Ecological resilience: literature review, article critique and experimental protocol

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Foreword

I present this paper in partial fulfillment of the doctoral program in biology at the Université du Québec à Montréal. My director, Christian Messier (Université du Québec à Montréal), originally proposed the topic of ecological resilience *sensu* Holling for this synthesis and provided the article dealing with this topic that I critique therein. The topic and article were later accepted by my co-director, Yves Bergeron (Université du Québec en Abitibi-Témiscamingue), and this *examen*'s committee members: Mike Flannigan (Canadian Forest Service) and Garry Peterson (McGill University). Thanks to Dominique Gravel for help with the successional index.

Abstract

This paper synthesizes elements of the theory and application of ecological resilience. It has three components. The first is a review of relevant literature concerning ecological resilience, with a focus on the work of ecologist Buzz Holling and his colleagues. Here, ecological resilience is a measure of the persistence of systems and of their capacity to absorb change and disturbance while maintaining the same structuring relationships between populations or state variables. The second component is an article critique of Peterson, G. D. 2002. Estimating resilience across landscapes. Cons. Ecol. **6**(1): 17. [online] URL: http://www.consecol.org/vol6/iss1/art17. This article deals with the measurement of resilience across a longleaf pine-dominated landscape in Florida where fire plays a key role in determining forest composition and structure and transition between stable states. I summarize the objectives, methods and results of the article as well as discuss the article's major strengths and weaknesses, including both general and specific comments on content and style. Third, I propose an experimental protocol designed to deal with issues raised by Peterson, in particular how structure and compositional diversity of component species relate to the notion that areas of cross-scale edge, a measure of resilience defined by Peterson, have low resilience. I conclude with reflections on how to effectively integrate ecological resilience into the sustainable management of resources.

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1. Introduction

Humanity's reach now extends further than ever before. In the last 150 yr, people have modified between one-third to one-half of Earth's terrestrial surface and we currently use more than half its accessible fresh water (Vitousek et al. 1997a; Groombridge and Jenkins 2002). We fix more atmospheric nitrogen than all natural terrestrial sources combined (Vitousek et al. 1997a) and have increased the concentration of carbon dioxide in the atmosphere by over 30 % since the Industrial Revolution (IPCC 2001). Humans are a root cause of what E.O. Wilson deems the sixth major wave of global biodiversity loss since the dawn of life on Earth (Wilson 1992). Largely as a consequence of habitat loss, extinction rates are about 100 to 1000 times greater than before humans grew to be a ubiquitous force (Pimm et al. 1995; Pimm and Raven 2000). For example, approximately one quarter of the bird species of the world are extinct as a result of human actions over the last 2000 yr (Steadman 1995) and overfishing since the advent of industrial harvest methods has dramatically altered ocean food webs and decreased the biomass of all top predators in the ocean by about 90 % (Jackson et al. 2001; Myers and Worm 2003). Invasions of exotic species through intentional and accidental anthropogenic introductions has resulted in a homogenization of the world's flora and fauna and reduced biodiversity on a global scale (Lövei et al. 1997; Vitousek et al. 1997b). It seems indisputable that humans now profoundly influence the diversity and evolution of life on our planet, and thereby the capacity of our ecosystems to continue providing the ecological services and goods on which our well-being depends.

This influence is poised to continue, indeed increase, in the foreseeable future with ongoing population growth, climate change and chemical contamination of the biosphere. This situation leads to some fundamental questions: How resilient are ecosystems to this rapid and pervasive ecological reorganization? How do we know when we are reaching thresholds of irreversible alteration of ecosystems? How can we maintain and build resilient ecosystems? Are humans actually capable of extracting goods and services from ecosystems without engendering what seems to be an inevitable long-term pattern of resource use that results in commercial resource extinction or lasting ecosystem degradation?

These questions are more pertinent with consideration of the remarkable consistency of overexploitation in the history of resource management (Clark 1973; Ludwig et al. 1993; Hilborn et al. 1995). Since management activities can reduce diversity and the capacity of ecosystems to absorb disturbances and deal with changing conditions (Holling and Meffe 1996; Scheffer et al. 2001), ecologists have argued for a refocusing of management goals away from specific targets such as

Maximum Sustainable Yield and towards the maintenance of resilience (Holling 1973; 1986; Peterson et al. 1998). In other words, managers should enhance the resilience of ecosystem states essential to the provision of ecosystem goods and services while decreasing the resilience of states that do not provide these services or that do so at low levels.

Here, I review literature that deals with ecological resilience, that is, the capacity of natural systems to absorb disturbances and withstand change to a fundamentally different state. I pay particular attention to the work of ecologist C. S. (Buzz) Holling and his collaborators who have, during the last 30 yr, developed a comprehensive multidisciplinary framework for understanding the resilience of natural and dynamic systems (Gunderson and Holling 2002). To scope this paper, I focus primarily on the ecological aspects of resilience rather than its social or economic dimensions, acknowledging that meaningful answers to the above questions rely on an integration of all these dimensions.

This paper has three major components: the first is a short review and synthesis of the literature concerning resilience, with an emphasis on its ecological dimension and its application in ecosystem research and management. The second component is an article critique, where I summarize and assess the strengths and weaknesses of Peterson (2002a) – an article dealing with resilience and how to measure it across a landscape of management interest. Third, I propose an experimental design that seeks to test and further develop the hypotheses presented in Peterson (2002a). Last, I conclude with some thoughts that address the questions raised above.

2. Literature review and synthesis

Attempts to understand how ecological communities and ecosystems remain stable in the face of disturbance and changing environmental conditions date back to at least Darwin (1859). Darwin (1859) proposed that the ecological stability of an area varies as a function of its species richness – in essence, the richer the diversity in a given system, the more stable the system. Other researchers built on this theme with observations that simpler communities are more prone to violent fluctuations in population density than complex communities and are more prone to successful invasions by exotic species (Odum 1953; Elton 1958). MacArthur (1955) further elaborated on these concepts by proposing that increasing the number of species in a community or ecosystem increases the number of ecological functions in an ecosystem and thereby its stability; essentially, if a variety of trophic links exists, the flow of energy and nutrients will be maintained through alternative links when a species becomes rare (MacArthur 1955; Holling 1973). These ideas were later challenged by May (1973) who showed that complex model communities were less likely to be stable than simpler ones, although he also suggested that more diverse model communities may have more stable equilibria than simpler ones and therefore exhibit enhanced persistence under changing conditions. More recently, it has been shown by experimentation in a grassland ecosystem that higher species richness at small spatial and temporal scales stabilizes or augments community stability and ecosystem processes such as primary production or carbon storage (Tilman 1996; Tilman et al. 2001). Currently, the diversity-stability debate seems to have reached consensus on the notion that diversity, on average, gives rise to ecosystem stability and now centres on the stabilizing roles of connectivity and the strength of interactions among components and trophic levels in an ecosystem (McCann 2000).

To further develop these ideas in the context of understanding how they relate to ecological resilience and resource sustainability, it is important to first define resilience and related key concepts. After reviewing key concepts, I describe an integrative theory of ecosystem change that links resilience with ecological structures and processes at multiple scales. I then describe the aspects of adaptiveness of this theory and the relation of biodiversity to resilience. Finally, I discuss resilience in managed systems and how managers and modellers can simplify the complexity of dynamic systems in attempts to manage for resilience. The conclusions are left for the end of the paper, following the article review and experimental protocol.

2.i. Key concepts

Ecological resilience

Holling (1973) first introduced the term resilience to the ecological literature three decades ago. In his seminal review of the theory and application of resilience, Holling (1973) defines resilience as a measure of the persistence of systems and of their capacity to absorb change and disturbance while maintaining the same relationships between populations or state variables. Resilience is therefore an emergent property of ecosystems that can measured by the magnitude of disturbance a system can absorb before changing to a different stable state (Holling 1973; Ludwig et al. 1996; Gunderson 2000). For example, resilience can be estimated by the frequency or intensity of fires or drought in an aspen parkland that results in conversion to grassland. This definition of resilience therefore assumes the existence of alternative stable states and is primarily concerned with persistence of a given state over time (Holling 1973; Gunderson 2000). In this paper, I evoke this definition when using the term resilience. Resilience can be desirable or not, depending on the system state of interest (Carpenter et al. 2001). For example, a polluted lake with low social utility (e.g. with turbid water or few game fish) may be an undesirable but highly resilient stable state.

To measure resilience, it is necessary to specify several qualitative characteristics. These include the system state being considered and its spatial scale (resilience *of* what), the perturbations of interest (resilience *to* what), and the time scale of interest (Carpenter et al. 2001). The temporal scale depends on the relevant aspects of the system of interest; for example, it will be considerably shorter in microcosm studies that in forest studies. It is also key to classifying the system components and processes as fast or slow i.e. as either variables or parameters in a model (Beisner et al. 2003). Resilience may also be measured as the probability that a given state will remain in a given state over the time period of interest (Peterson 2002a).

Alternative stable states

Depending on the scale and nature of inquiry, alternative stable states can have one of two meanings (Beisner et al. 2003). To population or community ecologists, a stable state refers to a relatively constant configuration or assemblage of individuals or species (Lewontin 1969; Sutherland 1974; Law and Morton 1993). In ecosystem ecology, a stable state refers to a set of mutually reinforcing structures and processes (Holling 1973; May 1977) – the definition used in this paper. In either sense, the term stable is somewhat misleading as a stable state is typically not static; rather, it typically displays oscillations within certain limits controlled by its internal structures or external forcing (Scheffer et al. 2001). When resilience is diminished and a new stable state emerges, the control of ecosystem function shifts from one set of interacting physical and biological processes to a different set (Holling 1996).

