

ORIGINAL ARTICLES

Ecological Resilience, Biodiversity, and Scale

Garry Peterson,^{1*} Craig R. Allen,² and C. S. Holling¹

¹Department of Zoology, Box 118525, University of Florida, Gainesville, FL 32611; and ²Department of Wildlife Ecology and Conservation, 117 Newins-Zeigler Hall, University of Florida, Gainesville, FL 32611, USA

ABSTRACT

We describe existing models of the relationship between species diversity and ecological function, and propose a conceptual model that relates species richness, ecological resilience, and scale. We suggest that species interact with scale-dependent sets of ecological structures and processes that determine functional opportunities. We propose that ecological resilience is generated by diverse, but overlapping, function within a scale and by apparently

redundant species that operate at different scales, thereby reinforcing function across scales. The distribution of functional diversity within and across scales enables regeneration and renewal to occur following ecological disruption over a wide range of scales.

Key words: biodiversity; cross-scale; ecological function; ecological organization; functional group; keystone; multiple stable states; resilience; scale; stability.

INTRODUCTION

One of the central questions in ecology is how biological diversity relates to ecological function. This question has become increasingly relevant as anthropogenic transformation of the earth has intensified. The distribution and abundance of species have been radically transformed as massive land-use changes have eliminated endemic species (Turner and others 1993), and the expansion of global transportation networks has spread other species (McNeely and others 1995). This biotic reorganization is co-occurring with a variety of other global changes, including climate change, alteration of nutrient cycles, and chemical contamination of the biosphere. Maintaining the ecological services that support humanity, and other life, during this extensive and rapid ecological reorganization requires understanding how ecological interactions among species produce resilient ecosystems.

Species perform diverse ecological functions. A species may regulate biogeochemical cycles (Vitousek 1990;

Zimov and others 1995), alter disturbance regimes (Dublin and others 1990; D'Antonio and Vitousek 1992), or modify the physical environment (Jones and others 1994; Naiman and others 1994). Other species regulate ecological processes indirectly, through trophic interactions such as predation or parasitism (Kitchell and Carpenter 1993; Prins and Van der Jeud 1993), or functional interactions such as pollination (Fleming and Sosa 1994) and seed dispersal (Brown and Heske 1990). The variety of functions that a species can perform is limited, and consequently ecologists frequently have proposed that an increase in species richness also increases functional diversity, producing an increase in ecological stability (Tilman and others 1996).

The idea that species richness produces ecological stability was originally proposed by Darwin (1859), reiterated by MacArthur (1955), and modeled by May (1973). Recently, Tilman and colleagues (Tilman 1996; Tilman and others 1996) experimentally demonstrated that in small systems, over ecologically brief periods, increased species richness increases the efficiency and stability of some ecosystem functions, but decreases

population stability. Despite the demonstrated link between species richness and ecological stability over small scales, the nature of this connection remains uncertain.

MODELS OF ECOLOGICAL ORGANIZATION

Many competing models attempt to describe how an increase in species richness increases stability. Following previous authors, we divide these models into four classes: “species richness–diversity” (MacArthur 1955), “idiosyncratic” (Lawton 1994), “rivet” (Ehrlich and Ehrlich 1981), and “drivers and passengers” (Walker 1992). These models all explicitly or implicitly assume that a species has ecological function, and that the function of a species can be represented as occupying an area of multidimensional ecological function space (Grinnell 1917; Hutchinson 1957; Sugihara 1980). For illustrative purposes, we compress multidimensional functional space into one dimension in which breadth represents the variety of a species’ ecological function (Clark 1954). For example, a species such as a beaver, that strongly influences tree populations, hydrology, and nutrient cycles, has a broad function, whereas a fig wasp that pollinates a single species of fig would have a narrow function. We represent the intensity of a species’ ecological function by height. For example, a “keystone species” (Paine 1969; Power and others 1996) has a stronger influence than a “passenger” species (Walker 1992).

We emphasize the differences between these models before discussing their similarities. We then present our model of “cross-scale resilience,” which incorporates scale into an expanded model of the relationship between diversity and ecological function.

Species Diversity

Darwin (1859) proposed that an area is more ecologically stable if it is occupied by a large number of species than if it is occupied by a small number. This idea was formalized by MacArthur (1955), who proposed that the addition of species to an ecosystem increases the number of ecological functions present, and that this increase stabilizes an ecosystem (Figure 1).

Although many experimental studies have demonstrated that increasing the number of species increases the stability of ecosystem function (Schindler 1990; Naeem and others 1994; Frost and others 1995; Holling and others 1995; Ewel and Bigelow 1996; Tilman 1996), apparently no investigations of the relationship between species richness and stability have indicated that additional species continue to increase stability at a constant rate, indicating

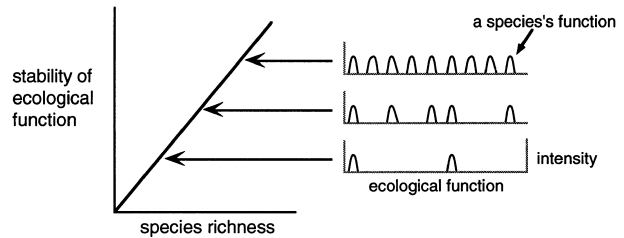


Figure 1. A representation of the Darwin/MacArthur model: increasing species richness increases the stability of ecological function. This model, and the other models we discuss, implicitly represents species ecological function as occupying a portion of a multidimensional ecological function space that is analogous to niche space (MacArthur 1955). As species accumulate, they fill this space. The width and height dimensions of the inset diagrams represent the breadth and intensity of a species’ ecological function. This model assumes that function space is relatively empty and therefore species can be continually added to a community without saturating it. It also assumes that the strength and breadth of ecological functions do not vary among species.

that the species–diversity model is excessively simplistic. Consequently, we focus our attention upon models that propose more complex relationships between species richness and ecological stability.

Idiosyncratic

A competing model of the relationship between species and ecological function proposes that strong ecological interactions among species result in an ecosystem that is extremely variable, and contingent on the particular nature of interspecific interactions (Lawton 1994). This model proposes that the degree of stability in a community depends idiosyncratically upon which species are present (Figure 2). For example, fire ants have had great impacts on ecosystems of the southeastern United States (Porter and Savignano 1990; Allen and others 1995), but have a much different role in the Pantanal of Brazil and Paraguay (Orr and others 1995). Such situations suggest that ecosystem function is contingent on the ecological history of a region and the evolutionary history of interacting species. However, ecosystems are not only products of historical contingency, ecosystem ecology has demonstrated that many ecosystems are similarly organized.

