

ECOLOGICAL RESILIENCE—IN THEORY AND APPLICATION

Lance H. Gunderson

Dept. of Environmental Studies, Emory University, Atlanta, Georgia 30322;
e-mail: lgunder@emory.edu

Key Words resilience, stability, stable states, biodiversity, adaptive management

■ **Abstract** In 1973, C. S. Holling introduced the word resilience into the ecological literature as a way of helping to understand the non-linear dynamics observed in ecosystems. Ecological resilience was defined as the amount of disturbance that an ecosystem could withstand without changing self-organized processes and structures (defined as alternative stable states). Other authors consider resilience as a return time to a stable state following a perturbation. A new term, adaptive capacity, is introduced to describe the processes that modify ecological resilience. Two definitions recognize the presence of multiple stable states (or stability domains), and hence resilience is the property that mediates transition among these states. Transitions among stable states have been described for many ecosystems, including semi-arid rangelands, lakes, coral reefs, and forests. In these systems, ecological resilience is maintained by keystone structuring processes across a number of scales, sources of renewal and reformation, and functional biodiversity. In practice, maintaining a capacity for renewal in a dynamic environment provides an ecological buffer that protects the system from the failure of management actions that are taken based upon incomplete understanding, and it allows managers to affordably learn and change.

INTRODUCTION

It has been almost three decades since the term resilience was introduced to the literature by the theoretical ecologist C. S. Holling (22). Since that time, multiple meanings of the concept have appeared (15, 40). Since most management actions are based upon some type of theory, these multiple meanings of resilience can lead to very different sets of policies and actions.

This review is divided into three parts. The first section reviews concepts and multiple meanings of resilience as they have appeared in the literature. That section reviews examples of modeling and field experiments that enrich our understanding of ecological change. The second section includes an assessment of how resilience is related to other key ecosystem properties. The review

concludes with a section on how ecological resilience is key to management of complex systems of people and nature.

Resilience, Stability and Adaptive Capacity

Resilience of a system has been defined in the ecological literature in two different ways, each reflecting different aspects of stability. Holling (22) first emphasized these different aspects of stability to draw attention to the distinctions between efficiency and persistence, between constancy and change, and between predictability and unpredictability. Holling (22) characterized stability as persistence of a system near or close to an equilibrium state. By contrast, resilience was introduced to indicate behavior of dynamic systems far from equilibrium, by defining resilience as the amount of disturbance that a system can absorb without changing state. The multiple meanings of resilience are related to assumptions about the presence of either single or multiple equilibria in a system (26), as described in the following sections.

Resilience and Global Equilibrium Many authors define the term resilience as the time required for a system to return to an equilibrium or steady-state following a perturbation (28, 39, 40, 44, 51). Implicit in this definition is that the system exists near a single or global equilibrium condition. Hence the measure of resilience is how far the system has moved from that equilibrium (in time) and how quickly it returns (35).

Other authors (22, 26, 35) consider return times as a measure of stability. Holling (26) described the return time definition of resilience as ‘engineering resilience.’ The return time definition arises from traditions of engineering, where the motive is to design systems with a single operating objective (9, 41, 54). On one hand, that makes the mathematics tractable, and on the other, it accommodates an engineer’s goal to develop optimal designs. There is an implicit assumption of global stability—i.e. there is only one equilibrium or steady state or, if other operating states exist, they should be avoided by applying safeguards. Other fields that use the term resilience, such as physics, control system design, or material engineering, all use this definition.

Resilience and Multiple Equilibrium The second type of resilience emphasizes conditions far from any steady state condition, where instabilities can flip a system into another regime of behavior—i.e. to another stability domain (22). In this case, resilience is measured by the magnitude of disturbance that can be absorbed before the system redefines its structure by changing the variables and processes that control behavior. This has been dubbed ecological resilience in contrast to engineering resilience (22, 57).

One key distinction between these two types of resilience lies in assumptions regarding the existence of multiple stable states. If it is assumed that only one stable state exists or can be designed to so exist, then the only possible definition and

measures for resilience are near equilibrium ones—such as characteristic return time as defined above. The concept of ecological resilience presumes the existence of multiple stability domains and the tolerance of the system to perturbations that facilitate transitions among stable states. Hence, ecological resilience refers to the width or limit of a stability domain and is defined by the magnitude of disturbance that a system can absorb before it changes stable states (22, 35).

