harvest, tensions such as those between single-species plans and ecosystem-based approaches persist. For example, in many US governmental agencies, the mandates for biodiversity conservation are separate from those for wildlife management despite the fact that federal programs such as State Wildlife Grants now focus on multiple species, declining species and overall biodiversity. In Canada, the Committee on the Status of Endangered Wildlife generally persists with a 'single-species' approach for its recovery plans, and multi-species plans are restricted to a few examples such as the Atlantic Coastal Plain flora (Government of Canada 2005).

Most wildlife agencies now focus on biodiversity conservation at some level, but their approaches often lack consistency. Classic strategies, such as managing for maximum sustained yield (MSY), have traditionally focused on optimizing a single quantity of interest, such as the abundance of a species, a habitat type or a particular state of an ecosystem. Decades of failure in the management of harvestable species, including examples such as the collapse of the cod fishery and the California anchovy fishery (Hutchings 2000), the mismanagement of fire regimes in the USA (Huggard & Gomez 2001), changes in life history traits (Proaktor et al. 2007) such as trophy size in big horn sheep (Coltman et al. 2003) and predator control measures that have had unintended side effects (Beschta 2005, Lessard et al. 2005, Tverra et al. 2007), have convincingly demonstrated many of the weaknesses of MSY or 'optimal-state' approaches. Attempts to optimize economic returns, physical connectivity or other single-system properties are typically doomed to failure in the long-term because of related, critical variables that are negatively affected by such management (Holling & Meffe 1996). Similarly, using one or a few species for the identification and development of reserve systems or conservation plans may result in the protection of one organism at the expense of others (Landres et al. 1988).

To counter the problems of using single species in conservation decision-making, the use of indicator species (Noss 1990), guilds (Verner 1984), umbrella species (Shafer 1990) or focal species (Watson et al. 2001) have been advocated as methods for identifying areas to conserve. Although each of these approaches has its own merits, they all tend to focus on a single variable or component in a system. Available evidence suggests that managing for single variables usually fails because such approaches do not account for potential feedbacks, thresholds and surprises arising from interactions with other components of the system (Holling & Meffe 1996). In short, such approaches ignore the true complexity of the system, including the complex interactions between human social systems and ecosystems (Mascia et al. 2003). Unfortunately, strategies for managing multiple variables are seldom applied, and if they are, appropriate factors for maintaining resilience are rarely identified, monitored or enforced.

The task of the manager is complicated by a set of social pressures that affect the application of science to management problems and are often poorly understood. Managers are employed by organizations with specific agendas. To achieve its agenda, an organization must negotiate acceptable compromises with other organizations and individuals that may have different and potentially conflicting agendas. Most wildlife managers have strong, vocal and longstanding constituencies that demand that certain things happen on a regular basis (e.g. winter deer counts and stocking of game fish). As a consequence, resources are often invested in such activities without considering the broader implications of a singular focus. Powerful constituencies and the division of mandates within wildlife agencies can promote a narrow focus on multiple implementations of single-species management. Managers are often forced to select between particular kinds of resource use, weighing different ecosystem services against one another (Millennium Ecosystem Assessment 2005, Rodríguez et al. 2005). If trade-offs between ecosystem services are ignored by resource managers, future problems may be created that can result in expensive attempts to achieve technological substitution of formerly free services.

A central problem in developing effective management strategies for wildlife is that social and ecological systems may not be aligned at the appropriate scales to achieve consistent regional and local management (Conroy et al. 2003, Cumming et al. 2006). It is not uncommon for national-level governmental policies to demand local management actions that are either impossible for local managers to comply with, or that are inappropriate to specific local circumstances. For example, standard hunting regulations may be inappropriate where local wildlife populations are overabundant or on the verge of extinction. Conversely, many ecosystem processes are difficult to manage at the local scale, and appropriate regional authorities and mandates may not exist.

Paradigms for multi-species and ecosystem management have existed for two decades, but their implementation within management agencies lags in acceptance, despite compelling arguments for their usefulness (Barrows et al. 2005). The failure of many federal, state or provincial management agencies to embrace ecosystem management may be attributable to a number of causes, including restrictive institutional mandates and agendas, inflexibility in their ability to adopt new approaches and avoidance of risk taking and/or lack of funding (particularly for the long-term monitoring and intensive schemes that ecosystem management often demands). Additionally, there are real and perceived short-comings in the associated science, in terms of both basic (theoretical) understanding of the system and in translating theory-derived guidelines into practical, unambiguous recommendations for managers.

For example, in the United States, the legal framework under which management must occur is not particularly well-suited to ecosystem management. In particular, the Endangered Species Act (ESA) was enacted in 1973, and is a species-based law, rather than an ecosystem-based law (Ruhl 2004). This creates a precarious situation, for as Ruhl (2004) notes, "the principal driver behind the imperilment of species is the condition of the ecosystems upon which species depend for their survival". Ruhl (2004) contends that the ESA is unlikely to be updated anytime soon, so it is incumbent upon wildlife managers to 'push the envelope' with respect to application of the ESA. There is also an increased awareness amongst legal scholars that in order for ecosystem management to occur, the 'front-end' approach, which entails intense procedural development in the initial process of policy formulation, is ill-suited for dealing with ecological systems characterized by non-linear dynamics and multiple regimes (Ruhl 2004).

Another limitation is the ESA's ability to facilitate adaptive management, which is critical to managing for resilience (Armitage et al. 2007). The ESA is focused upon species that are in precipitous or perhaps even irreversible decline, with no mechanism for making management decisions when signs of decline are evident (Ruhl 2004). Within the ESA framework, monitoring is required under section 4 of the Act, but that monitoring is only required 'at least once every five years', which simply is not sufficient for adaptive management (Ruhl 2004). The concept of adjusting policy based on monitoring is not explicitly required by ESA, which creates further problems for an adaptive management protocol, as adaptive management requires 'back-end' modification (Ruhl 2004).