Many ecosystem studies have revealed that despite dissimilar species compositions, ecosystems can have striking ecological similarities. For example, lake studies have demonstrated that similar ecological function can be maintained over a wide mix of species and population densities (Schindler 1990; Frost and others 1995). Mediterranean cli-

mate ecosystems provide a good example of functional convergence. The world's five Mediterranean climate regions, despite geographic and evolutionary isolation that has produced radically different floras and faunas, are extremely similar in ecological structure and function (Di Castri and Mooney 1973; Kalin Arroyo and others 1995). This convergence suggests that species are organized into functional groups, and that these groups are determined by regional ecological processes. Both the "rivet" (Ehrlich and Ehrlich 1981) and "drivers and passengers" (Walker 1992) models of functional diversity assume that some sort of functional redundancy exists, but they differ in the importance they assign to functional groups.

Rivets

Empirical evidence suggests that the effect of species removal from or addition to an ecosystem varies. Ehrlich and Ehrlich's (1981) rivet hypothesis, which is similar to Frost and colleagues' (1995) model of compensating complementarity, likens the ecological function of species to the rivets that attach a wing to a plane. Several rivets can be lost before the wing falls off. 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 (Figure 3).

In the rivet model, an ecological function will not disappear until all the species performing that function are removed from an ecosystem. Overlap of ecological function enables an ecosystem to persist. Compensation masks ecosystem degradation, because while a degraded system may function similarly to an intact system, the loss of redundancy decreases the system's ability to withstand disturbance or further species removal.

Drivers and Passengers

Walker's "drivers and passengers" hypothesis accepts the notion of species complementarity and extends it by proposing that ecological function resides in "driver" species or in functional groups of such species (Walker 1992, 1995). It is similar to Holling's (1992) "extended keystone hypothesis." Walker defines a driver as a species that has a strong ecological function. Such species significantly structure the ecosystems in which they and passenger species exist. Passenger species are those that have minor ecological impact. Driver species can take many forms. They may be "ecological engineers" (Jones and others 1994), such as beavers (Naiman and others 1994), or gopher tortoises (Diemer 1986), which physically structure their environments. Or drivers may be "keystone species" (Paine 1969),

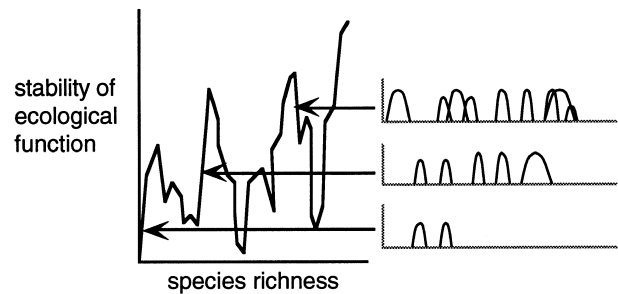


Figure 2. A representation of the idiosyncratic model (Lawton 1994). In this model, ecological function varies idiosyncratically as species richness increases. This model argues that the contribution of each species to ecological function is strongly influenced by interactions among species. Therefore, the effects of the introduction or removal of species to an ecosystem can be either insignificant or major, depending upon the nature of the species introduced or removed and the nature of the species with which it interacts.

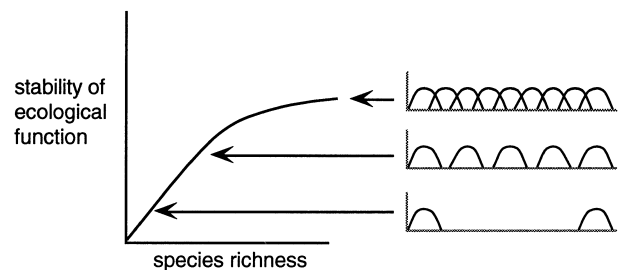


Figure 3. The "rivet" model of ecological function (Ehrlich and Ehrlich 1981) presumes that ecological function space is relatively small. Therefore, as species are added to an ecosystem, their functions begin to overlap or complement one another. This overlap allows ecological function to persist despite the loss of a limited number of species, since species with similar functions can compensate for the elimination or decline of other species. However, the increase of stability gained by adding new species decreases as species richness increases and functional space becomes increasingly crowded.

such as sea otters (Estes and Duggins 1995) or asynchronously fruiting trees (Terborgh 1986), that have strong interactions with other species (Power and others 1996). Walker (1995) proposes that since most ecological function resides in the strong influence of driver species, it is their presence or absence that determines the stability of an ecosystem's ecological function (Figure 4).

MODEL SYNTHESIS

Whereas the "rivet" hypothesis assumes that ecological function is evenly partitioned among species, Walker's model assumes there are large differences

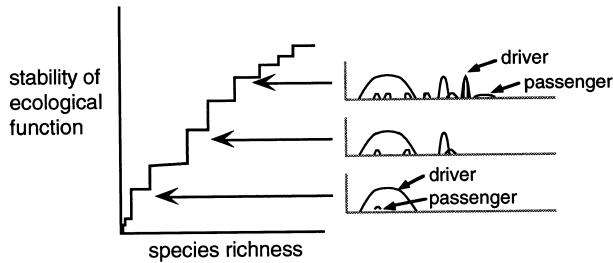


Figure 4. Walker's "drivers and passengers" model of redundant ecological function (1992, 1995) proposes that ecological function is unevenly distributed among species. Drivers have a large ecological impact, while passengers have a minimal impact. The addition of drivers increases the stability of the system, while passengers have little or no effect.

between drivers that have strong ecological function and passengers that have weak ecological function (Figure 4). Both hypotheses recognize that different types of ecological functionality are required to produce ecological stability, and that as additional species are added to an ecosystem the increasing redundancy of function decreases the rate at which ecological stability increases. The existence of some type of ecological redundancy is supported by experiments conducted in Minnesota grasslands, tropical rainforests, artificial mesocosms, and lakes (Schindler 1990; Naeem and others 1994; Ewel and Bigelow 1996; Tilman and others 1996).

Tilman, for example, demonstrated that more diverse plots (4×4 m) have greater plant cover and more efficiently utilize nitrogen (Tilman 1996). Tilman and colleagues demonstrated that ecological function was more stable in diverse communities despite, or perhaps because of, large fluctuations in populations of species (Tilman and others 1996). These results echo those of Frank and McNaughton (1991), who demonstrated that more diverse natural grass communities recovered faster than less diverse communities following drought.

In a series of experiments, Ewel and coworkers constructed a set of tropical ecosystems with different levels of species richness and compared their functioning to adjacent rainforest. They demonstrated that relatively few species, if drawn from different functional groups, can duplicate the ecological flows of a diverse rainforest (Ewel and others 1991). Herbivory per leaf area was lower and less variable in species-rich plots (Brown and Ewel 1987). They also demonstrated that a variety of ecosystem variables, such as soil organic matter, increase rapidly as one adds different functional types to a plot (Ewel and Bigelow 1996), and that simple agroecosystems function quite similarly to much

more species-rich rainforests, at least in areas of about $\frac{1}{3}$ ha (80×40 m) for 5 years (Ewel and others 1991).