Several different ecosystems display multiple stable states and shifts among them. Alternative stable states have been described in lakes, reefs, marine fisheries, benthic systems, wetlands, forests, savannas, and rangelands (Carpenter 2001; Scheffer et al. 2001). Shifts among states typically result from changes in slow processes that trigger responses in a fast process. For example, shallow lakes are known to rapidly shift between a clear-water, oligotrophic state with ample rooted vegetation to a turbid-water, eutrophic state with few submerged plants and abundant phytoplankton (Scheffer et al. 1993; Carpenter et al. 1999). While the state shift can result from a myriad of causes, such as sudden sediment inflows, reductions in algae-eating fish or removal of rooted vegetation, the gradual anthropogenic loading of nutrients, especially phosphorus, beyond a critical threshold is typically a dominant cause (Blindow et al. 1993; Scheffer et al. 2001). Each state is stabilized by the interactions among nutrients, vegetation type and light penetration (Gunderson 2000). For example, in the clear-water state, rooted vegetation stabilizes sediments, buffers nutrient loading, increases water clarity and provides predation cover for fish that eat phytoplankton. Alternatively, in the turbid state, the loss of rooted vegetation leads to high concentrations of suspended sediments that block the light needed for plant establishment and survival, thereby augmenting nutrient availability for phytoplankton and decreasing cover for phytoplanktivores (Scheffer et al. 1993).

The frequency and intensity of compounded disturbances is key for determining shifts between ecosystem states. Even large, infrequent disturbances at the extreme end of their range of intensity and size do not typically cause a lasting change in the fundamental character of a system (Paine et al. 1998). Large, infrequent disturbances often do not destroy the mechanisms that determine species composition, as the composition before and after a disturbance is similar (Turner et al. 1997). Ecosystems tend to display wholesale transition to fundamentally different states – “ecological surprises” – when multiple disturbances occur within the normal recovery time of the system i.e. when the spatial extent and especially the frequency of disturbance are at the extremes of their distribution and overwhelm the regenerative capacity of the system (Paine et al. 1998). Alterations in other aspects of disturbance such as seasonality are also important in determining shifts.

Stability

Holling (1973) makes a strong distinction between resilience and stability, where the latter refers to the ability of a system to remain near an equilibrium. Many authors, however, have used the term resilience in this sense (Pimm 1984; 1991; Tilman 1994, Tilman and Downing 1994; Ives 1995; Neubert and Caswell 1997; Mittelbach et al. 1995). In other words, these authors use the term resilience to refer to stability *sensu* Holling (1973) and measure it by the time required for a system to return to equilibrium or steady-state following disturbance. Holling (1996) describes this definition of resilience based on equilibrium return time as ‘engineering resilience’, recognizing it comes from the tradition of fields such as physics, control system design, or material engineering, where the goals are typically to design systems with a single operating objective and to develop optimal designs based on tractable mathematics (Gunderson 2000). This definition of resilience assumes one global equilibrium rather than many, or if alternative stable states (equilibria) do exist, they should be avoided by applying safeguards i.e. by building ‘system redundancy’ (Holling 1996).

Systems with high resilience are not necessarily stable. In fact, Holling (1973) argues a trade-off exists between stability and resilience, so that highly resilient systems can be very unstable and, conversely, highly stable systems exhibit low resilience. As evidence, he points to a 30-yr study of abundance data for forest insects across Canada showing insect populations in areas of extreme climatic conditions fluctuated widely but persisted despite these periodic extremes of fluctuation; on the other hand, insect populations in more benign climates were more constant but showed drastically lower ability to absorb extreme climate events (Watts 1968 as cited in Holling 1973).

Resistance

Resistance refers to the amount of external pressure needed to bring about a given level of change in a system (Carpenter et al. 2001). Resistant systems are capable of persistence in the face of high levels of external pressure. Resistance, therefore, represents a complementary aspect of resilience.

Adaptive capacity

Adaptive capacity refers to the capacity of an ecosystem to remain in a stability domain even as the domain itself changes (Gunderson 2000; Beisner et al. 2003). It may also be considered a type of resilience (Holling 2001).

Hysteresis

Hysteresis refers to a pattern of change between ecosystem states in which the forward and backward switches occur at different critical conditions (Ludwig et al. 1997; Scheffer et al. 2001; Figure 1). For example, in lakes that have undergone eutrophication, the shift back to an oligotrophic state happens at considerably lower rates of nutrient loading than those present when the original shift into the eutrophic state occurred (Carpenter and Cottingham 1997; Carpenter et al. 1999). Hysteresis has been shown in a variety of systems that undergo shifts between stable states, including lakes, climatic circulation patterns, deserts, and rangelands (Scheffer et al. 2001). In fact, hysteresis is often used as a defining characteristic that illustrates the presence of alternative stable states (Ludwig et al. 1997; Beisner et al. 2003).

2.ii. The ball and cup

The heuristic of a cup and ball is often used to illustrate resilience and related concepts (Figure 1; e.g. Carpenter et al. 1999; Scheffer et al. 2001; Beisner et al. 2003). The ball represents the system state, the arrow represents a perturbation, and cups represent the domain of attraction. Together, the set of attraction domains make up the stability landscape. Equilibria or stable states exist when the ball sits at the bottom of the cup. Engineering resilience relates to cup shape – the slope of the sides determines the system return time following a perturbation. Ecological resilience refers to the width of each cup. Adaptive capacity refers to the capacity to remain in a certain cup even as the shape of the cup or stability landscape changes. Hysteresis occurs when, following a state shift, the path of the ball to its original cup differs from the one taken during the initial shift.

2.iii. Panarchy: an integrative theory of change

Holling and colleagues describe a general theory of change in systems, termed Panarchy, that integrates resilience and ecosystem dynamics at multiple scales (Gunderson et al. 1995; Holling 2001; Gunderson and Holling 2002). Based on three decades of studies of regional ecosystems, this theoretical framework seeks to explain the behaviour of dynamic systems characterized by non-linear dynamics, time lags and thresholds of change. It has two principal components: the adaptive cycle and the hierarchical structure of ecosystem structures and processes. In summary, panarchy refers to how natural systems can evolve and persist thanks to an hierarchical structure that interconnects perpetual cycles of growth, accumulation, restructuring collapse and renewal at many scales (Carpenter and Turner 2001; Holling 2001). Panarchy should be viewed as a metaphor that generates testable hypotheses or to classify systems, rather than as a specific hypothesis itself (Carpenter et al. 2001; Holling and Gunderson 2002).

The adaptive cycle

The adaptive cycle has its basis on the notion that dynamical systems such as ecosystems or corporations do not simply tend towards an equilibrium condition (Holling 1986; Carpenter et al. 2001). Rather, they pass through four characteristic phases: rapid growth and exploitation (**r**), conservation (**K**), collapse or release ("creative destruction", **Ω**), and renewal or reorganization (**α**) (Figure 2). Each phase differs in its potential, connectedness, and resilience. **Potential** refers to the capability for change inherent in a system; in an ecosystem, potential refers to productivity or accumulated biomass and nutrients while in a corporation it can refer to its financial capital or "wealth" (Holling 2001). **Connectedness** refers to the degree of linkages among the components of a system and its controlling processes. It is a measure of the internal controllability of a system and reflects the degree of flexibility or rigidity of its internal controls (Holling 2001). The four stages of the adaptive cycle lump into the **front-loop** and **back-loop** (Figure 2), in which major change in the system occurs during the back-loop. Time does not flow evenly throughout the adaptive cycle (Figure 2). Rather, the progression in an ecosystem from the r phase to the K phase is slow, while the back-loop occurs relatively much more quickly.

The front-loop of the adaptive cycle is essentially ecological succession. This period of incremental change begins with a phase of exploitation (**r**) that is characterized by rapid colonization of recently disturbed areas. Exploitation gives way to a conservation phase (**K**), characterized by the slow accumulation and storage of energy and material[1]. Species with extensive dispersal abilities and rapid growth – r-strategists – typically dominate the exploitation phase in an arena of scramble competition ("whoever gets there first wins") while species with limited dispersal and slower growth – K-strategists – typically dominate the conservation or mature phase in an arena of contest competition (Gunderson 2000).

Throughout the front-loop, both the potential and connectedness of the system increase, and a transition occurs from exogenous control of the system behaviour to endogenous control. Pioneer species that can tolerate microclimatic extremes and capitalize on available resources gradually give way to species with narrower tolerance ranges but better capacity to compete for limited resources. For example, in the boreal forest, rapidly growing light-demanding species with light seeds such as white birch (*Betula papyrifera*) are gradually replaced by long-lived, slower growing species such as balsam fir (*Abies balsamea*) or white spruce (*Picea glauca*), shade tolerant species that compete with each other for water or nutrients. Moreover, as a stand ages, external recruitment sources such as seed rain from disturbance edges are gradually replaced by internal recruitment processes, such as pit-mound infilling from surrounding trees and layering.

Rapid change and reorganization characterize the back-loop. This dynamism is a consequence of an 'overconnected' system where gradually increasing slow variables surpass a threshold and trigger a rapid change in fast variables. In the boreal forest example, increases in connectedness and potential for change manifest themselves as the increased hazard of a catastrophic fire associated with a overall build-up in flammable fuels and increases in their horizontal and vertical continuity associated with stand development. A disturbance triggers the phase of collapse, Ω or creative destruction. Even a small perturbation can initiate Ω-phase, as it can easily propagate through the system and cause a large mobilization of energy and biomass, as occurs when a ground fire 'crowns out' after climbing fuel ladders and becomes a large mortality event. In this phase of rapidly collapsing dynamics, attributes or components of the system can be lost or dramatically changed. Following this phase, the system enters a reorganization phase, α. Innovation and novelty surge, uncertainty is high, internal controls are weak and external forces or variability can exert strong influence on the system e.g. seeds from veteran trees or trees outside the area affected by a disturbance exert a lasting influence on the composition of a regenerating stand. The system then enters back into the r-phase and begins anew to build complexity and connectedness.