However, in the United States, there is reason for optimism as there is no explicit prohibition in the ESA preventing federal agencies from managing species with ecosystem considerations taken into account (Ruhl 2004). Furthermore, Ruhl (2004) contends that section 7(a)(1) of the ESA could be an avenue by which agencies would be required to utilize adaptive management in their management decisions. However, this potential in the ESA has yet to be realized, and likely will not be without strong leadership within the U.S. Fish and Wildlife Service and National Marine Fisheries Service to push for adaptive management (Ruhl 2004). As in the United States, the difficulties of managing for resilience within the context of 'static' legal frameworks are present in many countries.

Biodiversity, stability and ecological function

Changes in wildlife management have been driven by changes in scientific understanding, as well as by a wide range of social and political changes. The usual goal of natural resource management is to ensure that one or more properties of a system of interest are maintained through time. This is often interpreted as a need for managers to either seek to maintain system stability, or maintain particular system components and relationships while allowing or encouraging the system to change. In considering the dynamics of management and system change, two areas of ecological research are particularly relevant: the relationships between biodiversity, stability and ecosystem function, and an understanding of ecological resilience.

Darwin (1859) proposed that an ecosystem becomes more stable when more species are present. MacArthur (1955) proposed that because adding species to an ecosystem increases the number of ecological functions present, increasing richness would increase stability. Studies of lake systems have demonstrated that a similar ecological function can be maintained over a wide mix of species and population densities (Schindler 1990). This suggests that functional groups are key to understanding stability. A competing hypothesis proposes that strong interactions among species result in stability that is contingent on the particular nature of interspecific interactions (Lawton 1994) and that stability depends idiosyncratically upon which species are present. For example, fire ants *Solenopsis invicta* have had strong negative impacts on ecosystems of the southeastern United States (Porter & Savignano 1990, Allen et al. 1995), but are more integrated into the Pantanal of Brazil and Paraguay (Orr et al. 1995).

The relationship between diversity and function is also unresolved. The model of compensating complementarity (Frost et al. 1995) is similar to the 'rivet' model (Ehrlich & Ehrlich 1981). This model proposes that the ecological functions of different species overlap, so that even if a species is removed, ecological function may persist because of the compensation of other species with similar functions. In the rivet model, an ecological function will not disappear until all the species performing that function are removed from an ecosystem. Walker's 'drivers and passengers' (Walker 1992, 1995) hypothesis accepts the notion of species complementarity but proposes that ecological function resides in 'driver' species or in functional groups of such species. Walker defines a driver as a species that significantly influences the ecosystems in which they and passenger species exist, whereas passenger species have minor ecological impact. Walker (1995) proposed that since most ecological function resides in the strong influence of driver species, it is their presence or absence that most strongly determines the stability of an ecosystem's ecological function.

The existence of some type of ecological redundancy is supported by experiments conducted in temperate grasslands, tropical rainforests, artificial mesocosms and lakes (Schindler 1990, Tilman 1996). These studies and others demonstrate that the stability of many, but not all, ecological processes increases with species richness. They suggest that ecological stability is generated more from richness in functional groups than from species richness. Elmqvist et al. (2003) concluded, from a range of studies of lakes, forests, rangelands and coral reefs, that the diversity of functional groups improves ecosystem 'performance', and that the diversity within functional groups (response diversity) promotes the 'stability' of that performance. The model that best describes an ecosystem appears to depend upon the variety of functions that are present, the evenness of the distribution of ecological function among species, and explicitly incorporates scale (Peterson et al. 1998).

Resilience

We describe resilience, following Holling (1973), as a measure of the amount of change or disruption that is required to transform a system from being maintained by one set of mutually reinforcing processes and structures to a different set of processes and structures. An alternative definition (e.g. Pimm 1991) places emphasis on the speed of return of a system to its equilibrium state. This 'engineering' interpretation does not account for the most important aspect of ecological disturbance and change, whether or not the system is able to recover. When a system can reorganize into an alternative state or regime (i.e. shift from one stability domain to another), the more relevant measure of ecosystem dynamics is ecological resilience (Holling 1973). Using this terminology, engineering resilience is a local measure and ecological resilience a global measure.

Resilience is a broader concept than stability. Although most models of the relationship between species richness and ecosystem stability fail to incorporate scaling, a growing body of knowledge suggests that ecological structure and dynamics are primarily regulated by a small number of ecological processes (Carpenter & Leavitt 1991, Levin 1992) that operate at characteristic temporal and spatial scales (Holling 1992). In a plant community, for example, at fine-grained and fast scales, biophysical processes control plant physiology and morphology, whereas at larger scales of broader extent and longer duration, processes such as patch dynamics and interspecific competition for resources determine local species composition and regeneration. At the scale of forest stands, mesoscale processes such as fire, storms, insect outbreaks and herbivory determine structure and dynamics at scales ranging from tens of meters to kilometers, and from years to decades. For landscapes, climate, geomorphologic and biogeographic processes alter ecological structure and dynamics across hundreds of kilometers and millennia. These processes can also self-organize: they can produce patterns which reinforce the processes that produced the patterns (Kauffman 1993).

The resilience of ecological processes, and therefore of ecosystems, depends in part upon the distribution of function within and across scales (Peterson et al. 1998). If animal species that are members of the same functional group operate at different scales, they provide mutual reinforcement that contributes to the resilience of a function, while at the same time minimizing competition among species within the functional group. The apparent redundancy is not truly redundant because the functions are occurring at different scales. For example, seed dispersal is an important function that occurs at multiple scales, ranging from the very small in the form of ant dispersal of spring ephemerals to large via large mammals such as elephants *Loxodonta* spp. At a single scale, resilience is enhanced by an imbrication of ecological function among species of different functional groups that operate at the same scales, providing a robust response to a diversity of perturbations that complements the cross-scale redundancy of responses. There is a strong link between scaling in animals and their functions and body size. These relationships have led to formal propositions relating body size to the distribution of function within and across scales and resilience (Allen et al. 2005), allowing for quantifiable measures of the relative resilience of different ecosystems.