Naeem and coworkers (1994) assembled replicate artificial ecosystems at a number of levels of species richness. They demonstrated that carbon dioxide consumption, vegetative cover, and productivity increased with species richness. These increases were greater between 9 and 15 species than between 15 and 31 species, providing support for the hypothesis that an increase in species richness increases ecological redundancy. Water and nutrient retention did not vary with species richness.

Frost and coworkers (1995) demonstrated that ecological function is preserved if population declines of zooplankton species are compensated for by population increases in other species with similar ecological functions. Their results suggest that lakes with fewer species in a functional group would exhibit decreased ability to compensate for population declines in other species. Similarly, Schindler (1990) observed that the largest changes in ecological processes and food-web organization occurred when species that were the only remaining member of a functional group were eliminated.

These studies demonstrate that the stability of many, but not all, ecological processes increases with species richness. They also suggest that the ecological stability is generated more by a diversity of functional groups than by species richness. These results suggest a possible synthesis of the various models relating stability to species richness.

The model that best describes an ecosystem appears to depend upon the variety of functional roles that are occupied in that system, and the evenness of the distribution of ecological function among species. An ecosystem consisting of species that each perform different ecological functions will be less redundant than an ecosystem consisting of the same number of species that each perform a wide variety of ecological functions. Similarly, if there is little difference between the ecological impact of different species, there is little point in differentiating driver and passenger species; they can all be considered rivets. We propose that these models of how species richness influences the stability of ecological function can be collapsed into a simple model that can produce specific versions of these models by varying the degree of functional overlap and the degree of variation in ecological function among species (Figure 5).

The experimental results just discussed suggest ecosystems possess considerable functional redundancy. Indeed, it is difficult to envision how ecosystems without redundancy could continue to persist in the face of disturbance. We assume that since no species are identical, redundancy does not reside in

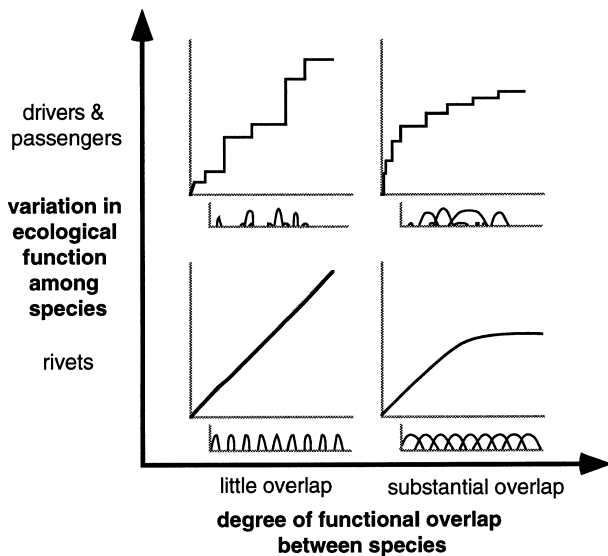


Figure 5. The relationship between stability and species richness varies with the degree of overlap that exists among the ecological function of different species and the amount of variation in the ecological impact of species ecological function. Overlap in ecological function leads to ecological redundancy. If the ecological impact of different species is similar they are “rivets,” whereas if some species have relatively large ecological impact they are “drivers” and others are “passengers.”

groups of species, but rather it emerges from the interactions of species. Therefore, it is not possible to substitute species for one another; rather, there are many possible combinations and organizations of species that can produce similar ecological functions. Redundancy quickly emerged in the experimental ecosystems, but these experiments were all conducted over relatively small areas and short time periods. Ewel and his coworkers (1991) conducted the longest and largest experimental manipulations of diversity, but even 5 years and a $\frac{1}{3}$ ha are small in comparison to the spatial and temporal dynamics of an ecosystem, or even the life span and home range of a medium-sized mammal.

Understanding of stability and ecological function developed at small scales can not be easily extended to larger scales, since the type and effect of ecological structures and processes vary with scale. At different scales, different sets of mutually reinforcing ecological processes leave their imprint on spatial, temporal and morphological patterns. Change may cause an ecosystem, at a particular scale, to reorganize suddenly around a set of alternative mutually reinforcing processes. For example, Hughes (1994) described an epidemic that caused a 99% decline in the population of an algae-eating fish in a Jamaican near-shore coral community. The loss of

these herbivores caused the community to shift from being dominated by corals to being dominated by fleshy macroalgae. Similar reorganizations are demonstrated in paleo-ecological (Carpenter and Leavitt 1991), historical (Prins and Jeud 1993), and long-term ecological research (Hughes 1994).

RESILIENCE

Assessing the stability of ecosystems that can reorganize requires more than a single metric. One common measure, what we term engineering resilience (Holling 1996), is the rate at which a system returns to a single steady or cyclic state following a perturbation. Engineering resilience assumes that behavior of a system remains within the stable domain that contains this steady state. When a system can reorganize (that is, shift from one stability domain to another), a more relevant measure of ecosystem dynamics is ecological resilience (Holling 1973). Ecological resilience is 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. Note that this use of resilience is different from its use by others [for example, Pimm (1984)], who define resilience as what we term engineering resilience (Holling 1996).

The difference between ecological and engineering resilience can be illustrated by modeling an ecological “state” as the position of a ball on a landscape. Gravity pulls the ball downward, and therefore pits in the surface of the landscape are stable states. The deeper a pit, the more stable it is, because increasingly strong disturbances are required to move an ecological state away from the bottom of the pit. The steepness of the sides of a stability pit corresponds to the strength of negative feedback processes maintaining an ecosystem near its stable state, and consequently engineering resilience increases with the slope of the sides of a pit (Figure 6).

Ecological resilience assumes that an ecosystem can exist in alternative self-organized or “stable” states. It measures the change required to move the ecosystem from being organized around one set of mutually reinforcing structures and processes to another. Using the landscape metaphor, whereas engineering resilience is a local measure of slope of the stability landscape, ecological resilience is a measure of regional topography. The ecological resilience of a state corresponds to the width of its stability pit. This corresponds to the degree to which the system would have to be altered before it begins

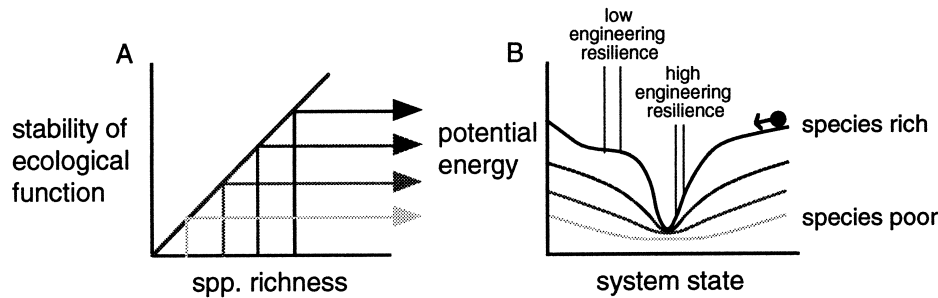


Figure 6. The relationship between stability and species richness can be represented by a set of stability landscapes. The dynamics of a system are expressed by a landscape, and its “state” is represented by a ball that is pulled into pits. Different landscape topographies may exist at different levels of species richness. In this model, the stability of a state increases with the depth of a pit. Zones of the stability surface that have low slopes have less engineering resilience than do areas that have steep slopes.