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[1] The names of the phases of the front-loop are drawn from the traditional designation of parameters of the logistic equation where r represents the instantaneous rate of growth of a population and K represents the carrying capacity or maximum size of a population that is sustainable.

Resilience in the adaptive cycle

Resilience varies with the phase of the adaptive cycle (Figure 3). As the front loop plays out, resilience is high at the beginning during the exploitation phase – the system is capable of absorbing a wide range of disturbances without shifting states – but gradually decreases through the K-phase as the system reaches its limits of conservative growth and rigidity and internal control of processes (connectedness) as well as its stored energy and biomass (potential) increase. The system is brittle and resilience is low so that even small perturbations can initiate a cascade of rapid structural changes throughout the over-connected system. At this point, the system is actually very stable i.e. it will rebound quickly from a small disturbance such as small windthrow, but its stability is narrow and local (Gunderson 2000). As the system undergoes the back loop, there is low connectedness and potential as well as weak internal control of system processes. Resilience at this point is therefore high because change in one component of the system has few consequences for other components. This condition allows creative experimentation within the system of new combinations of components with a low cost of failure (Holling 2001). As the α-phase unfolds, many experimental and innovative combinations of system components are 'tried' locally and most fail, as observed, for example, in the many diverse types of assemblages of trees and shrubs following the eruption of Mount St. Helens (Franklin and MacMahon 2000). It is during these periods of destruction and reorganization that a system is most vulnerable to change as a result of the behaviour in small, fast processes i.e. as it reorganizes around 'seeds' of order emerging from change in the lower levels (Gunderson et al. 1997; Peterson 2000).

Hierarchies in a "lumpy" world

A growing body of theoretical, modelling and empirical studies suggests that a small set of biotic and abiotic processes structure ecosystems across time and space and give rise to their hierarchical structure (Holling 1992; Levin 1992; Holling 1996; Peterson et al. 1998). In other words, ecosystems have discontinuous domains of influence or "lumps" in time and space. These lumps are nested within another and each is defined by a specific periodicity or frequency and spatial scale (Polis 1991; Holling 1992; Gunther and Folke 1993). The lumps are a consequence of thermodynamic constraints on the flow of matter and energy that result in "standing waves" of ecological pattern and processes (Ives and Jansen 1998). These principal scales of biological organization may be understood by scaling relationships that obey power laws (Holling 1992; Peterson 2000). For example, Holling (1992) reviews 23 examples of managed ecosystems and suggests that a small number of lumps or clusters of biotic and abiotic variables impose structure over a wide range of scale in all these ecosystems. He illustrates this point by showing strikingly similar gaps or discontinuities in the distribution of adult body mass for birds and mammals in the boreal forest and short-grass prairie, arguing these gaps are a consequence of how biota adapts to the complexity and number of "habitat quanta" across a landscape; in other words, the discontinuities in the distributions of body-mass are entrained by landscape or vegetation patterns (Holling 1992; Allen et al. 1999). Similar gaps in body-mass distributions have been detected for tropical forest birds (Restrepo et al. 1997), for mammals existing pre- and post- the Pleistocene extinction (Lambert and Holling 1998) and for animal communities in the wet savanna of Florida Everglades and the Australian Mediterranean (Allen et al. 1999). Architecturally simple landscapes have few lumps in the distribution of body mass of their component animals whereas complex landscapes have many lumps (Holling 1992; Holling et al. 2002).

The processes and structures that control ecosystem behaviour and give rise to the lumps described above can be understood as a cross-scale, nested set of adaptive cycles (Holling et al. 2002). For instance, in the boreal forest, Holling (1986) and Holling et al. (2002) recognize the following scales and their associated processes (Figure 4): at fine scales, pattern and process are dictated by biophysical forces that control plant physiology and morphology. At the coarser and slower scale of patch dynamics, competition among plants for nutrients, light and water determines local species composition and regeneration. The next coarser and slower scale is set by meso-scale contagious processes such as fire, insect outbreaks and large mammal herbivory that together determine structure and successional dynamics of stands at scales ranging from tens of meters to kilometres, and from years to decades. At the landscape scale, climate, geomorphological and biogeographical processes alter ecological structure over hundreds of kilometres and millennia. Generally, the smaller and faster cycles are constrained by larger and slower cycles.

The existence and feedback among adaptive cycles in this hierarchy provide the ecosystem with resilience and adaptiveness. The adaptive cycle has two complementary and sequential loops that foster both conservation and change (Holling 1986; 2001). The first loop maximizes production, conservation and accumulation while the second maximizes invention, variety and re-assortment. The lags between these periods of stability and bouts of strong selection and innovative rearrangement mean that diversity is perpetually created, thereby providing the elements for resilience over time across a large range of environmental conditions (Holling et al. 2002). The hierarchical structure of a system contributes to its adaptiveness because it performs two important functions: (i) to conserve and stabilize conditions for the smaller and faster levels i.e. interactions across scales in a hierarchy are asymmetrical so that larger, slower levels constrain behaviour of smaller, faster levels, and (ii) to generate and 'test' innovations such as mutations or new species assemblages by experiments occurring within each level (Simon 1974; Levin 1981; O'Neill et al. 1986; Holling 2001). In other words, finer-scale positive feedback creates heterogeneity and coarser-scale negative feedback stabilizes it (Levin 2000).

Remember and revolt

In the Panarchy metaphor, two types of connections exist among adaptive cycles – labelled "Revolt" and "Remember" that provide resilience and adaptiveness (Holling et al. 2002; Figure 5). These connections are important during times of change in adaptive cycles. Revolt refers to what occurs when a level in the panarchy enters the collapse (Ω) phase, and triggers a crisis in the next larger, slower cycle because the larger, slower cycle is itself in its K-phase, a phase of low resilience (Figure 5). In the boreal forest, this occurs when conditions are such that a locally ignited ground fire can spread to the crown of a tree, then to a patch of trees and eventually to the entire stand. If this revolt leads to another crisis in higher cycles undergoing a phase of low resilience, then a change in alternative stable states can be caused by an abrupt positive feedback chain of collapse (Holling 1996; Carpenter et al. 2001). Remember refers to the inter-level connection that occurs once a collapse begins at one level and its path of development is shaped by the accumulated biomass or potential of the next slower and larger level in its K-phase (Figure 5). For example, a forest can "remember" its pre-disturbance composition by the presence of veteran trees or clumps of trees that provide refugia from fire or seeds and nutrients to the regenerating stand (Holling et al. 2002).

2.iv. Complex adaptive systems

The notions of panarchy are applicable to **complex adaptive systems** (CAS) of which good examples are an economy or an organism capable of homeostasis, but of which the best example is likely an ecosystem. CAS are capable of **self-organization**; in other words, self-organized systems have structuring processes that create patterns in time and space and these patterns in turn reinforce the structuring processes (Kauffman 1993) e.g. jack pine (*Pinus banksiana*) can grow in tightly-spaced stands (pattern) that easily propagate crown fires (process) that in turn lead to more jack pine stands. In self-organized CAS, patterns at larger, slower levels in the hierarchy are an emergent property of interactions and selection processes that operate at smaller, faster levels in a CAS; in turn, the larger, slower structure constrains the behaviour of the small processes in such a way that the different levels mutually reinforce one another (Levin 1998; Peterson 2000). CAS have three essential elements (Levin 1998):

i. sustained individuality (i.e. spatial discreteness) of system components e.g. species or populations.

ii. localized interactions among the components e.g. competition, predation, or nutrient cycling.

iii. an autonomous process that selects from the components a subset for replication and enhancement, based on the outcomes of the localized interactions. In unmanaged ecosystems, this process is natural selection.

The occurrence of these elements creates systems with four basic properties: aggregation, nonlinearity, diversity and flows (Holland 1995; Levin 1998). Aggregation refers to the inhomogenities or "lumps" in how the elements of a CAS are organized (Polis 1991; Holling 1992). Nonlinearity refers to the change in the local rules of interaction among elements that occurs as the system evolves and develops, leading to path dependence in the development of ecosystems. Diversity is simply the variation in system components and functions that is continually maintained and created by the system itself (Hughes et al. 1997). Flows refers to the transfer of energy, nutrients, materials and information that interconnect the system components and transform it from a random collection into an integrated whole (Levin 1998). Understanding how management affects these properties of CAS can contribute to understanding its impacts on resilience, as well as to furthering development of theory and application of panarchy to systems such as economies, ecosystems and institutions.

2.v. Biodiversity, resilience and scale

Biodiversity is critically important for ecological resilience and for sustaining desirable stable states as environmental conditions change (Peterson et al. 1998; Bengtsson et al. 2003). It is well-established in the literature that (i) adequate performance of ecosystems depends on having species in all of the necessary functional groups (e.g. Schindler 1990) and (ii) the persistence of ecological function over time depends on the diversity of species within functional groups (Naeem et al. 1994). However, the relationship between biodiversity and resilience is not fully understood. For instance, the stability that diversity supposedly affords is not always observed – some very diverse systems are still prone to collapse as a result in decline of populations of just one or two species e.g. coral reefs (Bellwood et al. 2003). This type of observation has focused research on two related facets of ecological function in ecosystems: functional diversity and response diversity (Peterson et al. 1998). **Functional diversity** refers to the variety of species both within functional groups (functional redundancy or compensation) and across functional groups (functional complementarity). **Response diversity** is the variety of responses to environmental change among a group of species that contributes to the same ecological function (Elmqvist et al. 2003). The empirical evidence for these concepts comes from studies of production, respiration and nutrient cycling in lakes (Schindler 1990), nutrient or water cycling in Australian rangelands (Walker 1992; Walker et al. 1999), seed dispersal in tropical forests (Poulsen et al. 2002), and grazing in coral reefs (Nyström et al. 2000). For example, Schindler (1990) showed that similar ecological functions are maintained even though the mix or population densities of component species can vary widely.