Managing for resilience

Managing for resilience consists of actively maintaining a diversity of functions and homeostatic feedbacks, steering systems away from thresholds of potential concern, increasing the ability of the system to maintain its identity under a wide range of conditions (i.e. increasing 'attractor size') and increasing the capacity of the system to cope with change through learning and adaptation (Biggs & Rogers 2003). For example, management to maintain clear (swimmable and drinkable) water within a shallow lake might involve a combination of restocking a top predator, removing non-native carp *Cyprinus carpio* that stir up sediment from the bottom of the lake, applying policies to reduce the amount of phosphorus entering the lake and educating upstream landowners about appropriate riparian zone management practices to ensure that high quality water enters the lake (Carpenter et al. 1999, Bennett et al. 2001). In order to manage for resilience, the goal must be to generate improved understanding of the entire system of interest, rather than specific, detailed knowledge from parts of the system (Folke et al. 2005). It is important to bear in mind that systems in undesirable states can also be highly resilient (Zellmer & Gunderson 2009). In such cases, the manager's goal is to reduce the resilience of the system and help transform the system to a state that is desirable.

The core of managing for resilience thus involves 1) anticipating potentially unwanted regime shifts within the system and taking actions that prevent them from occurring (as in the lake example), 2) maintaining a diversity of the system elements and feedback interactions that keep a system within a particular desired state, for example through careful fire management, stocking a diverse range of herbivores or reintroducing key seed dispersers, and 3) working to reduce the likelihood of system crashes or flips into a different state, for instance by control of invasive species, monitoring and maintenance of hydrological processes or monitoring for emerging diseases. In order to operationalize the three core aspects of managing for resilience, we offer the following:

1) Wildlife managers must identify conditions that indicate loss of resilience for their particular systems (treated in detail in the following sections of this manuscript). Recent research shows that there are system-specific conditions that indicate that the system is losing resilience and approaching a regime shift (Brock et al. 2008, Biggs et al. 2009). For shallow lakes, the shift from an oligotrophic to a eutrophic regime can be preceded by an increase of the periphyton layer covering the macrophytes and a reduction in the proportion of piscivorous fish (Brock et al. 2008).
2) Enhancing resilience is important, and this may be possible by maintaining the patterns of distribution of ecological functions within and across scales. In a test of the cross-scale resilience model, Forys & Allen (2002) found that despite large turnover in the species composition of vertebrate fauna in south Florida, USA, functional group richness within scales and functional redundancy across scales did not change significantly. While the structure of the species assemblages remained somewhat static, the types of functions performed by species changed with species turnover (Forys & Allen 2002).
3) Adaptive management can help reveal the components of resilience. Adaptive management treats management interventions as experiments. Adaptive governance treats policy options as hypotheses to be put at risk, which could result in a shift in the type of environmental policy used to manage a system of interest (Garmestani et al. 2009a). Furthermore, institutional challenges are one of the greatest barriers for building resilience in ecological systems (Lant et al. 2008, Garmestani et al. 2009a). Bridging organizations, informal networks and shadow networks can facilitate communication between institutions and maintaining or building resilience in these systems.

Managing for resilience is based on a systems perspective. It cannot be adopted effectively in the absence of science and scientifically-derived monitoring, nor will it be successful if the dynamic interplay between ecosystems and society is ignored. Managing for resilience will be most effective where

Table 1. Contrast between the elements of resilient wildlife management and a worst-case example of traditional management.

Element of the system	Management	
	Traditional	Resilience
Species	Focus (icon emphasis)	Component (function emphasis)
Process	Implicit management goal	Explicit management goal
Structure	Conserved in its entirety	Selectively conserved
Management	Command & control	Adaptive
Scale	Single	Multiple
Uncertainty	Inhibited	Embraced
Variability	Inhibited	Embraced
Natural Disturbances	Dampened where possible	Maintained where possible
Crisis	Calamity	Opportunity
Novelty	Suppressed	Encouraged
Redundancy	Low	High
Potential for learning	Low	High

key elements and interactions in the system have been described; key uncertainties have been identified and reduced (where possible) through deliberate management experiments, and potential future perturbations have been listed, evaluated and responded to in advance (e.g. scenario planning). Adaptive management is an approach that is critical to resilience management, because it focuses on learning, reducing uncertainty and monitoring. Resilience-based management differs from optimization approaches because of its focus on general rather than specific properties of the system of interest (Table 1). Many current management strategies fail because they attempt to control disturbances or fluctuations, manage for only one or a few species or seek to optimize adaptive systems that are 'moving targets' (Holling & Meffe 1996, Gunderson 2000, Folke et al. 2004). Such strategies do not account for the unpredictable nature of complex systems. Appropriate management strategies vary with the uncertainty associated with the process that is to be managed and the ability of the manager to manipulate the system (Peterson et al. 2003). Traditional (MSY) approaches work well when uncertainty is low and the manager is able to manipulate the system. More flexible management and policy approaches, such as adaptive management, coupled with scenario planning (Peterson et al. 2003), are needed when uncertainty and/or the difficulty of achieving the desired manipulations are high.

Identification and recognition of appropriate temporal and spatial scales and cross-scale interactions is central to the management of ecological systems for resilience. For a system to be resilient implies that it maintains certain key properties (those that are central to its identity; Cumming & Collier 2005) through time, while responding and adapting dynamically to a changing environment. Thus, it shares some similarities to the concept of 'incorporation', introduced by Urban et al. (1987) > 20 years ago. Resilient systems are seldom at equilibrium, but will not overcompensate in response to perturbations or exhaust available resources. Habitat heterogeneity and connectivity may enhance or reduce resilience, depending on the species, the kinds of ecosystem processes and the kinds of perturbations that occur in the system (Terborgh et al. 2001).