The presence of multiple stable states and transitions among them have been described in a range of ecological systems. These include transitions from grass-dominated to woody-dominated semi-arid rangelands in Zimbabwe (60) and Australia (36, 59). In these cases the alternative states are described by dominant plant forms, and the disturbance is grazing pressure (59). Other examples include transitions from clear lakes to turbid ones (3, 46); alternative states are indicated by dominant assemblages of primary producers in the water or rooted macrophytes and disturbances include physical variables such as light and temperature. Alternative states are also described in populations levels created by interactions among populations (10, 11, 48, 62).

Carpenter et al. (3, 5) and Scheffer (46) have used the heuristic of a ball and a cup to highlight differences between these types of resilience. The ball represents the system state and the cup represents the stability domain (Figure 1). An equilibrium exists when the ball sits at the bottom of the cup and disturbances shake the marble to a transient position within the cup. Engineering resilience refers to characteristics of the shape of the cup—the slope of the sides dictate the return time of the ball to the bottom. Ecological resilience suggests that more than one cup exists, and resilience is defined as the width at the top of the cup. Implicit in both of these definitions is the assumption that resilience is a static property of

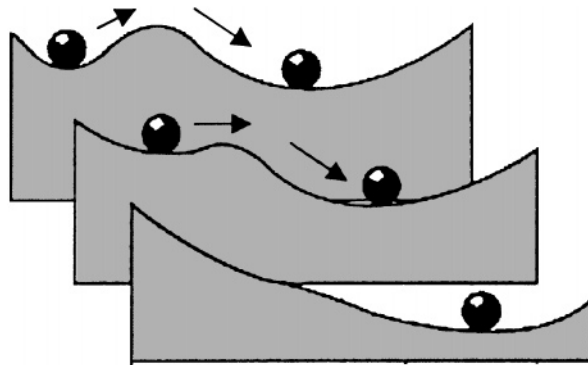


Figure 1 Ball and cup heuristic of system stability. Valleys represent stability domains, balls represent the system, and arrows represent disturbances. Engineering resilience is determined by the slopes in the stability landscapes, whereas ecological resilience is described as the width. Adaptive capacity refers to the ability of the system to remain in a stability domain, as the shape of the domain changes (as shown by the three slices or landscapes).

systems. That is, once defined, the shape of the cup remains fixed over time. But recent work indicates that stability domains are dynamic and variable.

Adaptive Capacity Many of the manifestations of human-induced state changes in ecosystems result from alteration of the key variables that influence the underlying stability domains. The key variables that configure these stability domains change at relatively slow rates (without human intervention). Examples include nutrients in wetlands and lakes (5, 46), species compositions in rangelands (56, 59) or trophic relationships (4). Using the ball in cup heuristic, the shape of the cup is subject to change, altering both stability (return time) and resilience (width of stability domain). Scheffer et al. (46) depict this as multiple stability landscapes (three slices in Figure 1). The property of an ecosystem that describes this change in stability landscapes and resilience is referred to as adaptive capacity (19).

Ecosystem Dynamics and Multiple Stable States

The previous section outlined a contrast among three views of resilience. All describe aspects of change in ecosystems and the degree of that change. But much of the literature over the last 30 years has addressed whether multiple stable states exist in ecosystems, and if so what mediates transition among them.

There is a growing body of literature that documents transitions among stability domains in a variety of ecosystems (4, 21, 35, 38, 59, 60). Many of those systems are influenced by human activities, which has led to a confounding problem around ecological resilience. Some authors (49) suggest that alternative stable states do not exist in systems untouched by humans, while others (10, 47) indicate that these are and have been part of the dynamics of systems with or without humans. Without treading on the question of whether people are or are not natural parts of ecosystems, three examples are presented suggesting that people do change the resilience of system. One involves lake systems, another wetlands, and the other semi-arid rangeland. In each example, the alternative states are discussed, as are the mechanisms that result in the transitions and those processes that contribute or detract from ecological resilience.