Data from Australian rangelands of functional attributes of graminoid species illustrate the concepts surrounding functional diversity and resilience. Walker et al. (1999) showed that the most abundant species in the rangelands exist far apart from each other when plotted in functional attribute space i.e. the dominant species differed in the functions they performed – i.e. they had functional complementarity. However, among the less dominant or minor species, at least one species performed very similar functions to dominant species – i.e. functional compensation. Furthermore, in a heavily disturbed site, the dominant species that had been eliminated by grazing was replaced by a functionally similar species that was a minor species in the lightly grazed site (Walker et al. 1999). Walker et al. (1999) therefore conclude that resilience is generated by response diversity, in other words, by the presence, within each functional type, of a number of species with a diversity of environmental response capacities e.g. capacity to withstand grazing.

Response diversity and resilience also depend on functional compensation *across* scales (Peterson et al. 1998). For example, avian predators in the boreal forest can control the initiation and intensity of outbreaks of the spruce budworm by a cross-scale predatory response that targets budworm over a range of budworm densities and spatial aggregations (Holling 1988). This cross-scale response occurs because the 31 different avian predators, for which Holling (1992) has discerned five distinct lumps in their body-mass distribution, search and consume budworm at different scales. Small birds like chickadees (*Parus* spp.) and Kinglets (*Regulus* spp.) search for and consume aggregated budworm at the scale of tufts of needles, medium birds at the scale of branches, and larger birds at stand and landscape scales. Therefore, both the size of birds and the distance they travel to prey on budworm increases with the size of the aggregations of the budworm and with increased budworm abundance in general (Peterson et al. 1998). This within and cross-scale ‘redundancy’ creates a resilient and diverse response of predation to budworm, and is quite effective at maintaining budworm abundances in check within young forest stands (Clark and Holling 1979; Holling 1988; Peterson et al. 1998).

2.vi. Resilience in managed ecosystems

Resource managers are often victims of their early success. Typically, at the onset of a management regime, managers do well at achieving a narrow set of well-defined objectives by controlling a target variable such allowable annual cut or rotation periods (Holling and Meffe 1996; Gunderson 2000).

This achievement is typically the result of a "command and control" strategy that seeks to standardize or minimize the natural variability of key ecosystem processes such a fire or regeneration (Pastor et al. 1998). Unfortunately, initial management successes have the simultaneous consequences of (a) encouraging people to grow dependent on the continuation of the management regime and (b) eroding ecological resilience in the long term by slowly changing other parts of the system and by creating ecosystems that have reduced variability in time and space (Holling and Meffe 1996; Peterson et al. 1998). This leads to a condition in which ecological change becomes increasingly undesirable yet more difficult to avoid. When dramatic change does arrive, it is typically a surprise and a policy crisis ensues (Gunderson et al. 1995; Gunderson 1999). Such is the "pathology of resource management" – any system of practices, institutions and regulations that manages an ecosystem for the consistent and predictable flow of goods or services results in reduced resilience, dependent societies and inflexible management agencies (Holling and Meffe 1996). For example, intensive forest management in New Brunswick greatly reduced the structural and age-class diversity across the landscape, a condition that resulted in a long-term decline in productivity and a chronic infestation of the spruce budworm (Baskerville 1985; 1988; Regier and Baskerville 1986).

2.vii. Minimal complexity

Albert Einstein said: "Keep things as simple as possible, but no simpler." This quote describes parsimonious nature of the minimal set of attributes that Holling et al. (2002) deem necessary for capturing the behaviour of a CAS while at the same time allowing managers or modellers to make sense of its complexity. This minimal set of attributes that allows understanding a panarchy and its adaptive cycles is:

- three to five key interacting components
- three qualitatively different speeds of variables
- nonlinear causation and multi-stable behaviour
- vulnerability and resilience that change as a function of the slow variables
- creation of structures by biota and reinforcements of biota from structure (legacies)
- spatially contagious processes to generate self-organized patterns

This set of attributes allows the emergence of multi-stable states with different stability domains as well as a stability landscape that is itself dynamic. Resilience changes according to the slow variables and the spatially contagious processes and legacies generate patterns that self-organize over different temporal and spatial scales (Holling 2001). Such a set of attributes should be the starting point of modellers or planners seeking to model a dynamic system and thereby gain insight into its resilience and sustainability (Holling et al. 2002).

3. Article critique

This section is a review of Peterson (2002a). Here, I begin with a summary of the objectives, methods and results of the article. I then discuss the article's major strengths and weaknesses, including both general and specific comments on content and style.

3.i. Article summary

The main objective of Peterson (2002a) is to evaluate whether cross-scale edge is a useful predictor of resilience across a landscape. **Cross-scale edge** is an empirical estimate of resilience based on landscape pattern, specifically, areas that are transitional (ecotones) between one of two alternative stable states: hardwood-dominated mesic forests (HW) or longleaf pine-dominated savannah (LL). Fire mediates the transition between these states: fire maintains LL and in the absence of fire sites convert to HW. The underlying assumption is that ecotones represent areas of low resilience because they are areas that result from changes in the processes that structure landscapes (i.e. fire) and where small changes in these processes can cause a switch from one state to another (Milne et al. 1996; Peterson 2002a).

To map cross-scale edge, Peterson (2002a) classifies each 60 x 60 m cell in his landscape model as either HW or LL. He then determines whether a cell of a given type can be considered an edge site by measuring the density of same-typed sites surrounding it across a range of window sizes (scales). If the density falls between a threshold range at any scale, it is considered an edge site, and, if it is within this range at a number of different window sizes, it is considered a cross-scale edge site (Figure 6). The usefulness of cross-scale edge as a predictor of areas vulnerable to transition to HW is tested by comparisons with probabilistic resilience. **Probabilistic resilience** is the probability of persistence of a given site (model cell) to persist over a specified period in a given state. This probability is determined in a stochastic landscape model run through Monte Carlo simulations starting with the same initial conditions. Peterson (2002a) assessed the efficacy of cross-scale edge by comparing how well it performs in predicting transitions between stable states under three alternative strategies of fire management: wildfire (no suppression), rotation (prescribed fire in different units across the landscape, all burned at an equal frequency), and responsive (LL areas burned at higher frequencies than HW areas).

Generally, cross-scale edge performed well at predicting resilience and transitions between states (Figure 8). Predictive success varied depending on the strategy of fire management and was best for wildfire strategy. In the wildfire case, errors were primarily (i) false positives i.e. cross-scale edge indicated changes that did not occur in the model, and (ii) where isolated LL sites occurred among HW areas. The success of prediction was relatively constant across scales (Figure 8A), while cumulative prediction success increased gradually to a plateau that differed for each management strategy (Figure 8D). Cross-scale edge was less accurate at predicting state transitions for the rotation and responsive strategies, largely because spatial pattern and contagion have a reduced role in these strategies for determining where fires occur. That is, management overwhelmingly influences the burn frequency rather than the vegetation itself. Cross-scale edge did not perform well at predicting transitions from LL to HW at individual scales (Figure 8C), although this performance improved for cumulative scales (Figure 8F).

3.ii. General Comments

Overall, I found the article very interesting and well-written. The notion of an easy metric for estimating and mapping resilience is very attractive conceptually and devising such a metric represents a formidable challenge. Therefore, I think this article was well-worth publishing.

Importance and interest to journal's readers – The topics introduced in Peterson (2002a) are central to the interests of readers of Conservation Ecology. This online journal, published by the Resilience Alliance, is one of the principal fora for discussion of the theory and application of resilience. The concepts introduced in the article are original and represent a useful contribution to the dialogue of how to operationalize resilience in a management context. Indeed, a primary contribution of this article is as a nexus of ideas for further development, a way of stimulating dialogue or generating testable hypotheses regarding resilience in managed landscapes. Examples of how Peterson (2002a) advances the theory and application of resilience include (i) the introduction of two methods of assessing resilience in landscape models i.e. cross-scale edge and probabilistic resilience, and (ii) an elaboration of the role that disturbance contagion plays in shaping resilience across landscapes – a theme he further develops in another recent publication (Peterson 2002b).

Organization and clarity – Peterson writes clearly and concisely, stating objectives and assumptions explicitly and guiding the reader along an interesting, logical and well-organized path. In general, the methods seem scientifically sound, well-grounded in ecological theory, and appropriately described to allow replication by another researcher. The figures illustrate the results and discussion well, and the appended information added significantly to my understanding of the concepts, especially Appendix 1.

3.iii. Criticisms

A general criticism in terms of content and structure is that Peterson (2002a) probably tried to do too much in one article. Rather than testing three different strategies of fire management, I would have focused on one vital aspect of fire regime known to have a profound influence on resilience in this landscape and over which managers have some degree of control, namely, fire frequency (Glitzenstein et al. 2003). Modelling fire frequency over a wide range and exploring the consequences of this variation for resilience and the predictive power of cross-scale edge, while more limited in scope than what Peterson (2002a) covers, would have perhaps provided similar insights in a simpler fashion. Other criticisms follow.

Lack of supporting empirical evidence – Although the article presents a very interesting theoretical concept with potential management applications, it fails to deliver – presently – a useable management tool. To support his conclusion that cross-scale edge is an accurate predictor of resilience, Peterson (2002a) compares the pattern of an abstracted and simplified landscape with the results of a simulation model i.e. he predicts pattern from another pattern. He bases this prediction on the notion that the current distribution of vegetation across the landscape reflects the combined effects of the historical processes such harvesting, fire, seed dispersal. It is impossible to discern from the information provided in the article the possible role that programming played in determining the higher tendency of edge areas to change i.e. was this tendency to change simply a tautology of the way the simulation model was structured? By the end of the article, I was not sure that Peterson (2002a) had detected a pattern (and an underlying process) actually occurring 'on the ground'. I would thus hesitate to make management decisions based on cross-scale edge or to have much confidence in its applicability in other systems. To build confidence, I would need to have empirical evidence of the ecological processes behind the pattern.