Enhancing spatial and temporal resilience in management requires the maintenance of key processes of a system within and across multiple scales. Some ecosystem processes are local, such as the deposition of soil nutrients from leaf fall, while others, such as climate regulation and groundwater recharge, are regional. Many organisms have both local and regional components to their lifecycles, ranging from local needs for food to regional dispersal and seasonal movements. Resilient wildlife management takes into account such processes, and thus necessitates the design and implementation of conservation strategies that integrate both across scales and among ecosystem components, and anticipates anthropogenic impacts on the environment and land-use tenure. Although the basic structure of some ecosystems that are highly perturbed, such as the Florida Everglades (Forys & Allen 2002) or nutrient enriched lakes (Havlicek & Carpenter 2001), appears conservative to these perturbations (at least for short-time periods), the rapid collapse and subsequent reorganization of other ecosystems, including coral reefs (Hughes 1994), shallow lakes (Carpenter 2001) and terrestrial systems (Carpenter & Leavitt 1991, Peterson 2002) demonstrates that many others are not. Learning how to recognize and manage for resilience in these systems is necessarily a high priority.

A key aspect of managing for resilience is to understand and maintain essential feedbacks between different system components. Tight feedbacks, in which the interactions between cause and effect are large, fast or strong, can facilitate rapid local adaptation (Levin 2000). By contrast, looser (slower and weaker) feedbacks often enhance diversity. If tight feedbacks are restricted to a limited spatial scale or segment of a food web, they can produce compartments, which are system subsets that exhibit locally independent dynamics. Mutualisms and many classical predator*prey interactions occur in compartmentalized food webs (Bascompte et al. 2003, Rezende et al. 2009). The lack of strong external controls on large predators can lead to interactions where feedbacks from predator to prey and prey to predator are tight, whereas feedbacks from resource to prey or from predator to the broader ecosystem are loose. In a broader context, there are also many feedbacks between ecological and social systems. For example, the return of revenue from a protected area to a local community can provide an incentive for conservation. Disruption of feedbacks can have profound effects on resilience. It is critical to understand feedbacks, because they can play a large role in maintaining or reducing system cohesion and can push the system over a threshold.

A central question in management is how to maintain essential functions and processes within a system while allowing it to respond and adapt to changing environmental conditions. Complex systems theory suggests that the conservation of function is strongly dependent on diversity, selection and the number and nature of feedbacks between different system components (Garmestani et al. 2009b). Consequently, it is important that management should both facilitate the maintenance of diversity and allow adaptation and evolution, suggesting that managers should be sensitive to changes within their systems and resist the temptation to focus on reintroductions or habitat mitigation for locally rare or extirpated species that are fundamentally unsuited to current conditions.

A focus of management on resilience, rather than on reducing variability of one or a few of the components of the system in order to achieve greater efficiency of production of a particular component or ecosystem service, therefore has several important facets. Embracing uncertainty and allowing and encouraging variability is critical. Understanding and incorporating disturbance is necessary. Key scales and entraining variables need to be identified, and conservation must be focused upon structures and processes rather than on individual species. We next consider how this conceptual discussion of resilience management translates into practical recommendations for managers.

Operationalizing resilience management

We consider the following three questions to be of particular importance for the practice of resilience management: 1) "How do I apply resilience management principles to the system I manage?", 2) "Are there examples where managing for resilience has been or is being successfully implemented?", and 3) "If I manage for resilience in my own system, how do I know whether or not I am getting it right?". Although we do not claim to have definitive answers to these questions, we can offer some practical recommendations that will facilitate the application of resilience management, and collectively allow managers to begin to discover the answers to these questions. One method of learning more about system dynamics and thus learning how to better manage through safe-to-fail experiments is via an adaptive management approach (Garmestani et al. 2009a, Allen et al. 2011).

With regard to the first question, the first step is to determine what is known about the system, in terms of both data and conceptual understanding. Managing for resilience requires active exploration of current and potential changes in the study system. Consequently, it is important to monitor spatial and temporal change in the system and to develop a data baseline against which change can be assessed (Litvaitis 2003). Appropriate data can reveal the critical processes and the scales at which they occur. For many ecosystems, it takes 30-40 years of data collection before key processes and dynamics become apparent (at the mesoscales, about which we often know the least). Monitoring schemes should ideally incorporate a range of cross- and multi-scale processes and the variables that govern them. They should also include monitoring of both social and ecological variables. Feedbacks between different system components and processes are of particular importance. Negative feedbacks create homeostasis, or stability; positive feedbacks create instability. Disruption of processes and feedbacks can have unexpected consequences, and self-reinforcing feedbacks often create the possibility for alternate regimes. Regime shifts occur when a system approaches and then exceeds a threshold; the identification of thresholds is valuable, because awareness of a possible trap is the first step in avoiding it. In social-ecological systems, this means determining alternative system configurations (Walker & Meyers 2004) and then understanding how a system may transform. Thresholds between alternate system regimes may be marked by change in the direction or intensity of feedbacks or by increasing variance in key parameters (Carpenter & Brock 2006, Wardwell & Allen 2009). Of particular interest in a resilience context is the identification of 'traps'; undesirable, self-reinforcing system configurations from which the system may find it difficult to escape (Carpenter & Brock 2008).

Next, managing for resilience requires managers to treat management efforts as experimental manipulations (i.e. adaptive management), and cherished notions of system function as hypotheses that can be falsified. Management activity where nothing is learned should be viewed as wasted effort. An important part of learning is to maintain some form of memory that can be passed on to others; for example, records of data collected, the exact kinds and locations of management activities that were undertaken and the underlying hypotheses that drove the management. Crises can create opportunities for the development of novel approaches, and can serve as catalysts for change in human perceptions. Learning can often be achieved by experimentally varying regulations, such as bag limits or incidental take. Examples from irrigation and other systems that persisted for long periods (Ostrom 1990, Forbes et al. 2009) show that a regime of alternating rules in the social domain in response to changing environmental conditions can help social-ecological systems avoid crossing an unwanted ecological threshold. In this context, it may be critical to involve stakeholders, to have stakeholders verbalize their mental models of ecological systems, as well as their relationships and influence upon them, and to envision alternative and competing plausible scenarios of future conditions based on the mental models (Andrade 2009, Browne et al. 2009). Indigenous peoples may have vastly different mental models, and goals and objectives for wildlife management, yet their knowledge, frequently overlooked, can be critical (Berkes 2008).