Shallow Lakes Limnologists have long recognized the existence of qualitative differences in the state of lakes. In shallow lakes, two alternative states can be characterized as (a) clear water and rooted macrophytes or (b) turbid water with planktonic algae (45, 46). Each of these states is relatively stable due to interactions among nutrients, the types of vegetation, and light penetration (Figure 1). In the clear water state, sediments, and nutrient cycling are stabilized by rooted vegetation (45, 46). The turbid state persists when wind-driven mixing resuspends sediments. The sediments and phytoplankton in the water column decrease light penetration, thereby curtailing establishment of benthic vegetation (45, 46).

Transitions between these two states can be mediated by trophic relationships. Decreasing stocks of planktivorous fish can create a shift from a turbid to a clear

lake. As predation on herbivorous zooplankton decreases, their populations increase, leading to an increase in herbivory and a reduction in phytoplankton biomass. Increased light penetration and available nutrients then lead to establishment of rooted vegetation (45). In the other direction, shifts from the clear to turbid state can result from overgrazing of benthic vegetation by fish or waterfowl (45). The shift between stable states is hysteretic—the disturbances that influence change in one direction do not have similar impacts in the opposite direction (45).

Wetlands Nutrient enrichment in the freshwater marshes of the Everglades caused the loss of resilience. The Everglades is an oligotrophic wetland, limited primarily by phosphorus (50). For the past 5000 years or so, the ecosystem effectively self-organized around this low nutrient status, pulsed by annual wet/dry cycles and by decadal recycling associated with fires (17). The resulting landscape mosaic was comprised of sawgrass marshes and wet prairies interspersed with small tree islands (7, 33, 50).

In the late 1970s and early 1980s, large-scale vegetation changes were noticed in the regions downstream from the Everglades agricultural area. Sawgrass marshes and wet prairies had become dominated by a single species—cattail (8). The conversion was attributed to a slow increase in the concentration of soil phosphorus, and a disturbance, such as fire, drought or freeze.

Key ecosystem processes and structures occur at various spatial and temporal scales. The vegetation structures represent the most rapidly changing variables, with plant turnover times on the order of 5 to 10 years (8). Fires operate on return frequencies of 10 to 20 y (20, 53). Other disturbances such as freezes and droughts occur on multiple decade return times (20, 53). The soil phosphorus concentrations are the slowest of the variables, with turnover times on the order of centuries (8).

The resilience of the freshwater marshes is related to the soil nutrient content. The alternative stability domains are characterized by the dominant plant species; sawgrass or wet prairie communities dominate on sites with low nutrients, and cattail dominates on sites with higher soil phosphorus concentrations. Following a disturbance, it is the soil phosphorus level that determines which of these species dominate.

Semi-arid Rangelands Savanna rangelands are found in climatic regimes of hot, rainy summers and mild, dry winters. These systems have high productivity and support a diverse assemblage of perennial and annual grasses and few woody plants. Key biophysical processes in these systems include variation in rainfall, fires, and grazing. Walker (59) and Ludwig et al. (36) identify alternative stable states as either woody/grass coverage, or woody thicket. The transition between these states is mediated by grazing pressures that remove either drought-tolerant or perennial grasses (36, 59). If grazing pressures are high, the perennial grass abundance is decreased, leading to an increased abundance of woody plants. Once

the woody community is established, fires burn less frequently (if the thickets burn at all) and the woody community persists for decades. Walker and Ludwig et al (36, 59) suggest that the woody/grass assemblage can be reestablished, either through collapse of matured woody plants or through manipulation of fire and drainage processes (36). The role of functional biodiversity in contributing to the ecological resilience is discussed in the next section.

Resilience in Ecosystems—Patterns and Process

Resilience is an emergent property of ecosystems and is related to self-organized behavior of those ecosystems over time. In this sense, self-organization is the interaction between structure and process that leads to system development, regardless of initial conditions. Self-organization also implies that for certain scale ranges, structure and process are not easily separable and interact in an organic way to generate emergent patterns. The adaptive cycle or four-phase model of Holling (24, 25) describes how patterns and processes change over time in many ecosystems, especially those with disturbance regimes.