Corroboration needed – Presently, cross-scale edge needs corroboration of its predictive efficacy. That is, cross-scale edge is not useable as a stand-alone measure of resilience because each landscape has specific scaling relationships that determine where in the landscape thresholds of connectivity, and thereby areas of cross-scale edge, exist (Peterson 2000). Therefore, some corroborative way of understanding the capacity of cross-scale edge to gauge resilience is needed before it can be applied with rigour e.g. results from a stochastic model (as Peterson uses), historical records or observations of transition in the cross-scale edge areas, or detected changes in forest cover using satellite imagery or air photos.

Important limitations to applicability – Peterson (2002a) does a good job of outlining the limitations of cross-scale edge in the discussion. These limitations are not trivial and, without a better understanding of why cross-scale edge works, currently limit the applicability of this method in a management context or in other systems. For example, it is uncertain how applicable cross-scale edge is in systems where contagious processes such as fire or seed dispersal are not the principal mediators of change between stable states. As Peterson (2002a) points, cross-scale edge works well in the modelled longleaf pine system because the state of a cell hinges on fire spread and regeneration from adjacent cells e.g. fire will spread readily among LL cells but will be inhibited among HW cells. It is therefore likely that cross-scale edge will not have the same predictive capacity in other systems where non-contagious disturbances such as wind or ice storms are the principal disturbances or where regeneration for major species depends on fine-scale processes such as rain of heavy seeds, suckering or layering e.g. temperate deciduous forests. Moreover, in the case of the longleaf pine ecosystem, the presence or absence of single disturbance – ground fire – regulates transitions between stable states and this role is well understood (Glitzenstein et al. 2003). For systems where multiple disturbances and their interactions regulate pattern (e.g. the pine forests of central interior British Columbia shaped by the interactions between fire and the mountain pine beetle [*Dendroctonus ponderosae*]), where contagion is not as important, or where transitions occur among multiple stable states, cross-scale edge may not perform with the same efficacy as that observed by Peterson (2002a).

Cross-scale edge is not really that easy to apply – Although Peterson (2002a) proposes cross-scale edge is a simple metric to understand and use as a potential management tool, I did not find it particularly user-friendly. First, while certainly simpler than building a stochastic model of landscape dynamics, the use of cross-scale edge requires (i) an understanding of the ecological theory and evidence surrounding resilience, (ii) a grasp of novel ecological concepts (e.g. percolation theory) and (iii) specialized tools for measurement (e.g. rastarized version of landscape, roving window analysis). Second, cross-scale was not very robust in detecting change in the areas of greatest management concern as outlined in the article – although it does a very good job at predicting overall conversion, it did not perform well at predicting LL to HW conversion (40 % or less). Third, I was left uncertain what a manager should do with the information that cross-scale provides, in particular what cross-scale edge meant for the landscape in its entirety i.e. as a sum of the individual sites modeled. Presumably, a manager should orient management policies and practices to maximize the area of the stable state that generates the most value and change practices in cross-scale edge areas to increase (or decrease, depending on their state) their resilience. Discussion of examples of such practices or further detail in this regard would have been very helpful.

3.iv. Specific Comments

Errors **–** The caption in Fig. 9 is incorrect. It makes references to sub-figures as Fig. 8a, 8b, etc. rather than Fig. 9a, 9b, etc.

Abstract structure **–** The abstract is poorly structured and does not adequately convey the article content. Four of its total six sentences are introductory, while only one pertains to the methods and one to results and conclusions. To make the abstract more effective, I would delete its first three sentences, expand the methods description, and add a two or three sentences pertaining to results and discussion.

Replicability **–** Three areas were unclear and could hamper efforts to replicate this study. First, the description of the classification scheme for how landscape was simplified into a binary arrangement (LL and HW) is essentially non-existent. This classification scheme has important implications for the geometry and abundance of stable states and thereby the distribution of cross-scale edge across the landscape. Knowing the criteria for how this simplification occurred would be useful for someone seeking to measure and test cross-scale edge in another landscape. Second, a detailed description of the calculations behind the determination of probabilistic resilience was not provided. To be fair, Peterson (2002a) encourages readers who need more information to read his dissertation for further details. Third, although Peterson (2002a) is clear about where edge sites occur, he never explicitly tells the reader how cross-scale edge is determined, leaving us to conclude based on his Fig. 7 that cross-scale must be where edge is detected with at least two or more window sizes.

3.v. Conclusion of article critique

Given the complexity of devising a user-friendly metric for resilience, Peterson (2002a) succeeded in building a solid foundation to launch further work. Subsequent studies should provide details on the mechanistic underpinnings of how and why resilience varies across a landscape. Such studies would be very helpful to managers seeking to develop and implement practices that influence resilience.

4. Experimental protocol

4.i. Introduction

The principal hypothesis of Peterson (2002a) is that the persistence of a site is affected by the status of its neighbouring sites, and as such, cross-scale edge represents areas of low resilience. Given my criticism above of the lack of specifically-related data that provides proximate understanding of why cross-scale has predictive power, I propose an experimental design below that is both empirical and experimental. This approach represents an attempt to 'ground-truth' the concept of cross-scale edge by conducting a "BACI" experiment (Before/After/Control/Impact; Green [1979]) that complies with criteria for fruitful adaptive management (Holling 1996; Holling 2001): the experiment (i) has a low-cost of failure i.e. it allows understanding of resilience and associated processes without diminishing ecosystem services, and (ii) discerns viable explanations from among a set of hypotheses concerning ecological process and pattern.

The longleaf pine woodlands of south eastern United States have been labelled the "fire forests" (Engstrom et al. 2003). These forests historically burned more than any other forest type in North America (Engstrom et al. 2003). It thus seems reasonable that *all* of their dominant species are somehow adapted to fire and that diverse fire strategies have evolved, even among oak-dominated communities (Brewer 2001). Therefore, the hypotheses tested by this experimental protocol revolve around the central notion that resilience of the two states in the longleaf pine ecosystem is a function of the diversity, abundance and connectedness of the species that influence the behaviour of ground fire. For example, resilience of LL sites is a function of the diversity and abundance of pyrogenic species such as longleaf pine, slash pine (*P. caribaea*), and wiregrasses (*Aristida* spp.). Alternatively, resilience of HW sites is a function of the diversity and abundance of species with relatively fire-retardant qualities such as scrub oaks (*Quercus* spp.) or red gum trees (*Liquidamber styraciflua*), so that when fires do occur during severe fire weather, fuel is sufficiently accumulated to generate fires hot enough to kill longleaf pines and transfer the competitive advantage to sprouting oak species (Heyward 1939). This pathway of change is akin to the hypothesis of disturbance severity of threshold change proposed by Holling (1981) and Frelich and Reich (1998).

Many of the mechanisms that mediate fire and its effects on diversity are already well-understood for longleaf pine forests. For example, Rebertus et al. (1989) have shown that regenerating turkey oaks (*Q. laevis*) rarely survive needle-fuelled fires in the vicinity of longleaf pines. Moreover, researchers have elucidated aspects of how seasonality and frequency of fire influence the diversity and structural composition of understory and ground-layer vegetation (Hiers et al. 2000; Drewa et al. 2002;

Glitzenstein et al 2003; Heuberger and Putz 2003). Rather than seeking to replicate aspects of these studies, the protocol below, which represents a possible Ph.D. dissertation, is proposed as a complementary project to the Peterson (2002a) study. In other words, it is an explicit attempt to understand how structural and compositional diversity and their response to fire relate to cross-scale edge as a measure of landscape resilience in longleaf pine forests. This study would require strong cooperation and coordination with the management agencies operating in the Elgin Air Force Base.

4.ii. Hypotheses

This experimental protocol tests hypotheses concerning the characteristics that sites of low resilience should possess according to the Panarchy metaphor and according to the relationships between resilience and biodiversity presented above. More specifically, areas of low resilience should have high potential for change, high connectedness among system components, and, relative to sites with higher resilience, should have lower diversity in key functional groups.

1. Abundance and diversity of component species

Hypothesis: areas of cross-scale edge have lower connectedness and diversity of species that mediate fire[2] than areas not classed as cross-scale edge.

Predictions:

i. LL (edge) areas will have a lower abundance and diversity of pyrogenic species than LL areas.
ii. HW (edge) areas will have a lower abundance and diversity of fire retardant species than HW areas.

2. Successional tendency

Hypothesis: The establishment of propagules of species from other sites lowers the resilience of a site. That is, sites open to dispersal to species from sites in other states will have lower resilience. Cross-scale edge areas therefore display successional tendencies away from the dominant canopy cover while areas not classed as cross-scale edge display successional tendencies that maintain current canopy composition.

Predictions:

i. Successional index will point to hardwood transition in LL (edge) areas as a result of higher understory diversity and abundance (density) of mesic oak species than pine species.
ii. Successional index will point to transition to pine species in HW (edge) areas as a result of higher understory diversity and abundance (density) of pine than hardwood species.

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[2] It would be necessary to generate a list of species that mediate the behaviour of fires, based on literature and local knowledge, and class or rank them as pyrogenic or relatively fire-retardant.

iii. Successional index will point to oak maintenance in HW areas and pine maintenance in LL areas.

3. Fuel loading

Hypothesis: Cross-scale edge areas have higher and compositionally distinct loads of ground fuel than areas not classed as cross-scale edge

Predictions:

i. Cross-scale edge areas will have deeper and more connected litter layers than areas not classed as cross-scale edge.
ii. LL (edge) areas will have deeper litter layers with higher oak or fire-retardant species composition than LL areas.
iii. HW (edge) areas will have shallower litter layers with more pyrogenic species composition than HW areas.

4. Response to disturbance

Hypothesis: Areas not classed as cross-scale edge respond faster than cross-scale edge areas to re-establish pre-disturbance composition.