Third, managing for resilience involves spreading the risk by employing a diversity of management strategies. It is important to identify those elements of the system that can be subjected to manipulation and experimentation. Changing environmental conditions will select the successful approaches over the failures, but a lack of diversity in management activities creates the possibility for a catastrophic failure. Risk can be minimized by maintaining diversity within the system. Management should encourage variability in processes and in the scales at which the processes operate. Diversity is important in times of change, when alternative options (which may be species, technologies or connectivity) may prove to be more viable. Similarly, management should incorporate disturbance at multiple spatial and temporal scales, and be proactive. In many cases, particular kinds of perturbation are likely to occur, even though their timing and severity may be hard to predict. Rather than engineering the system to attempt to avoid those events, and so reduce resilience, a better approach is to manage the system so that when unexpected events occur, the system is resilient enough to recover.

A pragmatic and innovative example of an approach to resilience management is the 'Thresholds of Potential Concern' (TPC) approach used in the Kruger National Park, South Africa (Biggs & Rogers 2003). TPCs are a set of operational goals that together define the spatio-temporal heterogeneity of conditions for which the Kruger ecosystem is managed. The approach concedes that because it is not possible to monitor, or research, all components of wildlife, vegetation, soils and waterways, the most effective approach is to develop conceptual models of the system, with the goal of identifying possible threshold effects and regime shifts. These are paid special attention, and when routine monitoring indicates that the system is approaching a potential threshold, more effort is put into research.

How does a manager know when he or she is getting it right? Because resilience management is unlikely to be adopted synchronously and uniformly by multiple agencies, managers who are interested in managing for resilience will be able to contrast the outcome of their management activities with those of other comparable systems that are managed in more traditional ways. Another measure of success will be the degree to which managing for resilience solves chronic problems that have not been amenable to other approaches. One of the areas where we believe that resilience management could make a substantial contribution is in enhancing the alignment of the scales of management and the scales at which ecological processes occur (Cumming et al. 2006).

Panarchy is a useful model for characterizing ecological systems and the formal institutions that manage these systems (Gunderson & Holling 2002). One of the most critical aspects in the panarchy of ecological systems and formal institutions appears to be a bridging organization that can monitor the status of the system, and manifest rapid change if conditions are deteriorating (Kinzig et al. 2003, Olsson et al. 2007). Bridging organizations can facilitate cross-scale linkages, in order for formal management entities operating at discrete scales to improve communication channels and create opportunities for collaboration. These results will allow for management to set new target levels, and modify policy to reach those target levels, as new information is generated on scale-specific system attributes (Karkkainen 2002). This resilience management framework, which incorporates panarchy, adaptive management and bridging organizations, could serve as one scenario in the suite of policy options for actualizing ecosystem management (Garmestani et al. 2009a).

We expect that managing for resilience will sustain diversity, permit natural perturbations, facilitate the action of natural processes and integrate both social and ecological dimensions of sustainability. Its strongest test will probably be the ability of the managed system to cope with large and catastrophic perturbations such as tsunamis or hurricanes, which come as a surprise. Monitoring must be linked to an underlying model of the system's dynamics, i.e. the expected vs actual consequences of drivers and shocks to the system. A key component of active adaptive management (Walters 1986) is the forecast vs actual outcome of a management intervention. The forecast outcome requires a model of some sort, whether implicit (a mental model) or explicit. Managing for resilience requires the same kind of developing understanding of the dynamics of the system in response to either purposeful management actions or natural surprises.

One of the key aspects of managing for resilience is awareness that the present is not necessarily what we thought it would be. Future changes are very difficult to predict accurately, but it is possible to identify the major sources of uncertainty that would affect our predictions. Scenario planning offers a structured way of considering uncertainty that links both quantitative and qualitative approaches (Peterson et al. 2003). It is particularly appropriate when uncertainty is high and the ability of the manager to control or regulate the system is low. Scenarios can play an important role in envisioning the future resilience of the system and the likelihood that a system may be disrupted in some way. Depending on the outcome of scenario planning, managers may feel either that they can continue with business as usual, or that some actions are necessary to prepare for likely future perturbations.

Costs and benefits

Adopting a resilience-centered approach to management will carry both costs and benefits. The focus of resilience on long-term persistence and social-ecological linkages assumes that the world is constantly changing, humans are inextricably part of ecosystems and that wise managers will attempt to prepare their systems for future change. Managing for resilience implies that overexploitation, maximization, variance reduction and optimization are to be avoided because they erode the capacity of the system to cope with change or fail to acknowledge the constancy of change in ecological systems (Holling & Meffe 1996).

The underlying theory suggests that managing for resilience comes most fully into its own during times of crisis. When crises are unknown but anticipated, it is the responsibility of the manager to try to develop the greatest possible capacity within the system to respond and adapt to crises without transforming the state of the system (i.e. causing a regime shift). In the same way that sections of the global community have started to respond to the crisis of species loss by investing more heavily in protected areas, so must managers respond to anticipated threats by investing more heavily in activities that will facilitate system persistence under new conditions or heightened variability. Although such thinking has begun to pervade both the social and ecological sciences, resilience thinking has yet to be substantially translated to policy because it is perceived as risky.

In cases where the environment remains constant over long periods of time, the extra effort and resources that managing for resilience entails may be perceived as wasteful. Maintaining response diversity within a system may be costly, and society will be asked to bear these costs in exchange for a greater likelihood that a system will meet stated goals of long-term persistence. The value added by a resilience approach is partly dictated by the cost of failure. Surprises are inevitable, and historical long-term constancy and persistence is no guarantee of future stability (Janssen et al. 2007). If the potential cost of failure is greater than the increase in costs that managing for resilience would require, then it is worthwhile to implement a resilience approach.