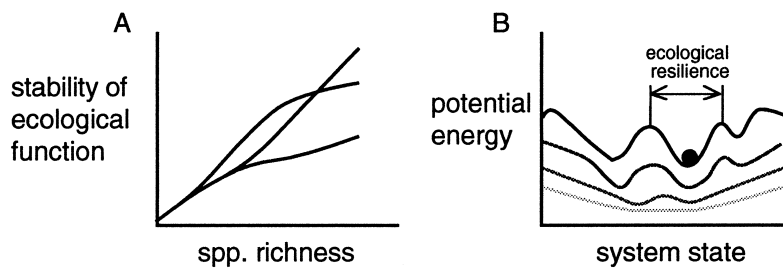


Figure 7. A system may be locally stable in a number of different states. Disturbance that moves the system across the landscape and slow systemic changes that alter the shape of the landscape both drive the movement of a system between states. The stability of a state is a local measure. It is determined by the slope of the landscape at its present position. The resilience of a state is a large-scale measure, as it corresponds to the width of the pit the system is currently within.

to reorganize around another set of processes (Figure 7).

Ecological and engineering resilience reflect different properties. Ecological resilience concentrates on the ability of a set of mutually reinforcing structures and processes to persist. It allows ecologists or managers to focus upon transitions between definable states, defined by sets of organizing processes and structures, and the likelihood of such occurrence. Engineering resilience, on the other hand, concentrates on conditions near a steady state where transient measurements of rate of return are made following small disturbances. Engineering resilience focuses upon small portions of a system’s stability landscape, whereas ecological resilience focuses upon its contours. Engineering resilience does not help assess either the response of a system to large perturbations or when gradual changes in a system’s stability landscape may cause the system to move from one stability domain to another. For these reasons we concentrate on ecological resilience.

SCALE

Ecosystems are resilient when ecological interactions reinforce one another and dampen disruptions. Such situations may arise due to compensa-

tion when a species with an ecological function similar to another species increases in abundance as the other declines (Holling 1996), or as one species reduces the impact of a disruption on other species. However, different species operate at different temporal and spatial scales, as is clearly demonstrated by the scaling relationships that relate body size to ecological function (Peters 1983).

We define a scale as a range of spatial and temporal frequencies. This range of frequencies is defined by resolution below which faster and smaller frequencies are noise, and the extent above which slower and larger frequencies are background. Species that operate at the same scale interact strongly with one another, but the organization and context of these interactions are determined by the cross-scale organization of an ecosystem. Consequently, understanding interactions among species requires understanding how species interact within and across scales.

Many disturbance processes provide an ecological connection across scales. Contagious disturbance processes such as fire, disease, and insect outbreaks have the ability to propagate themselves across a landscape, which allows small-scale changes to drive larger-scale changes. For example, the lightning

ignition of a single tree can produce a fire that spreads across thousands of square kilometers. Such disturbances are not external to ecological organization, but rather form integral parts of ecological organization (Holling 1986). Disturbance dynamics affect and are affected by species and their ecological functions (D'Antonio and Vitousek 1992). Consequently, the processes regulating contagious disturbances are as much determinants of ecological resilience as are more local interactions among species.

Current models of the relationship between species richness and stability implicitly model species and their ecological functions at the same scale; however, ecological systems are not scale invariant. A growing body of empirical evidence, theory, and models suggests that ecological structure and dynamics are primarily regulated by a small set of plant, animal, and abiotic processes (Carpenter and Leavitt 1991; Levin 1992; Holling and others 1995). Processes operate at characteristic periodicities and spatial scales (Holling 1992). Small and fast scales are dominated by biophysical processes that control plant physiology and morphology. At the larger and slower scale of patch dynamics, interspecific plant competition for nutrients, light, and water influences local species composition and regeneration. At a still larger scale of stands in a forest, mesoscale processes of fire, storm, insect outbreak, and large mammal herbivory determine structure and successional dynamics from tens of meters to kilometers, and from years to decades. At the largest landscape scales, climate, geomorphological, and biogeographical processes alter ecological structure and dynamics across hundreds of kilometers and over millennia (Figure 8). These processes produce patterns and are in turn reinforced by those patterns; that is, they are self-organized (Kauffman 1993).

Ecological processes produce a scale-specific template of ecological structures that are available to species (Morse and others 1985; Krummel and others 1987; O'Neill and others 1991). Ecological structure and patterns vary across landscapes and across scales. Many species may inhabit a given area, but if they live at different scales they will experience that area quite differently. For example, a wetland may be inhabited by both a mouse and a moose, but these species perceive and experience the wetland differently. A mouse may spend its entire life within a patch of land smaller than a hectare, while a moose may move among wetlands over more than a thousand hectares (Figure 8). This scale separation reduces the strength of interactions between mice and moose relative to interactions among animals that operate at similar scales (Allen and Hoeks-

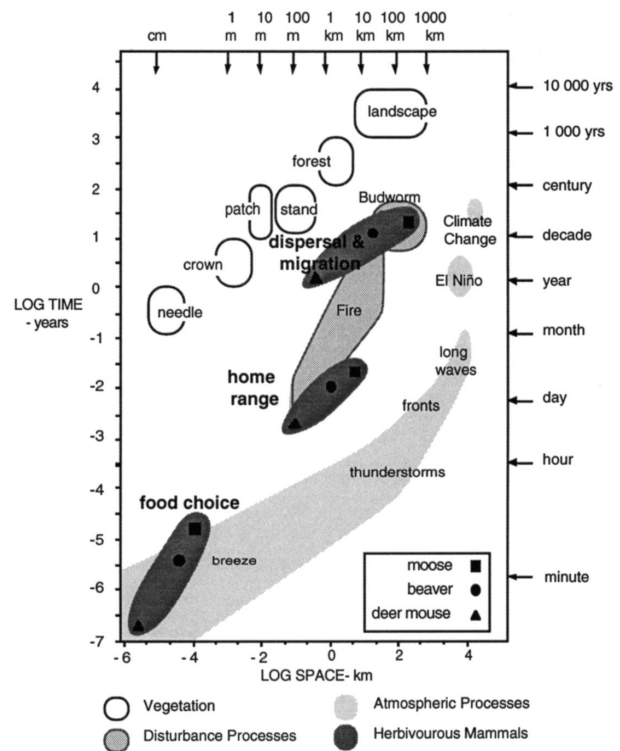


Figure 8. Time and space scales of the boreal forest (Holling 1986) and their relationship to some of the processes that structure the forest. These processes include insect outbreaks, fire, atmospheric processes, and the rapid carbon dioxide increase in modern times (Clark 1985). Contagious mesoscale disturbance processes provide a linkage between macroscale atmospheric processes and microscale landscape processes. Scales at which deer mouse, beaver, and moose choose food items, occupy a home range, and disperse to locate suitable home ranges vary with their body size (Holling 1992; Macdonald 1985; Nowak and Paradiso 1983).

tra 1992). In the next section, we propose a conceptual model that relates species richness, ecological resilience, and scale.