Predictions:

i. Percent mortality following fire will be lower in pine regeneration in LL than in LL(edge) areas.
ii. Percent cover for pyrogenic grasses will be higher in LL than in LL (edge) areas.
iii. Percent mortality for oak regeneration and canopy trees will be higher in HW (edge) than in HW areas.
iv. Regeneration density of oaks will be higher in HW than in HW (edge) areas.
v. Growth rates of regeneration will be higher in LL and HW areas than in LL (edge) and HW (edge), respectively.
vi. Direction of successional index will remain unchanged for LL and HW but will change for LL (edge) and HW (edge).

4.iii. Methods

In a GIS, randomly allocate across the landscape 3060-m wide transects[3] that traverse areas of cross-scale edge by initiating in 'pure' HW or LL areas. Within each transect, randomly locate 60 x 60 m quadrats[4] in areas of HW, HW (edge), LL (edge), and LL (Figure X). Quadrats where possible should be placed in (i) mesic sites to standardize variation in composition, structure and fire behaviour

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[3] This width corresponds to largest window size used by Peterson (2002).

[4] This size corresponds to the cell size in the model used by Peterson (2002).

resulting from differences in soil moisture regime (Heyward 1939; Kirkman et al. 2001; Ferguson et al. 2002; Foster and Brooks 2002), and (ii) areas with similar time since last fire to standardize for variation associated with succession. For each quadrat, determine species, DBH, height and density of all dominant[5] canopy trees. Within each quadrat, randomly locate sub-quadrats[6] to measure the following:

i. Density of 'grass-stage' and emergent[7] ('rocket stage') longleaf pine regeneration.
ii. Height growth rates as determined by distance between branch whorls.
iii. Diversity and abundance (percent cover) of pyrogenic perennial bunchgrasses, such as wiregrass[8] and broad-leaf grasses.
iv. Density of oak regeneration (seedlings and saplings[9]).
v. Type (pine or oak) and abundance (percent cover) of leaf litter.
vi. At each corner of the sub-quadrat, determine type and measure depth of litter layer.

After this sampling is complete, randomly divide the transects into 2 groups: a prescribed burn group and a control group. All other fires in the experimental area will be actively suppressed during the experiment. In the burn group, conduct prescribed burns of the similar intensity in each quadrat at the end of the growing season. At the end of the following season, re-measure the quadrats for the vegetation attributes described above as well as mortality of any canopy dominants or regeneration.

Statistical analyses

Statistical tests – ANOVAs and multivariate tests such as correspondence canonic analyses will be used to test for significant differences in variables (e.g. percent cover among different area-types and before and after burning) and for understanding how variability is partitioned among dependent variables. An *a priori* analysis of statistical power will be performed to determine the minimum number of transects needed to have Power $\geq 80\%$. Significant differences will be assigned when $P \leq 0.05$.

Index of compositional divergence (ICD) – This index is measure of successional tendency, based on a comparison of the relative composition of pine or oak species in each stratum (Austin 1977; Goff and

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[5] A threshold DBH for determining canopy dominance would need to be set *a priori* from existing stocking information.

[6] The size will depend on pilot analyses of species-area relationships.

[7] A threshold stem diameter for the sapling class would need to be set *a priori*, based on literature or expert judgment, beyond which the probability of surviving to canopy ascendance is high.

[8] Wiregrasses have several physical attributes that encourage fire. For example, their leaves overlap with adjacent clumps to act as a net to catch fallen pine needles, thereby allowing air to circulate along the savannah floor and keep the ground primed for burns. Their bunched structure allows fire to spread easily from clump to clump, prolongs decomposition of the pine needles over a two- to three-year cycle and results in the maintenance of higher fuel loading than sites without wiregrass (Crofton 2003).

[9] See footnote 7.

Zedler). It is a static measure of succession that assumes the sapling stratum is representative of the future canopy[10]. The index is calculated as:

$$\text{ICD} = \frac{\text{Hardwood density}_{\text{canopy}}}{\text{Hardwood density}_{\text{canopy}} + \text{Pine density}_{\text{canopy}}} - \frac{\text{Hardwood density}_{\text{saplings}}}{\text{Hardwood density}_{\text{saplings}} + \text{Pine density}_{\text{saplings}}}$$

Depending on the sampled composition, the index is a value between 1 and -1. An index of 1 occurs when hardwoods compose 100 % of the canopy with no hardwood regeneration beneath. Conversely, an index of -1 occurs when pines fully dominate the canopy while hardwood fully dominate the regeneration. In this way, a positive value indicates a transition towards pines, a negative value towards hardwoods, and a zero value indicates a stable composition.

Caveat

A caveat about scaling effects is necessary about this experimental protocol. The structural and compositional patterns that this protocol targets possibly operate at a smaller spatial scale than the scale at which the contagion-dependent aspects of cross-scale edge operate (Peterson 2000). The relatively small scale of the quadrats and sub-quadrats proposed in the protocol are essentially a compromise of feasibility i.e. they represent what would be possible for one graduate student to achieve within two field seasons.

5. Conclusion

Understanding resilience may hold the key to overcoming the challenges inherent to the sustainable use resources as well as resolving the fundamental mismatch between the dynamics of natural systems and the dynamics of human management systems (Levin 2000) e.g. maintaining the cycles that create biodiversity and provide soil nutrients associated with old-growth forests vs. economic forest rotations. This mismatch makes it difficult (i) to see the signs of possible irreversible change until that change is underway (Scheffer et al. 2003), (ii) to understand the impacts of individual behaviour on coarse scales, and (iii) for individuals to feel that their actions can influence sustainability since it is the actions of billions that dictate the dynamics of the global commons (Levin 2000). The emergence of a cross-disciplinary research body seeking to understanding resilience in managed ecosystems that views

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[10] This is not the only assumption inherent in the ICD. In fact, several others are made that require careful interpretation of results, including assumptions about survival probabilities, size-age correlations, and confusion between environmental effects and successional gradients (Austin 1977). Therefore, this index provides simply an idea of the direction of potential change existing at the time of sampling.

humans as a profound and integrated force is encouraging in terms of the prospects of finding ways to achieve sustainability of use of ecosystem goods and services (e.g. Gunderson and Holling 2002). The resolution of sustainability issues raised in the introduction may come from developing policies and practices of resource use that recognize the following:

- Ecosystems are prone to catastrophic change when managed in a way that minimizes variation of key environmental variables such as fire regime or when subjected to long-term anthropogenic stresses such as overharvesting (Holling and Meffe 1996; Carpenter et al 2001).
- The globalization and intensification of anthropogenic stresses such as introduced species and climate change are expected to increase the frequency and intensity of compounded perturbations and thereby the frequency of both adaptive and catastrophic shifts within ecosystems (Paine et al. 1998; Reiger and Kay 2002).
- Institutions that allow persistence and sustainable use of common property resources in an equitable manner share two fundamental elements: access limitation and investment of resources back into the socio-ecological systems (Ostrom et al. 1999). In the case of forests, operationalizing these elements into a management regime may be easier than for other common property resources such as fisheries because forest resources are tractable, ample knowledge exists about ecosystem function and dynamics, and there is an increasing social willingness to see them managed for use by future generations (Ostrom et al. 1999; Scheffer et al. 2000).
- Acceptance by practitioners, politicians and the public that due of the panarchical nature of ecosystems, uncertainty will always be present, as the systems themselves are perpetually changing, and that surprises are inevitable even though managers may make the most rational decisions given the available information (Holling 2001; Peterson et al. 2003). Monitoring and adaptive management are therefore central to sustainability and learning from doing (Holling 1978; Walters 1997).
- Reductionist science, which by its nature is conservative and unambiguous by being incomplete and fragmented, plays a non-trivial role in developing practices and policies that contribute to a loss of ecological resilience (Levin 1992; Holling 1993; Gunderson 2000). Traditional fisheries science is a poignant example of how a scientific approach that breaks management issues into parts for analysis can lead to proposed solutions or practices that are piecemeal and, in the long term, largely ineffective at prediction or sustainable management (Hilborn et al. 1995). Of

course, even the best scientific recommendations will be ineffective in this respect in the absence of meaningful political and social will for sustainability or practices driven by greed.

- The developing science of socio-ecological systems (SES) holds considerable promise for understanding on how we can manage ecosystems across scales for resilience and long-term sustainability e.g. how changes at one level or scale of biological organization will affect emergent patterns or processes at another level of organization (Hartvigsen et al. 1998) or how interactions across slow and fast time scales can foster predictions of impending environmental change (Carpenter and Turner 2001). This field views people as an integral part of managed systems and recognizes that humans are a key agent behind changes and the maintenance of resilience (Kates et al. 2001, Folke et al. 2002; Berkes et al. 2003). Therefore, perhaps most importantly, SES studies can provide insight into how to effectively integrate the role of people towards meeting the sustainability goal after identifying points of vulnerabilities in cycles of change e.g. by inclusion of incentive structures that foster sustainable resource use (Scheffer et al. 2000; Carpenter et al. 2003).

The integration of all of the above represents a formidable, and perhaps insurmountable, challenge. However, as Ostrom et al. (1999) point out, we have only one Earth on which to experiment and this creates but one option for managers and researchers concerned with the sustainability of resources and inter- and intra-generational equity: to try. Holling (2001) provides some hope in this respect by recognizing that human systems represent a variant of the panarchy as we are capable of foresight and forward-looking behaviour and are endowed with significant technological and communication capacity. It may therefore be possible that we are capable of building resilience, legacy, learning and diversity on a global scale and thereby dampen the amplitude of a collapse-phase that looms large (Folke et al. 2002).