Conclusions

The world is transforming and is doing so at an increasing rate (Millenium Ecosystem Assessment 2005). Humans increasingly dominate ecological goods and services (Vitousek et al. 1997). Potential rapid climate change is exacerbated by a reduction in many habitats upon which species rely (including humans), increased fragmentation of the remainder and an increasing homogenization of the world's taxa. Remnant ecosystems and species are increasingly challenged by such transformations, and the adaptive potential of those ecosystems and their components is constrained. Management of these systems to date has often been reactionary. A better approach to the management of wildlife and the systems within which they reside is necessary in a rapidly transforming world rife with uncertainty at multiple scales. An approach to management that maintains and enhances the resilience of these complex adaptive systems is called for. Resilience theory is still developing, but is a rapidly growing focus of ecological, social and economic inquiry. Wildlife professionals should consider embracing the principles of resilience theory, because management based upon them is more likely than traditional alternatives to sustain wildlife populations in a world where human and natural system boundaries are increasingly blurred.

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References

Allen, C.R., Fontaine, T.J., Pope, K.L. & Garmestani, A.S. 2011: Adaptive management for a turbulent future. - Journal of Environmental Management 92(5): 1339-1345.

Allen, C.R., Gunderson, L. & Johnson, A.R. 2005: The use of discontinuities and functional groups to assess relative resilience in complex systems. - Ecosystems 8(8): 958-966.

Allen, C.R., Lutz, R.S. & Demarais, S. 1995: Red imported fire any impacts on Northern Bobwhite populations. - Ecological Applications 5(3): 632-638.

Andrade, G.I. 2009: Closing the Frontier? Reflections on the new social construction of protected nature in Colombia. - Revista De Estudios Sociales 32: 48-58.

Armitage, D., Berkes, F. & Doubleday, N. 2007: Adaptive Co-Management: Collaboration, Learning and Multi-level Governance. - UBC Press, Vancouver, Canada, 344 pp.

Barrows, C.W., Swartz, M.S., Hodges, W.L., Allen, M.F., Rotenberry, J.T., Li, B., Scott, T.A. & Chen, X. 2005: A framework for monitoring multiple species conservation plans. - Journal of Wildlife Management 69(4): 1333-1345.

Bascompte, J., Jordano, P., Melian, C.J. & Olesen, J.M. 2003: The nested assembly of plant-animal mutualistic networks. - Proceedings of the National Academy of Sciences of the United States of America 100(16): 9383-9387.

Baxter, G.S., Hockings, M., Carter, R.W. & Beeton, R.J.S. 1999: Trends in wildlife management and the appropriateness of Australian university training. - Conservation Biology 13(4): 842-849.

Bennett, E.M., Carpenter, S.R. & Caraco, N.F. 2001: Human impact on erodable phosphorus and eutrophication: a global perspective. - BioScience 51(3): 227-234.

Berkes, F. 2008: Sacred Ecology. - Routledge Publishers, New York, New York, USA, 336 pp.

Beschta, R.L. 2005: Reduced cottonwood recruitment following extirpation of wolves in Yellowstone's northern range. - Ecology 86(2): 391-403.

Biddle, P.B., Cross, D.H., Jennings, D.P., Sojda, R.C. & Solomon, R.C. 1995: Information needs and technology applications of the Department of the Interior natural resource professionals. - Wildlife Society Bulletin 23(4): 627-630.

Biggs, R., Carpenter, S.R. & Brock, W.A. 2009: Turning back from the brink: Detecting an impending regime shift in time to avert it. - Proceedings of the National Academy of Sciences 106(3): 826-831.

Biggs, H.C. & Rogers, K.H. 2003: An adaptive system to link science, monitoring, and management in practice. - In: du Toit, J.T., Rogers, K.H. & Biggs, H.G. (Eds.); The Kruger experience: ecology and management of savanna heterogeneity. Island Press, Washington, D.C., USA, pp. 59-80.

Brock, W.A., Carpenter, S.R. & Scheffer, M. 2008: Regime shifts, environmental signals, uncertainty, and policy choice. - In: Norberg, J. & Cumming, G.S. (Eds.); Complexity theory for a sustainable future. Columbia University Press, New York, New York, USA, pp. 180-206.

Browne, M., Pagad, S. & De Poorter, M. 2009: The crucial role of information exchange and research for effective responses to biological invasions. - Weed Research 49(1): 6-18.

Carpenter, S.R. 2001: Alternate states of ecosystems: evidence and its implications. - In: Press, M.C., Huntly, N. & Levin, S. (Eds.); Ecology: achievement and challenge. Blackwell, London, UK, pp. 357-383.

Carpenter, S.R. & Brock, W.A. 2006: Rising variance: a leading indicator of ecological transition. - Ecology letters 9(3): 311-318.

Carpenter, S.R. & Brock, W.A. 2008: Adaptive capacity and traps. - Ecology and Society 13: 40.

Carpenter, S.R, Brock, W.A. & Hanson, P. 1999: Ecological and social dynamics in simple models of ecosystem management. - Conservation Ecology 3(2): 4.

Carpenter, S.R. & Leavitt P.R. 1991: Temporal variation in paleolimnological record arising from a trophic cascade. - Ecology 72(1): 277-285.

Coltman, D.W., O'Donoghue, P., Jorgenson, J.T., Hogg, J.T., Strobeck, C. & Festa-Bianchet, M. 2003: Undesirable evolutionary consequences of trophy hunting. - Nature 426: 655-658.

Conroy, M.J., Allen, C.R., Peterson, J.T., Pritchard, L., Jr. & Moore, C.T. 2003: Landscape change in the southern piedmont: challenges, solutions, and uncertainty across scales. - Conservation Ecology 8(2): 3.

Cumming, G.S. & Collier, J. 2005: Change and identity in complex systems. - Ecology and Society 10(1): 29.

Cumming, G.S., Cumming, D.H.M. & Redman, C.L. 2006: Scale mismatches in social-ecological systems: causes, consequences, and solutions. - Ecology and Society 11(1): 14.

Cutler, M.R. 1982: What kind of wildlifers will be needed in the 1980s? - Wildlife Society Bulletin 10(1): 75-79.