Holling (24, 25) describes ecosystem succession in the first two phases of the cycle. The exploitative phase is characterized by rapid colonization of recently disturbed areas. This phase gives way to a conservation phase, as material and energy are accumulated and stored. The exploitative phase is characterized by rapid growth in an arena of scramble competition, while the species that dominate in the later phase tend to have slower growth rates and survive in an arena of exclusive competition. The mature or conservative phase is followed by a phase when a disturbance influences the structure that has accumulated in previous phases. This phase is called creative destruction. Disturbance agents such as forest fires, insect pests, or intense pulses of grazing suddenly release accumulated ecological capital. The system enters the fourth phase, or reorganization. The system passes through the reorganization phase and then enters another exploitative phase.

Resilience is related to the phase of Holling's adaptive cycle. During the exploitation phase, ecological resilience is high—the system can absorb a wide range of disturbances. When the system is reaching the limits to its conservative growth, it becomes increasingly brittle and its accumulated capital is ready to fuel rapid structural changes. The system is very stable, but that stability is local and narrow. A small disturbance can push it out of that stable domain into catastrophe. The nature and timing of the collapse-initiating disturbance determines, within some bounds, the future trajectory of the system. Therefore this brittle state presents the opportunity for a change at a small scale to cascade rapidly through the over-connected system, bringing about its rapid transformation. Either internal conditions or external events can initiate collapse, but typically it is internally induced brittleness (because of high connectivity and accumulated capital) that sets the conditions for collapse. The system becomes “an accident waiting to happen” (24)

During the reorganization phase, a system becomes most vulnerable to changing stability domains. There is little local regulation and stability, so that the system can easily be moved from one state to another. Resources for growth are present, but they are disconnected from the processes that facilitate and control growth. In such a weakly connected state, random seedings can generate multiple trajectories, which then establish the exploitative path along which the system develops. The previous system pattern may reassert itself, or the system may reorganize itself into a novel structure.

Resilience and Biodiversity

The relationship between biological diversity and ecological stability has been an ongoing discussion in ecology (37, 51, 52). Tilman (51, 52) has demonstrated that, over ecologically brief periods, an increase in species number increases the efficiency and stability of some ecosystem functions, but decreases the stability of the populations of the species. While this work is important and interesting, it focuses upon how an ecosystem behaves near some steady state. The role of ecological diversity over a much broader range of variations and especially the relationship between diversity and resilience have only been recently addressed (31, 43, 55, 56).

When grappling with this broader relationship between diversity and resilience Walker (58) developed a driver and passengers analogy. Walker proposed that functional groups of species can be divided into 'drivers' and 'passengers.' Drivers are keystone species that control the future of an ecosystem, while the passengers live in but do not alter significantly this ecosystem. However, as conditions change, endogenously or exogenously, species shift roles. In this model, removing passengers has little effect, but removing drivers can have a large impact. Ecological resilience resides both in the diversity of the drivers, and in the number of passengers who are potential drivers. Walker has more recently shown how the diversity of functional groups also maintains the resilience of ecosystem structure and function (56). Such diversity provides robustness to ecosystem functions and resilience to the system behavior. Moreover, this seems the way many biological processes are regulated—overlapping influences by multiple processes, each one of which is inefficient in its individual effect but together operating in a robust manner.

Recent models indicate that biodiversity provides a cross-scale resilience (43). Species combine to form an overlapping set of reinforcing influences that help spread risks and benefits widely to retain overall consistency in performance independent of wide fluctuations in the individual species. Because of the robustness of this redundancy within functional groups, and the non-linear way behavior suddenly flips from one pattern to another and one set of controls to another, gradual loss of species involved in controlling structure initially would have little perceived effect over a wide range of loss of species. As loss of those species continued, different behavior would emerge more and more frequently in more and

more places. To the observer, it would appear as if only the few remaining species were critical when in fact all add to the resilience. Although behavior would change suddenly, resilience measured as the size of stability domains (22) would gradually contract. The system, in gradually losing resilience, would become increasingly vulnerable to perturbations that earlier could be absorbed without change in function, pattern, and controls.