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Figures

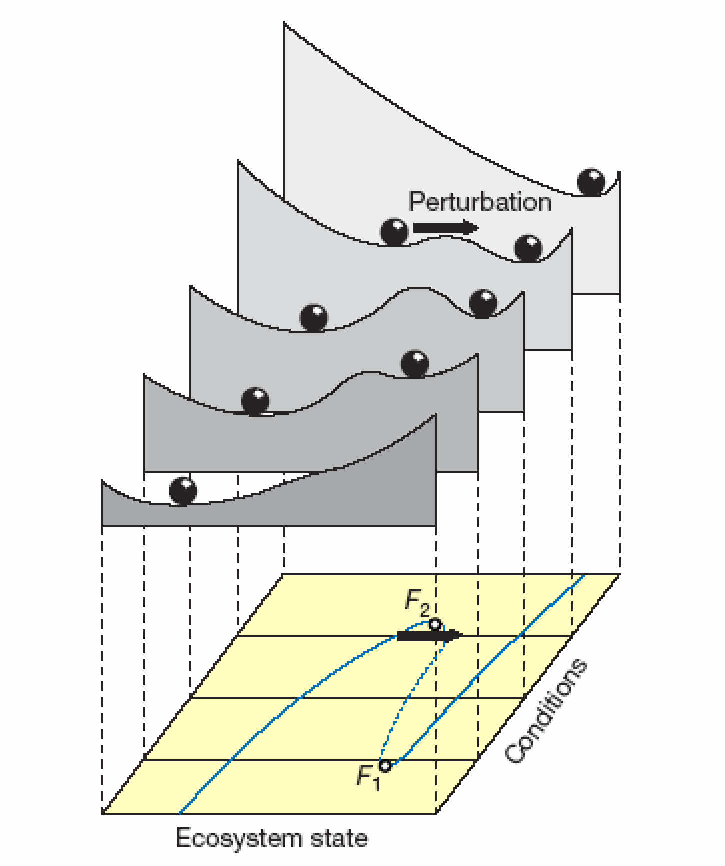

Figure 1 - The resilience of multiple stable states with respect to perturbations and varying external conditions. Resilience is denoted by the width of the valleys that cradle the ecosystem (ball). The arrow denotes the direction of a perturbation. Figure from Sheffer et al. (2001).

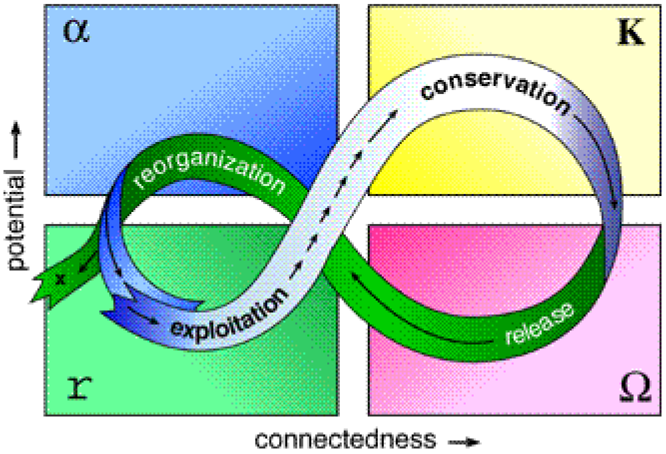

Figure 2 - The adaptive cycle of a complex adaptive system. The arrows indicate the speed of change in the cycle where short, narrowly spaced arrows indicate slow change whereas long arrows indicate rapid change. The exit from the adaptive cycle on the lower left suggests where in the cycle the potential of a system can leak away and where a switch into a system with lower productivity and organization is most likely to occur. Figure from Gunderson and Holling (2002).

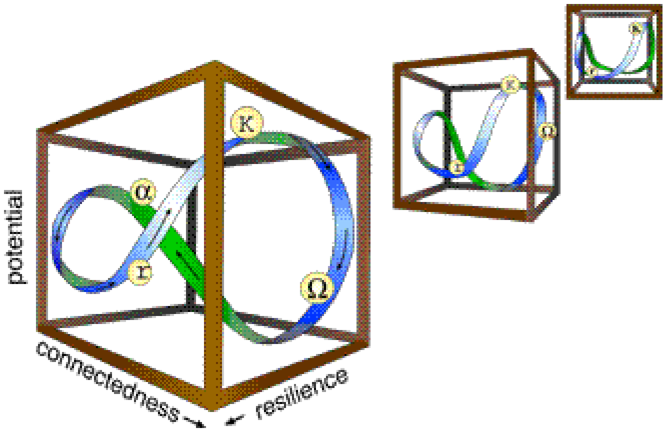

Figure 3 - Resilience as a third dimension in the adaptive cycle. Resilience changes throughout the cycle, shrinking as the cycle moves toward K and expanding as the cycle rapidly shifts toward the back-loop to reorganize accumulated resources for a new cycle initiation. Figure from Gunderson and Holling (2002).

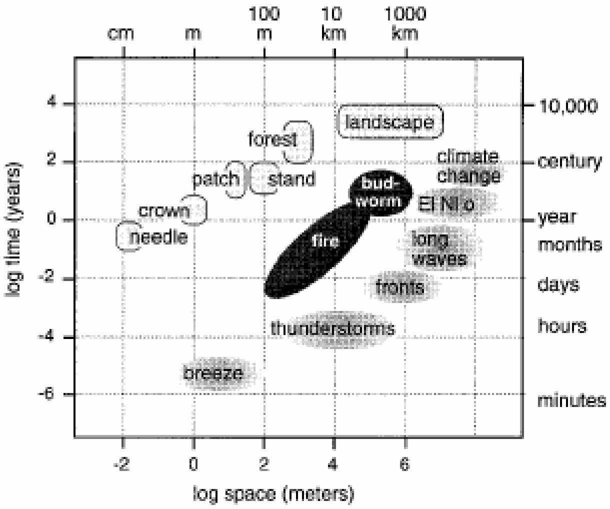

Figure 4 - Time and space scales in the boreal forest (Holling 1986) and the atmosphere (Clark 1985) illustrating relationships among some of the processes that structure the forest. The interactions among the slow vegetation processes and faster atmospheric processes are mediated by meso-scale contagious processes like fire or outbreaks of the spruce budworm. Figure from Holling (2001).

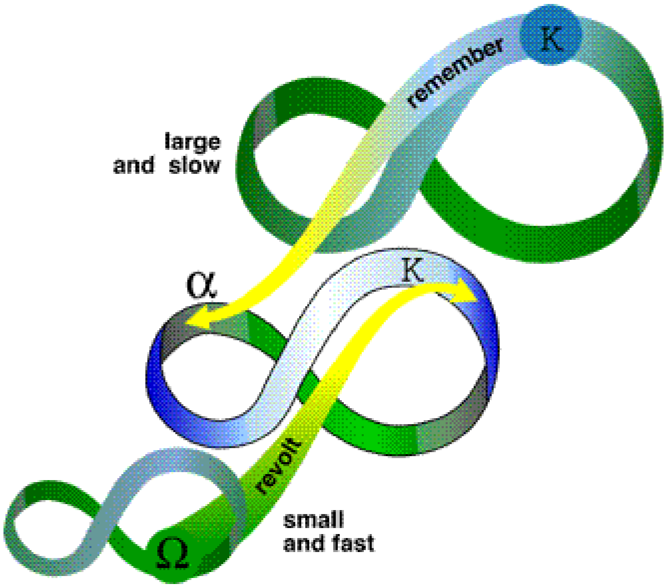

Figure 5 - Connections among adaptive cycles in a Panarchy. “Revolt” refers to how a critical change in one cycle can cascade upwards to a vulnerable stage in a larger, slower cycle e.g. when conditions in a forest are such that a locally ignited ground fire can spread to the crown of a tree, then to a patch of trees and eventually to the entire stand. “Remember” refers to how renewal is facilitated at one cycle by drawing on the accumulated potential in a larger, slower cycle e.g. by the presence of veteran trees providing refugia from fire or seeds and nutrients for the regenerating stand. Figure from Gunderson and Holling (2002).

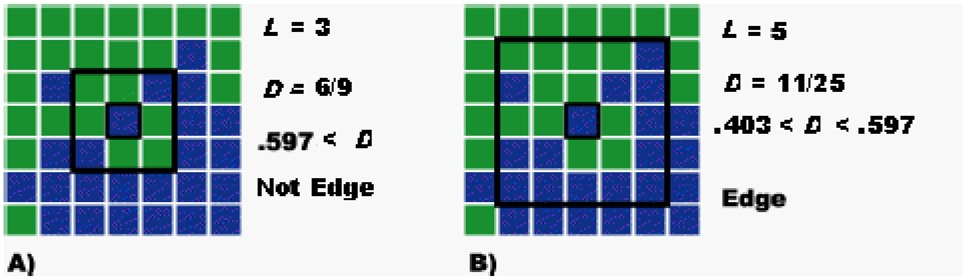

Figure 6 - Estimation of edge. Density (*D*) is a scale-dependent measure i.e. the density of the green cells within a window varies according to the window size (*L*). In A), the middle cell is not an edge site when the window is *L* is small (*L* =3). In B), the middle cell is an edge site when the *L* = 5. Figure from Peterson (2002).