Darwin, C. 1859: On the origin of species: by means of natural selection or the preservation of favoured races in the struggle for life (reprinted in 1964). - Harvard University, Cambridge, Massachusetts, USA, 512 pp.

Ehrlich, P.R. & Ehrlich, A.H. 1981: Extinction: the causes and consequences of the disappearance of species. - Random House, New York, New York, USA, 305 pp.

Elmqvist, T., Folke, C., Nystrom, N., Peterson, G., Bengston, J., Walker, B. & Norberg, J. 2003: Response diversity, ecosystem change and resilience. - Frontiers in Ecology and Environment 1(9): 488-494.

Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L. & Holling, C.S. 2004: Regime shifts, resilience, and biodiversity in ecosystem management. - Annual Review of Ecology, Evolution, and Systematics 35: 557-581.

Folke, C., Hahn, T., Olsson, P. & Norberg, J. 2005: Adaptive governance of social-ecological systems. - Annual Review of Environment and Resources 30: 441-473.

Forbes, B.C., Stammler, F., Kumpula, T., Meschtyb, N., Pjunen, A. & Kaarlejarvi, E. 2009: High resilience in the Yamal-Nenets social-ecological system, West Siberian Arctic, Russia. - Proceedings of the National Academy of Sciences 106(52): 22041-22048.

Forys, E.A. & Allen, C.R. 2002: Functional group change within and across scales following invasions and extinctions in the Everglades ecosystem. - Ecosystems 5(4): 339-347.

Frost, T.M., Carpenter, S.R., Ives, A.R. & Kratz, T.K. 1995: Species compensation and complementarity in ecosystem function. - In: Jones, C.G. & Lawton, J.H. (Eds.); Linking species and ecosystems. - Chapman and Hall, New York, New York, USA, pp. 224-239.

Garmestani, A.S., Allen, C.R. & Cabezas, H. 2009a: Panarchy, adaptive management and governance: policy options for building resilience. - Nebraska Law Review 87: 1036-1054.

Garmestani, A.S., Allen, C.R. & Gunderson, L. 2009b: Panarchy: discontinuities reveal similarities in the dynamic system structure of ecological and social systems. - Ecology and Society 14 (1): 15.

Government of Canada 2005: Species at Risk Registry. - Available at: http://www.sararegistry.gc.ca/ (Last accessed on 10 August 2005).

Groom, M.J., Meffe, G.K. & Carroll, C.R. 2006: Principles of Conservation Biology. 3rd edition. - Sinauer Associates, Sunderland, Massachusetts, USA, 779 pp.

Gunderson, L.H. 2000: Ecological resilience: in theory and application. - Annual Review of Ecology and Systematics 31: 425-439.

Gunderson, L. & Holling, C.S. 2002: Panarchy: understanding transformations in systems of humans and nature. - Island Press, Washington, D.C., USA, 508 pp.

Havlicek, T.D. & Carpenter, S.R. 2001: Pelagic species size distributions in lakes: are they discontinuous? - Limnology and Oceanography 46(5): 1021-1033.

Holling, C.S. 1973: Resilience and stability of ecological systems. - Annual Review of Ecology and Systematics 4: 1-23.

Holling, C.S. 1992: Cross-scale morphology, geometry and dynamics of ecosystems. - Ecological Monographs 62(4): 447-502.

Holling, C.S. & Meffe, G.K. 1996: Command and control and the pathology of natural resource management. - Conservation Biology 10(2): 328-337.

Huggard, C.J. & Gomez, A.R. 2001: Forests under fire: a century of ecosystem mismanagement in the southwest. - University of Arizona Press, Tuscon, Arizona, USA, 307 pp.

Hughes, T.P. 1994: Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. - Science 265(5178): 1547-1551.

Hutchings, J.A. 2000: Collapse and recovery of marine fishes. - Nature 406: 882-885.

Jacobson, S.K. & McDuff, M.D. 1998: Training idiot savants: the lack of human dimensions in conservation biology. - Conservation Biology 12(2): 263-267.

Janssen, M.A., Anderies, J.M. & Ostrom, E. 2007: Robustness of social-ecological systems to spatial and temporal variability. - Society and Natural Resources 20: 1-16.

Karkkainen, B.C. 2002: Collaborative ecosystem governance: scale, complexity and dynamism. - Virginia Environmental Law Journal 21: 189-243.

Kauffman, S.A. 1993: Origins of order: self-organization and selection in evolution. - Oxford University, Oxford, UK, 734 pp.

Kinzig, A., Starrett, D., Arrow, K., Aniyar, S., Bolin, B., Dasgupta, P., Ehrlich, P., Folke, C., Hanemann, M., Heal, G., Hoel, M., Jansson, A., Jansson, B.O., Kautsky, N., Levin, S., Lubchenco, J., Maler, K.G., Pacala, S.W., Schneider, S.H., Siniscalco, D. & Walker, B. 2003: Coping with uncertainty: a call for a new science-policy forum. - Ambio 32(5): 330-335.

Landres, P.B., Verner, J. & Thomas, J.W. 1988: Ecological uses of vertebrate indicator species: a critique. - Conservation Biology 2(4): 316-328.

Lant, C.L., Ruhl, J.B. & Kraft, S.E. 2008: The tragedy of ecosystem services. - BioScience 58(10): 969-974.

Lawton, J.H. 1994: What do species do in ecosystems? - Oikos 71(3): 367-374.

Levin, S.A. 1992: The problem of pattern and scale in ecology. - Ecology 73(6): 1943-1967.

Levin, S.A. 2000: Fragile dominion: complexity and the commons. - Perseus Publishing, Cambridge, Massachusetts, USA, 272 pp.

Lessard, R.B., Martell, S., Walters, C.J., Essington, T.E. & Kitchell, J.F.K. 2005: Should ecosystem management involve active control of species abundances? - Ecology and Society 10(2): 1.

Litvaitis, J.A. 2003: Are pre-Columbian conditions relevant baselines for managed forests in the northeastern United States? - Forest Ecology and Management 185(1-2): 113-126.