SPECIES, SCALE, AND ECOLOGICAL FUNCTION

Species can be divided into functional groups based upon their ecological roles (Clark 1954; Körner 1996). Species can be also be divided into groups based upon the specific scales that they exploit. The ecological scales at which species operate often strongly correspond with average species body mass, making this measure a useful proxy variable for determining the scales of an animal's perception and influence (Holling 1992). We propose that the resilience of ecological processes, and therefore of the ecosystems they maintain, depends upon the

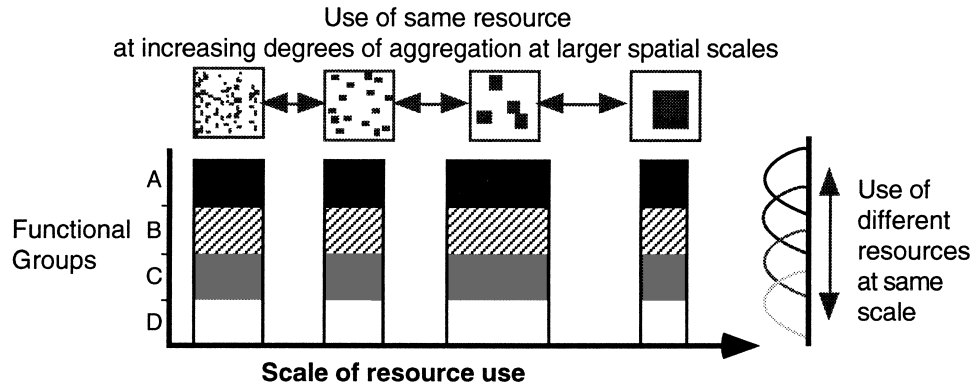


Figure 9. Our hypothesized relationship between the scale of species interactions and their membership in a functional group. Different species use resources at different spatial and temporal scales. Members of a functional group use similar resources, but species that operate at larger scales require those resources to be more aggregated in space than do species that operate at smaller scales. Within scales, the presence of different functional groups provides robust ecological functioning, whereas replication of function across scales reinforces ecological function. The combination of a diversity of ecological function at specific scales and the replication of function across a diversity of scales produces resilient ecological function.

distribution of functional groups within and across scales.

We hypothesize that if species in a 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 (Figure 9). This cross-scale resilience complements a within-scale resilience produced by overlap of ecological function among species of different functional groups that operate at the same scales. Competition among members of a multitaxa functional group may be minimized if group members that use similar resources exploit different ecological scales. Ecological resilience does not derive from redundancy in the traditional engineering sense; rather, it derives from overlapping function within scales and reinforcement of function across scales.

We illustrate these two features of resilience by summarizing the effects of two functional groups on ecosystem dynamics and diversity in two different systems. The first example summarizes the results of field and modeling investigations of the role of avian predators in the dynamics of spruce/fir forests of eastern North America. The second summarizes field and modeling studies of the role of mammalian seed dispersers in the tropical forests of East Africa.

Avian Predation of Insect Defoliators

The combination of within-scale and cross-scale resilience enables an ecological function such as predation of keystone defoliators to be maintained despite sudden variations in resource availability or environmental conditions. It is well known that if a particular insect

becomes more common, species that would not normally exploit it may switch to using it (Murdoch 1969). This occurs as the increasing relative abundance of a resource makes its utilization less costly. We argue that as resources become increasingly aggregated they become available to larger animals that are unable to exploit dispersed resources efficiently. This mechanism introduces strong negative feedback regulation of resource abundance over a wide range of resource densities.

A well-studied example of such a situation is found in the forests of New Brunswick, Canada, where outbreaks of a defoliating insect, spruce budworm (*Choristoneura fumiferana*), periodically kill large areas of mature boreal fir forest. The initiation of these outbreaks is controlled by the interactions between the slowly changing volume of a growing forest susceptible to budworm, the more quickly changing densities and feeding responses of budworm's avian predators, and rapidly changing weather conditions (Morris 1963; Clark and Holling 1979).

Avian predation on budworm regulates the timing of budworm outbreaks by having its largest influence when budworm densities are low and forests stands are young. At least 31 species of birds prey upon budworm (Holling 1988). These bird species can be divided into five distinct body-mass classes or body-mass lumps, separated by gaps in their body-mass distributions (Holling 1992). The existence of budworm predators in these different body-size classes makes the influence of predation robust over a broad range of budworm densities. This robustness emerges not because the predators

exhibit redundant functional forms of predation, but rather because the scales at which predators are effective overlap, spreading their impact over a wide range of densities and spatial aggregations of budworms.

The predatory effectiveness of a bird is largely determined by its body size. The amount of food that a bird can consume—its functional response (Holling 1959)—is a function of its body size, and a bird's search rate is greatly influenced by the scale at which it searches. Kinglets (*Regulus* sp.), chickadees (*Parus* sp.) and warblers (Emberizidae), small birds with an average body mass of about 10 g, concentrate on recognizing prey at the scale of needles or tufts of needles. Medium-sized birds focus their foraging upon branches, while larger birds such as evening grosbeaks (*Coccothraustes vespertinus*, 45 g) react to stand-level concentrations of food such as irruptions of seeds during good mast years or stand-level budworm outbreaks. The movement of birds over a landscape also is scaled to its body size. Larger birds forage over wider areas than do smaller birds. Consequently, both the body mass of birds attracted to budworm and the distance from which they are attracted will increase as the size of local aggregations of budworm increase. A diversity of foraging strategies within and across scales thus provides a strong and highly resilient predation on budworm populations (Holling 1988), particularly at low densities of budworm within stands of young trees (<30 years old).

Members of functional groups maintain and therefore determine the resilience of ecosystems by spreading their influence over a range of scales. When a functional group consists of species that operate at different scales, that group provides cross-scale functional reinforcement that greatly increases the resilience of its function. This interpretation of the partitioning of ecological function suggests that what is often defined as redundancy, is not. The apparent redundancy of similar function replicated at different scales adds resilience to an ecosystem: because disturbances are limited to specific scales, functions that operate at other scales are able to persist. The production of resilience by cross-scale functional diversity can be illustrated in a model of seed dispersal.