As humans struggle to manage these key ecosystem attributes of function and pattern, there is a growing recognition of the importance of ecological resilience. Ecological resilience is recognized as the property that allows for managers and other actors to learn from and adapt to the unpredictability inherent in these ecosystems. This idea is developed in the final section in which the interaction between ecosystem management and resilience is discussed.

Managing for Resilience in Policy and Practice

A growing number of case histories of large-scale, bureaucratic resource systems (16, 29) and traditional management systems (2) demonstrate patterns of surprise, crises, and reformation. Shifts between alternative conditions are usually signaled as a resource crisis. That is, a crisis occurs when an ecosystem behaves in a surprising manner or when observations of a system are qualitatively different from expectations of that system. Such surprises occur when variation in broad scale processes (such as a hurricane or extreme drought), intersects with internal changes in an ecosystem due to human alteration. Examples of human induced shifts include woody invasion of semi-arid rangelands (59, 60) or algae blooms in freshwater lakes (15) as described earlier. These shifts in stability domains are chronicled as resource crisis. Understanding how and why people chose to react is key to managing for resilience.

When faced with shifting stability domains and resulting crises, management options fall into one of three general classes of response. The first is to do nothing and wait to see if the system will return to some acceptable state. One consequence of this option is that the social benefits of the desired state are foregone while waiting to see if the system will return to the desired state. The second option is to actively manage the system and try to return the system to a desirable stability domain. The third option is to admit that the system is irreversibly changed, and hence the only strategy is to adapt to the new, altered system.

The ecological resilience of the system provides some measure of ease of transition among states and is a key consideration regarding how management actions should or can be structured. This theme is developed in the following two sections, one on how building understanding provides resilience and the second on how to maintain or restore resilience in managed systems.

Uncertainty, Understanding, and Resilience

During most of the 20th century, the goal of technologically-based resource management has been to control the external sources of variability in order to seek

a single goal, such as maximization of yield (trees, fish) or controlling levels of pollution. This 'command and control' approach focuses on controlling a target variable, but then slowly changes other parts of the system (27). That is, isolating and controlling the variables of interest (i.e. assuming that the uncertainty of nature can be replaced with the certainty of control) has resulted in erosion of resilience. The manifestation of that erosion is the pattern of policy crisis and reformation as mentioned above and elsewhere (16). Much of subsidized agriculture, where incentives are set up to deal with changes in markets and costs, as well as variability from nature, falls into this category (6).

Much of the 'command and control' resource management that leads to loss of ecological resilience is based upon the presumed predictability of complex ecological systems and driven by the myth that disciplinary science will resolve most uncertainties of management. But there has been a growing sense that traditional scientific approaches are not working, and, indeed, make the problem worse (34). One reason why rigid scientific and technological approaches fail is because they presume a system near equilibrium and a constancy of relationships. In this case, uncertainties arise not from errors in tools or models but from lack of appropriate information for the models. Another reason for failure is that few approaches account for inherent complex relationships among variables that lead to inherent unpredictabilities in ecological systems. Scientific disciplines tend to break the management issue into parts for analysis, and have historically generated piecemeal sets of policies as solutions (16, 61). Yet, recent models by Carpenter and others (5) that integrate ecologic, economic, and social dynamics around a flipping lake system indicate that ecosystem resilience must be continually probed.

Different views of science can contribute to a loss of ecological resilience. One mode of science focuses on parts of the system and deals with experiments that narrow uncertainty to the point of acceptance by peers; it is conservative and unambiguous by being incomplete and fragmentary. The other view is integrative and holistic, searching for simple structures and relationships that explain much of nature's complexity. This view provides the underpinnings for an approach to dealing with resource issues called adaptive management, which assumes surprises are inevitable, that knowledge will always be incomplete, and that human interaction with ecosystems will always be evolving (16, 23, 30, 61).