MacArthur, R.H. 1955: Fluctuations of animal populations and a measure of community stability. - Ecology 36(3): 533-536.

Mascia, M., Brosius, J.P., Dobson, T., Forbes, B.C., Nabhan, G. & Tomforde, M. 2003: Conservation and the social sciences. - Conservation Biology 17(3): 649-650.

Millennium Ecosystem Assessment 2005: Ecosystem and human well-being: general synthesis. - Island Press, Washington, D.C., USA, 160 pp.

Noss, R.F. 1990: Indicators for monitoring biodiversity: a hierarchical approach. - Conservation Biology 4(4): 355-364.

Olsson, P., Folke, C., Galaz, V., Hahn, T. & Schultz, L. 2007: Enhancing the fit through adaptive co-management: Creating and maintaining bridging functions for matching scales in the Kristianstads Vattenrike Biosphere Reserve Sweden. - Ecology and Society 12: 28.

Orr, M.R., Seike, S.H., Benson, W.W. & Gilbert, L.E. 1995: Flies suppress fire ants. - Nature 373: 292-293.

Ostrom, E. 1990: Governing the Commons: The Evolution of Institutions for Collective Action. - Cambridge University Press, Cambridge, UK, 298 pp.

Pimm, S.L. 1991: The Balance of Nature. - University of Chicago Press, Chicago, Illinois, USA, 448 pp.

Peterson, G.D. 2002: Resilience of southern pine forests. - In: Gunderson, L.H. & Pritchard, L., Jr. (Eds.); Resilience and the behavior of large scale ecosystems. Island Press, Washington, D.C., USA, pp. 227-246.

Peterson, G., Allen, C.R. & Holling, C.S. 1998: Ecological resilience, biodiversity and scale. - Ecosystems 1(1): 6-18.

Peterson, G.D., Cumming, G.S. & Carpenter, S.R. 2003: Scenario planning: a tool for conservation in an uncertain world. - Conservation Biology 17(2): 358-366.

Porter, S.D. & Savignano, D.A. 1990: Invasion of polygyne fire ants decimates native ants and disrupts arthropod community. - Ecology 71(6): 2095-2116.

Proaktor, G., Coulson, T. & Milner-Gulland, E.J. 2007: Evolutionary responses to harvesting in ungulates. - Journal of Animal Ecology 76(4): 669-678.

Rezende, E.L., Albert, E.M., Fortuna, M.A. & Bascompte, J. 2009: Compartments in a marine food web associated with phylogeny, body mass, and habitat structure. - Ecology Letters 12(8): 779-788.

Rodríguez, J.P., Beard, T.D., Jr., Agard, J., Bennett, E., Cork, S., Cumming, G., Deane, D., Dobson, A.P., Lodge, D.M., Mutale, M., Nelson, G.C., Peterson, G.D. & Ribeiro, T. 2005: Interactions among ecosystem services. - In: Carpenter, S.R., Pingali, P.L., Bennett, E.M. & Zurek, M.B. (Eds.); Ecosystems and human well-being: scenarios (Volume 2). Findings of the Scenarios Working Group, Millennium Ecosystem Assessment. Island Press, Washington, D.C., USA, pp. 431-448.

Ruhl, J.B. 2004: Taking adaptive management seriously: a case study of the Endangered Species Act. - Kansas Law Review 52: 1249-1284.

Schindler, D.W. 1990: Experimental perturbations of whole lakes as tests of hypotheses concerning ecosystem structure and function. - Oikos 57(1): 25-41.

Shafer, C.L. 1990: Nature reserves: Island Theory and Conservation Practice. - Smithsonian Institution Press, Washington, D.C., USA, 208 pp.

Terborgh, J., Lopez, L., Nunez, P., Rao, M., Shahabuddin, G., Orihuela, G., Riveros, M., Ascanio, R., Adler, G.H., Lambert, T.D. & Balbas, L. 2001: Ecological meltdown in predator-free forest fragments. - Science 294(5548): 1923-1926.

Tilman, D. 1996: Biodiversity: population versus ecosystem stability. - Ecology 77(2): 350-363.

Tverra, T., Fauchald, P., Yoccoz, N.G., Ims, R.A., Aanes, R. & Høgda, K.A. 2007: What regulates and limits reindeer populations in Norway? - Oikos 116(4): 706-715.

Urban, D.L., O'Neill, R.V. & Shugart, H.H., Jr. .1987: Landscape ecology. - BioScience 37(2): 119-127.

van Heezik, Y. & Seddon, P.J. 2005: Structure and content of graduate wildlife management and conservation biology programs: an international perspective. - Conservation Biology 19(1): 7-14.

Verner, J. 1984: The guild concept applied to management of bird populations. - Environmental Management 8(1): 1-14.

Vitousek, P.M., Mooney, H.A., Lubchenco, J. & Melillo, J.M. 1997: Human domination of Earth's ecosystems. - Science 277(5325): 494-499.

Walker, B. 1992: Biological diversity and ecological redundancy. - Conservation Biology 6(1): 18-23.

Walker, B. 1995: Conserving biological diversity through ecosystem resilience. - Conservation Biology 9(4): 747-752.

Walker, B. & Meyers, J.A. 2004: Thresholds in ecological and social-ecological systems: a developing database. - Ecology and Society 9(2): 3.

Walters, C. 1986: Adaptive Management of Renewable Resources. - Macmillan, New York, New York, USA, 374 pp.

Wardwell, D. & Allen, C.R. 2009: Variability in population abundance is associated with thresholds between scaling regimes. - Ecology and Society 14(2): 42.

Watson, J., Freudenberger, D. & Paull, D. 2001: An assessment of the focal-species approach for conserving birds in variegated landscapes in southeastern Australia. - Conservation Biology 15(5): 1364-1373.

Zellmer, S. & Gunderson, L. 2009: Why resilience may not always be a good thing: Lessons in ecosystem restoration from Glen Canyon and the Everglades. - Nebraska Law Review 87: 893-949.