Mammalian Seed Dispersal in an African Tropical Forest

In Uganda's Kibale National Park, seed dispersers vary in size from small mice that range over areas of less than a hectare, to chimpanzees that range over tens of square kilometers. In a simple model of seed dispersal, when the area disturbed annually and the

total amount of dispersal are held constant, the population growth rate of mammal-dispersed trees is determined by the distance over which its seeds are dispersed and the size of disturbance. A diverse set of dispersers, functioning at different scales, enables the tree population to persist despite disturbance. If, however, large, long-distance seed dispersers are absent, the tree population declines, especially when large disturbances occur (Figure 10). Mammal-dispersed trees are more aggregated when dispersal is only by small mammals that move the seeds small distances. When disturbance sizes are large, this limited dispersal is unable to maintain populations of mammal-dispersed trees (G. Peterson and C. A. Chapman, unpublished data).

Due to cross-scale functional reinforcement, and the nonlinear fashion in which ecosystem behavior can suddenly flip from one set of mutually reinforcing structures and processes to another, the gradual loss of species in a functional group may initially have little apparent effect, but their loss would nevertheless reduce ecological resilience. This decrease in resilience would be recognized only at specific spatial and temporal scales, and even then may be compensated for within or across scales. However, the ecosystem would become increasingly vulnerable to perturbations that previously could have been absorbed without changes in function or structure.

An indirect consequence of species loss is that it limits the potential number of ways a system can reorganize. Especially troubling is the possibility that the loss of large species, such as moose (Pastor and others 1993) or elephants (Dublin and others 1990), that generate mesoscale ecological structure may also eliminate forms of ecological organization. This may have occurred during the Pleistocene extinctions of megaherbivores (Owen-Smith 1989; Flannery 1994; Zimov and others 1995). These losses appear to be particularly difficult to reverse even with large-scale ecological engineering projects (Flannery 1994).

POTENTIAL TESTS OF CROSS-SCALE RESILIENCE

Our model expands theory relating biodiversity to ecological resilience by incorporating scale. The scaling relationships we propose can be tested through the analysis of empirical data, simulation, and field experimentation.

The proposition that ecological function is distributed across scales can be tested by analyzing the distribution of ecological function of an ecosystems species, and determining whether species belonging

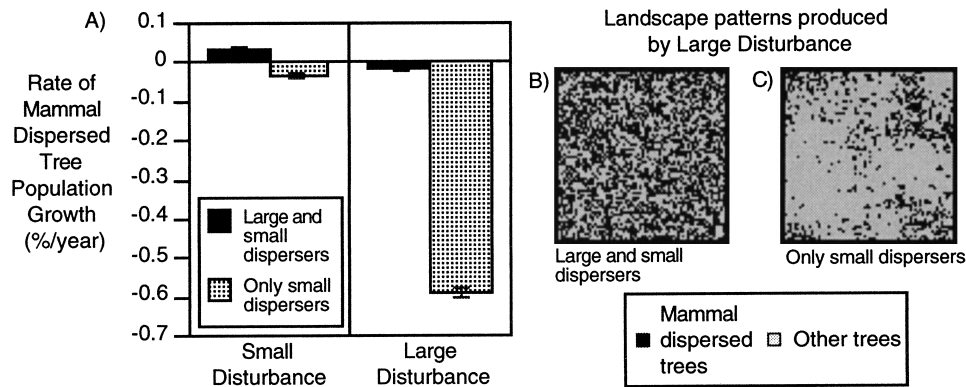


Figure 10. Results from a simple model of forest dynamics and seed dispersal by mammalian frugivores in Kibale National Park, Uganda. (A) Forest disturbance size interacts with the disperser community to determine the success of mammal-dispersed trees. When both large and small seed dispersers are present, the mammal-dispersed trees are resilient to both small and large disturbance events. When large dispersers are absent, mammal-dispersed trees slowly decline after small disturbances, but rapidly decline after large disturbances. Large differences in landscape pattern can be seen after 200 years, when the forest is subjected to large disturbances, between (B) a forest containing both large and small seed dispersers and (C) a forest with only small seed dispersers. The model demonstrates that seed dispersal at a diversity of scales is more resilient to disturbance than is seed dispersal over small scales. The model assumes lottery colonization of disturbed sites (Hubbell 1979) by either mammal-dispersed or other tree species (Chapman and Chapman 1996). Total mammal seed dispersals assumed to be constant. Dispersal range was estimated for large mammals (1010 m for *Cercocebus albigena*, and 1930 m for *Pan troglodytes*) and small mammals (355 m for *Cercopithecus mitus*, 245 m for *Cercopithecus ascanius*, and 30 m for various Rodentia) (C. A. Chapman, unpublished data). The disturbance rate was held constant at 1.5%/year in the model, with only the spatial scale of disturbance varying between the small (0.04 ha) and large (10.24 ha) disturbance regimes.

to the same guild or functional group are dispersed across scales as we predict. The proposition that competition within a scale drives the dispersion of guilds across scales can be tested by determining whether species are more evenly morphologically dispersed within a scale than across scales.

Our model of cross-scale resilience can be tested by creating simulations that use various assemblages of species, divided by function and scale, to assess the resilience of a system to a fluctuating environment. We advocate two approaches, one focusing on the role of scale in function, and the other focusing on the plausibility of our model of ecological organization. The first approach is the one followed in the model of Kibale Forest that was just described. An ecological function that is performed by a number of species at different scales can be modeled, and then this model may be perturbed by disrupting function and species composition to analyze ecological resilience. Our idea that ecological resilience derives from cross-scale functional redundancy resulting from strong within-scale interactions can be tested by simulating an evolving community of organisms that compete for a set of resources. Allowing the resource preference and scale of the organisms to evolve allows one to evaluate our hypothesis that competitive interactions could lead to the distribution of similar func-

tion across scales and functional diversity within scales.

Finally, field experiments can be designed to test the response of species to resource availability at different scales. We hypothesize that limited, nonaggregated resources will be used by species that live at small scales (for example, small birds such as warblers), whereas if resources are aggregated they will be used by larger species. We predict that resource utilization by animals is determined by the density of resources at their foraging scale. Since density is a scale-dependent measure, as resources are increasingly aggregated we expect that they will be used by larger animals.

These tests will provide partial evaluation of our model. To test our theory more fully, and better understand ecological resilience in general, requires long-term and extensive experiments that manipulate species composition and ecological structure at different scales.

CONCLUSIONS

We argue that ecosystems are usefully considered not as fixed objects in space, but as interacting, self-organized sets of processes and structures that vary across scales. Our approach integrates existing models of the relationship between species and

ecological function, and extends these models to incorporate scale. Ecological organization at a specific scale is determined by interactions between species and processes operating within that scale. Competitive interactions are strongest among species that have similar functions and operate at similar scales. These interactions encourage functional diversity within a scale, and the distribution of ecological function across scales, enhancing cross-scale resilience. We suggest that it is possible to identify critical scales of landscape change that may be altered by species extinctions or introductions, or alternatively to identify which species may be affected by changes in landscape structure. Ultimately, we argue that understanding interactions between the scaling of species and scaling of ecological processes should be a central goal of ecology.