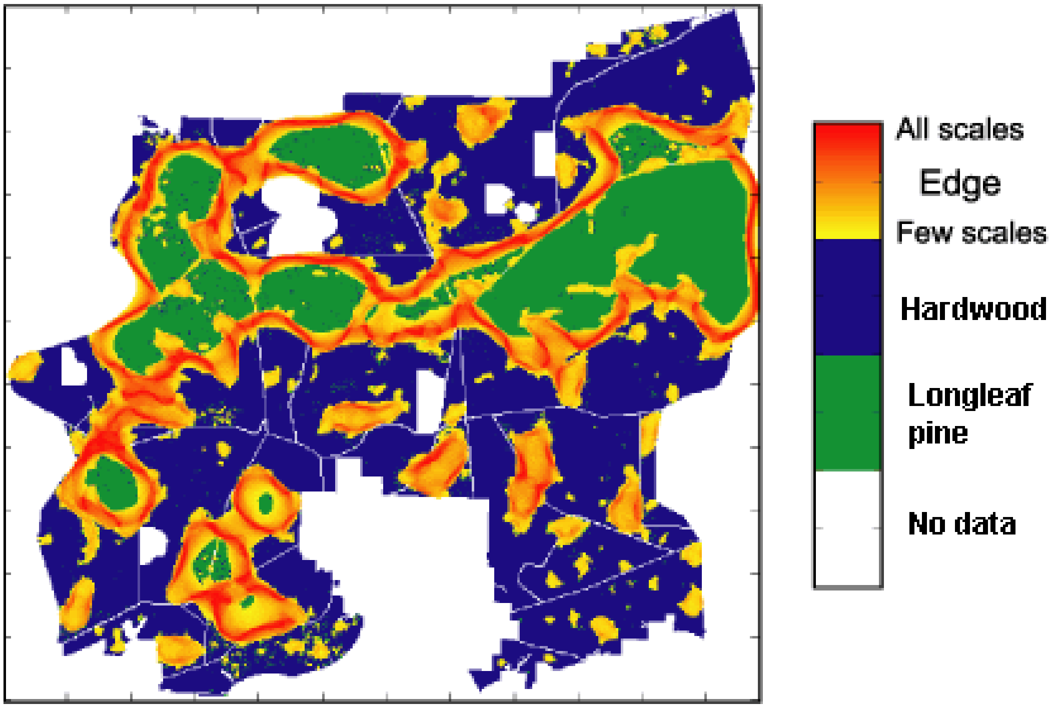

Figure 7 - Cross-scale edge in the Elgin Air Force Base. Figure from Peterson (2002).

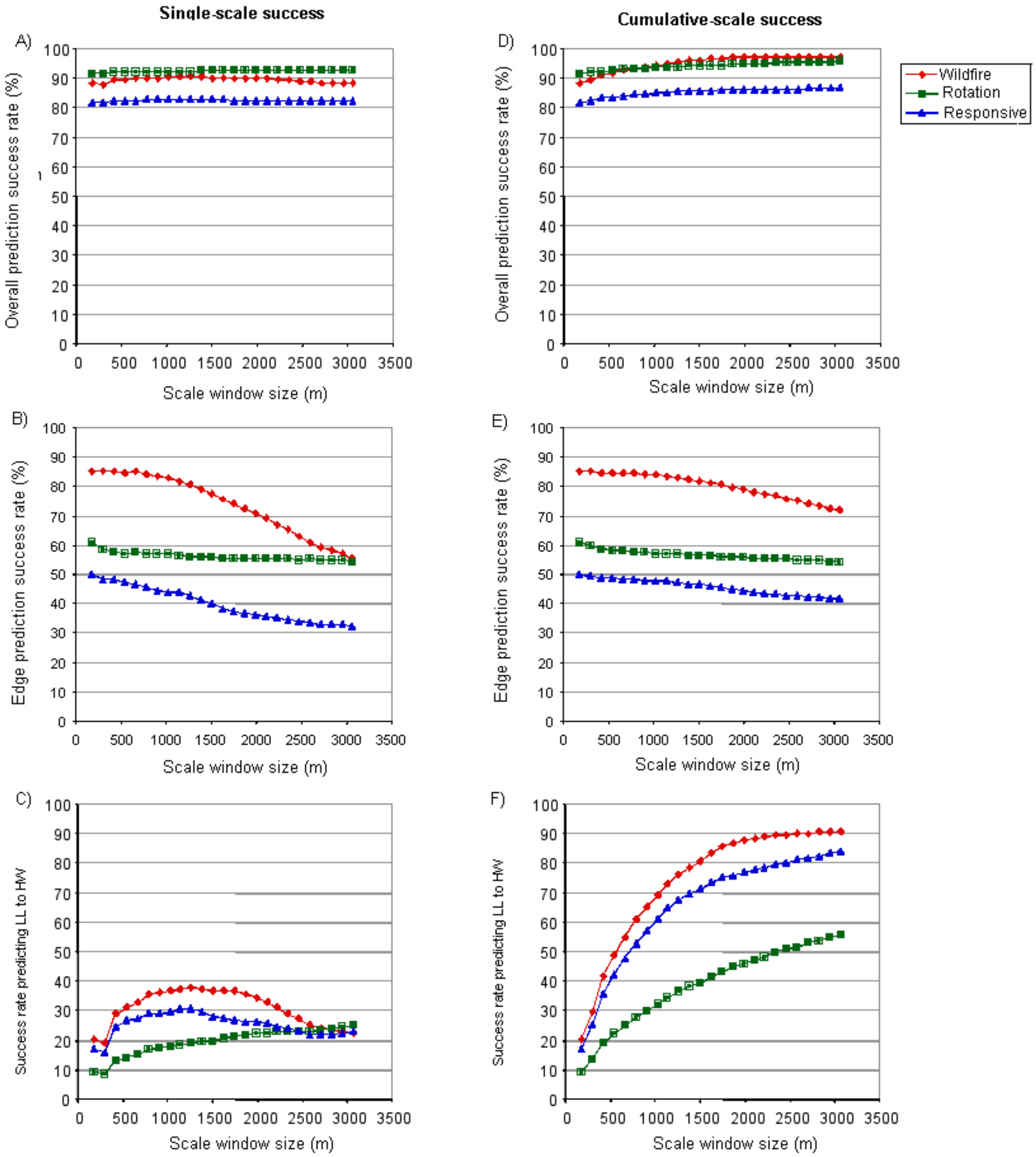

Figure 8 - Predictive success of cross-scale edge at single scales (A, B, and C) and across scales (D, E, and F) for three different regimes of fire management. Overall predictive success measures how well cross-scale edge classifications predicted the persistence of LL and HW sites as well as transitions to HW within the cross-scale edge sites in modeled future landscape. Edge prediction success is the proportion of sites in the modeled future landscape that actually are HW. Success rate predicting LL to HW shows how accurately cross-scale edge predicted transitions from LL to HW. Figure from Peterson (2002).

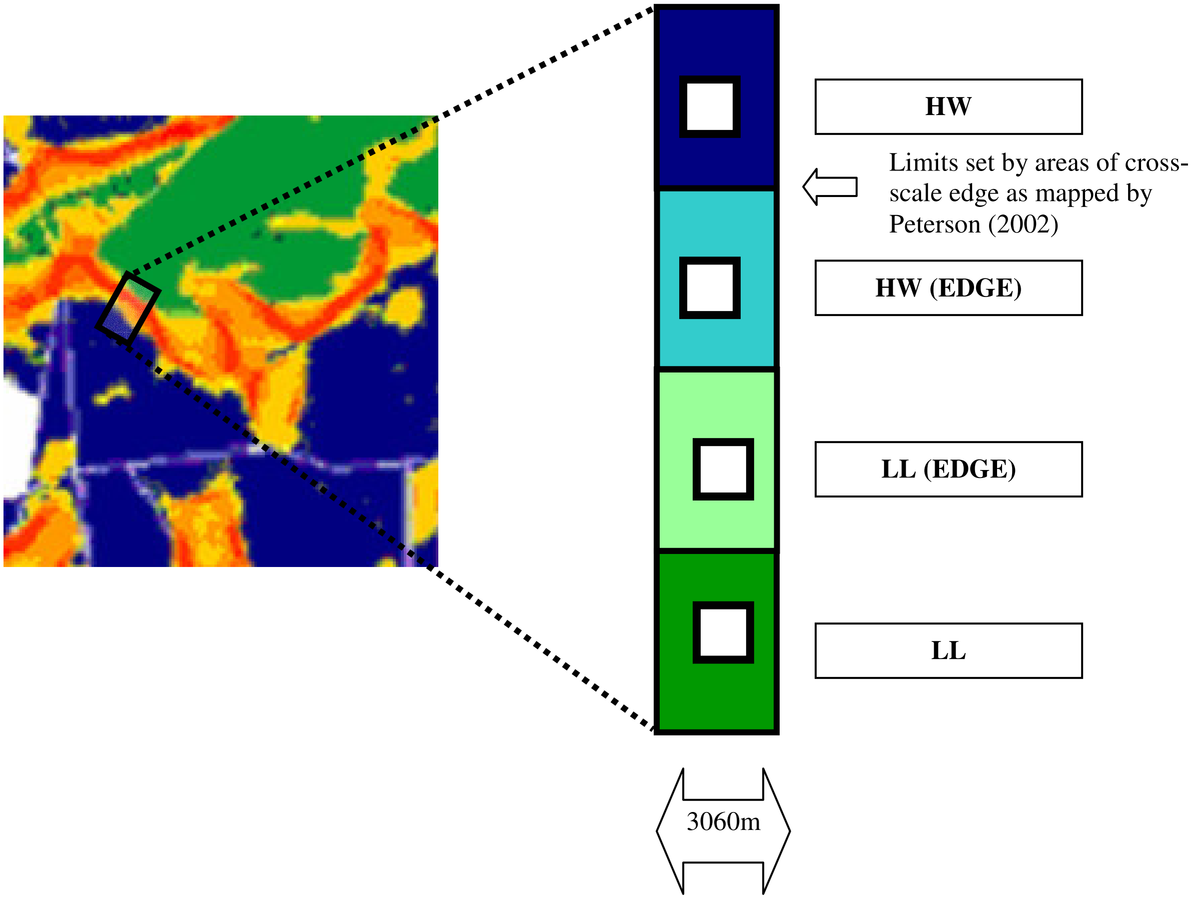

Figure 9 - Sampling design for experiment testing relationships among compositional and structural diversity with cross-scale edge. Figure adapted from Peterson (2002). Quadrats are white boxes with black borders (not to scale). Sub-quadrats not shown but would be randomly located within quadrats. See text for details.