Our model of cross-scale resilience has several consequences for ecological policy. The history of resource exploitation and development reveals that ecological crisis and surprises often emerge from unexpected cross-scale interactions (Holling 1986; Regier and Baskerville 1986; Gunderson and others 1995). Management of natural resources often produces high short-term yields and, either purposefully or unintentionally, creates ecosystems that are less variable and diverse over space and time. Management channels ecological productivity into a reduced number of ecological functions and eliminates ecological functions at many scales. This simplification reduces cross-scale resilience, leaving systems increasingly vulnerable to biophysical, economic, or social events that otherwise could have been absorbed—disease, weather anomalies, or market fluctuations. In Jamaica, for example, off-shore fishing reduced the diversity of herbivorous fish species, leading to the replacement of coral reefs by macroalgae (Hughes 1994). Similarly, in New Brunswick, forestry eliminated landscape and age-class diversity, leading to a long period of chronic spruce budworm infestation (Regier and Baskerville 1986). In both of these cases, management reduced the resilience of these ecosystems, leaving the existing people and biota vulnerable to abrupt ecological reorganization. To avoid repeating the ecological management disasters of the past, it is necessary that ecologists understand how the scale-dependent organization of ecosystems and functional reinforcement across scales combine to produce ecological resilience.

We propose that ecological resilience is generated by diverse, but overlapping, function within a scale and by apparently redundant species that operate at different scales. The distribution of functional diversity within and across scales allows regeneration

and renewal to occur following ecological disruption over a wide range of scales. The consequences of species loss may not be immediately visible, but species loss decreases ecological resilience to disturbance or disruption. It produces ecosystems that are more vulnerable to ecological collapse and reduces the variety of possible alternative ecological organizations. Ecological resilience must be understood if humanity is to anticipate and cope with the ecological crises and surprises that accelerating global change will bring.

ACKNOWLEDGMENTS

We appreciate the support of a NASA/EOS Interdisciplinary Scientific Investigations of the Earth Observing Systems grant (NAG 2524), a NASA Terrestrial Ecology grant (NAG 3698), and a NASA Earth System Science Fellowship to G.P. Our manuscript was improved by comments from S. Bigelow, C. Chapman, K. Sieving, F. Putz, T. Allen, T. Frost, and S. Carpenter.

REFERENCES

- Allen CR, Lutz RS, Demarais S. 1995. Red imported fire ant impacts on Northern Bobwhite populations. *Ecol Appl* 5: 632–8.
- Allen TFH, Hoekstra TW. 1992. *Toward a unified ecology*. New York: Columbia University.
- Brown BJ, Ewel JJ. 1987. Herbivory in complex and simple tropical successional ecosystems. *Ecology* 68:108–16.
- Brown JH, Heske EJ. 1990. Control of a desert-grassland by a keystone rodent guild. *Science* 250:1705–7.
- Carpenter SR, Leavitt PR. 1991. Temporal variation in paleolimnological record arising from a trophic cascade. *Ecology* 72: 277–85.
- Chapman CA, Chapman LJ. 1996. Frugivory and the fate of dispersed and non-dispersed seeds of 6 African tree species. *J Trop Ecol* 12:491–504.
- Clark GL. 1954. *Elements of ecology*. New York: John Wiley.
- Clark WC. 1985. Scales of climate impacts. *Climatic Change* 7:5–27.
- Clark WC, Holling CS. 1979. Process models, equilibrium structures, and population dynamics: on the formulation and testing of realistic theory in ecology. *Popul Ecol* 25:29–52.
- D'Antonio CM, Vitousek PM. 1992. Biological invasions by exotic grasses, the grass/fire cycle and global change. *Annu Rev Ecol Syst* 23:63–87.
- 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 1964]. Cambridge (MA): Harvard University.
- Di Castri F, Mooney HA. 1973. *Mediterranean type ecosystems: origins and structure*. New York: Springer-Verlag.
- Diemer JE. 1986. The ecology and management of the gopher tortoise in the southeastern United States. *Herpetologica* 42: 125–33.
- Dublin HT, Sinclair ARE, McGlade J. 1990. Elephants and fire as causes of multiple stable states in the Serengeti-Mara woodlands. *J Anim Ecol* 59:1147–64.

- Ehrlich PR, Ehrlich AH. 1981. Extinction: the causes and consequences of the disappearance of species. New York: Random House.
- Estes JA, Duggins DO. 1995. Sea otters and kelp forests in Alaska: generality and variation in a community ecological paradigm. *Ecol Monogr* 65:75–100.
- Ewel JJ, Bigelow SW. 1996. Plant life-forms and tropical ecosystem functioning. In: Orians GH, Dirzo R, Cushman JH, editors. Biodiversity and ecosystem processes in tropical forests. Heidelberg: Springer-Verlag, p 101–26.
- Ewel JJ, Mazzarino MJ, Berrish CW. 1991. Tropical soil fertility changes under monocultures and successional communities of different structure. *Ecol Appl* 1:289–302.
- Flannery T. 1994. The future eaters: an ecological history of the Australasian lands and people. New York: George Braziller.
- Fleming TH, Sosa VJ. 1994. Effects of nectarivorous and frugivorous mammals on reproductive success of plants. *J Mammal* 75:845–51.
- Frank DA, McNaughton SJ. 1991. Stability increases with diversity in plant communities: empirical evidence from the 1988 Yellowstone drought. *Oikos* 62:360–62.
- Frost TM, Carpenter SR, Ives AR, Kratz TK. 1995. Species compensation and complementarity in ecosystem function. In: Jones CG, Lawton JH, editors. Linking species and ecosystems. New York: Chapman and Hall. p 224–39.
- Grinnell J. 1917. The niche relations of the California thrashers. *Auk* 34:427–33.
- Gunderson L, Holling C, Light S. 1995. Barriers and bridges to the renewal of ecosystems and institutions. New York: Columbia University.
- Holling CS. 1959. The components of predation as revealed by a study of small mammal predation of the European pine sawfly. *Can Entomol* 91:293–320.
- Holling CS. 1973. Resilience and stability of ecological systems. *Annu Rev Ecol Syst* 4:1–23.
- Holling CS. 1986. The resilience of ecosystems: local surprise and global change. In: Clark WC, Munn RE, editors. Sustainable development of the biosphere. Cambridge (UK): Cambridge University. p 292–317.
- Holling CS. 1988. Temperate forest insect outbreaks, tropical deforestation and migratory birds. *Mem Entomol Soc Can* 146:21–32.
- Holling CS. 1992. Cross-scale morphology, geometry and dynamics of ecosystems. *Ecol Monogr* 62:447–502.
- Holling CS. 1996. Engineering resilience versus ecological resilience. In: Schulze P, editor. Engineering within ecological constraints. Washington (DC): National Academy, p 31–44.
- Holling CS, Schindler DW, Walker BW, Roughgarden J. 1995. Biodiversity in the functioning of ecosystems: an ecological synthesis. In: Perrings C, Mäler K-G, Folke C, Holling CS, Jansson B-O, editors. Biodiversity loss: economic and ecological issues. New York: Cambridge University. p 44–83.
- Hubbell SP. 1979. Tree dispersion, abundance, and diversity in a tropical dry forest. *Science* 203:1299–309.
- Hughes TP. 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265:1547–51.
- Hutchinson GE. 1957. Concluding remarks. *Cold Spring Harbor Symp Quant Biol* 22:415–27.
- Jones CG, Lawton JH, Shachak M. 1994. Organisms as ecosystem engineers. *Oikos* 69:373–86.
- Kalin Arroyo MT, Zedler PH, Fox MD. 1995. Ecology and biogeography of Mediterranean ecosystems in Chile, California, and Australia. New York: Springer-Verlag.
- Kauffman SA. 1993. Origins of order: self-organization and selection in evolution. Oxford: Oxford University.
- Kitchell JF, Carpenter SR. 1993. Synthesis and new directions. In: Carpenter SR, Kitchell JF, editors. The trophic cascade in lakes. New York: Cambridge University. p 332–50.
- Körner C. 1996. Scaling from species to vegetation: the usefulness of functional groups. In: Schulze E-D, Mooney HA, editors. Biodiversity and ecosystem function. New York: Springer-Verlag. p 117–40.
- Krummel JR, Gardner RH, Sugihara G, O'Neill RV, Coleman PR. 1987. Landscape patterns in a disturbed environment. *Oikos* 48:321–24.
- Lawton JH. 1994. What do species do in ecosystems? *Oikos* 71:367–74.
- Levin SA. 1992. The problem of pattern and scale in ecology. *Ecology* 73:1943–67.
- MacArthur RH. 1955. Fluctuations of animal populations and a measure of community stability. *Ecology* 36:533–6.
- Macdonald D. 1985. The encyclopedia of mammals. New York: Facts On File.
- May RM. 1973. Stability and complexity in model ecosystems. Princeton (NJ): Princeton University.
- McNeely JA, Gadgil M, Leveque C, Padoch C, Redford K. 1995. Human influences on biodiversity. In: Heywood V, editor. Global biodiversity assessment. Cambridge (UK): Cambridge University. p 711–822.
- Morris RF. 1963. The dynamics of epidemic spruce budworm populations. *Mem Entomol Soc Can* 31:1–322.
- Morse DR, Lawton JH, Dodson MM. 1985. Fractal dimension of vegetation and the distribution of arthropod body lengths. *Nature* 314:731–3.
- Murdoch WW. 1969. Switching in general predators: experiments on predator specificity and stability of prey populations. *Ecol Monogr* 39:335–54.
- Naeem S, Thompson LJ, Lawler SP, Lawton JH, Woodfin RM. 1994. Declining biodiversity can alter the performance of ecosystems. *Nature* 368:734–7.
- Naiman RJ, Pinay G, Johnston CA, Pastor J. 1994. Beaver influences on the long-term biogeochemical characteristics of boreal forest drainage networks. *Ecology* 75:905–21.
- Nowak RM, Paradiso JL. 1983. Walker's mammals of the world. Baltimore: John Hopkins University.
- O'Neill R, Turner SJ, Cullinam VI, Coffin DP, Cook T, Conley W, Brunt J, Thomas JM, Conley MR, Gosz J. 1991. Multiple landscape scales: an intersite comparison. *Landscape Ecol* 5:137–44.
- Orr MR, Seike SH, Benson WW, Gilbert LE. 1995. Flies suppress fire ants. *Nature* 373:292–3.
- Owen-Smith N. 1989. Megafaunal extinctions: the conservation message from 11,000 years B.C. *Conserv Biol* 3:405–11.
- Paine RT. 1969. A note on trophic complexity and community stability. *Am Nat* 103:91–3.
- Pastor J, Dewey B, Naiman RJ, McInnes PF, Cohen Y. 1993. Moose browsing and soil fertility in the boreal forests of Isle Royale National Park. *Ecology* 74:467–80.
- Peters RH. 1983. The ecological implications of body size. Cambridge (UK): Cambridge University.

- Pimm SL. 1984. The complexity and stability of ecosystems. *Nature* 307:321–6.
- Porter SD, Savignano DA. 1990. Invasion of polygyne fire ants decimates native ants and disrupts arthropod community. *Ecology* 71:2095–116.
- Power ME, Tilman D, Estes JA, Menge BA, Bond WJ, Mills LS, Daily G, Castilla JC, Lubchenco J, Paine R. 1996. Challenges in the quest for keystones. *BioScience* 46:609–20.
- Prins HHT, Van der Jeud HP. 1993. Herbivore population crashes and woodland structure in East Africa. *J Ecol* 81:305–14.
- Regier HA, Baskerville GL. 1986. Sustainable redevelopment of regional ecosystems degraded by exploitive development. In: Munn WC, Munn RE, editors. *Sustainable development of the biosphere*. Cambridge (MA): Cambridge University. p 75–101.
- Schindler DW. 1990. Experimental perturbations of whole lakes as tests of hypotheses concerning ecosystem structure and function. *Oikos* 57:25–41.
- Sugihara G. 1980. Minimal community structure: an explanation for species abundance patterns. *Am Nat* 116:770–87.
- Terborgh J. 1986. Keystone plant resources in the tropical forest. In: Soulé ME, editor. *Conservation biology: the science of scarcity and diversity*. Sunderland (UK): Sinauer. p 330–44.
- Tilman D. 1996. Biodiversity: population versus ecosystem stability. *Ecology* 77:350–63.
- Tilman D, Wedin D, Knops J. 1996. Productivity and sustainability influenced by biodiversity in grasslands ecosystems. *Nature* 379:718–20.
- Turner BL, Clark WC, Kates RW, Richards JF, Mathews JT, Meyer WB. 1993. *The earth as transformed by human action*. New York: Cambridge University.
- Vitousek PM. 1990. Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. *Oikos* 57:7–13.
- Walker B. 1992. Biological diversity and ecological redundancy. *Conserv Biol* 6:18–23.
- Walker B. 1995. Conserving biological diversity through ecosystem resilience. *Conserv Biol* 9:747–52.
- Zimov SA, Chuprynin VI, Oreshko AP, Chapin IFS, Reynolds JF, Chapin MC. 1995. Steppe-tundra transition: a herbivore-driven biome shift at the end of the Pleistocene. *Am Nat* 146:765–94.