Adaptive management is an integrated, multidisciplinary method for natural resources management (23, 61). It is adaptive because it acknowledges that the natural resources being managed will always change, so humans must respond by adjusting and conforming as situations change. There is and always will be uncertainty and unpredictability in managed ecosystems, both as humans experience new situations and as these systems change because of management. Surprises are inevitable. Active learning is the way in which this uncertainty is winnowed. Adaptive management acknowledges that policies must satisfy social objectives but also must be continually modified and be flexible for adaptation to these surprises (16, 23, 30, 61). Adaptive management therefore views policies as hypotheses—that is; most policies are really questions masquerading as answers.

Since policies are questions, then management actions become treatments in the experimental sense. The process of adaptive management includes highlighting uncertainties, developing and evaluating hypotheses around a set of desired system outcomes, and structuring actions to evaluate or 'test' these ideas (16, 23, 30, 61). Although learning occurs regardless of the management approach, adaptive management is structured to make that learning more efficient. Trial and error is a default model for learning while managing; people are going to learn and adapt by the simple process of experience. Just as the scientific method promotes efficient learning through articulating hypotheses and testing those hypotheses, adaptive management proposes a similar approach to resolving uncertainties of resource issues.

A unique property of human systems in response to uncertainty is the generation of novelty. Novelty is key to dealing with surprises or crises. Humans are unique in that they create novelty that transforms the future over multiple decades to centuries. Natural evolutionary processes cause the same magnitude of transformation over time spans of millennia. Examples are the creation of new types and arrangements of management institutions after resource crises in the Everglades or Columbia River Basin (30, 32).

Restoration and Maintenance of Resilience

At least two aspects of managing for resilience can be identified; strategies that people employ in order to restore or maintain ecological resilience and properties that contribute to resilience in human organizations. In order to add resilience to managed systems, at least three strategies are employed: increasing the buffering capacity of the system, managing for processes at multiple scales, and nurturing sources of renewal (18). Most activities for buffering tend to address the engineering type of resilience, that is, mitigating the effects of unwanted variation in the system in order to shorten the return time to a desired equilibrium. In many agricultural systems, resistance to change is dealt with by a combination of barriers to outside forces (tariffs, fences, etc.) and internal adjustments such as water or cost control mechanisms (6). Water resource systems can be designed for resilience by increasing the buffering capacity or robustness through redundancy of structures (and flexibility of operations) rather than fewer, larger structures and rigid operational schemes (12). Folke, Berkes and collaborators (1, 2, 13, 14) suggest that traditional approaches (they define as traditional ecological knowledge) buffer systems by allowing smaller scale perturbations to enter the system, thereby lessening the impact of unpredictable or large perturbations. One such example is that the Cree fisherman use a mixed-size mesh net to harvest multiple ages classes, thereby preserving an age class structure that mimics a natural population (1). This age structure helps buffer widely varying reproductive success.

Resource systems that have been sustained over long time periods increase resilience by managing processes at multiple scales. Returning to the example of the Cree in northern Canada, Berkes (1) argues that multiple spatial domains are part

of their fishing practices and multiple temporal domains in their hunting practices. While fishing within a season, the Cree monitor catch per unit effort. When they notice the rate dropping, they immediately move to different areas and do not fish those areas for a number of years. Over longer time frames, they rotate fishing effort to more remote sites (1). Similarly, they retain information through belief systems, e.g. that caribou will return for hunting at annual and decadal cycles or periods. Similarly, the Everglades water management system has changed to manage across multiple time frames. In the mid 1970s water deliveries to Everglades Park were based upon a seasonally variable, but annually constant volume of water. This system was changed in the mid 1980s to a statistical formulation that incorporated interannual variation into the volumetric calculation (32).

Folke and Berkes (2) argue that local communities and institutions co-evolve by trial and error at time scales in tune to the key sets of processes that structure ecosystems within which the groups are embedded. Many of the crises chronicled by Gunderson et al. (16) were created by an inherent focus on one scale for management, and reformations of learning recognized the multiple scales by which the ecosystem was functioning. Institutions (defined broadly as the set of rules and structures that allow people to organize for collective action) can add resilience to a system. Young and McCay (63) argue that adding flexibility and renewable structure to property rights regimes will increase ecosystem resilience. They indicate that market-based property right schemes (licenses, leases, quotas or permits) should include termination schemes, with stable arrangements (entitlements, obligations) in the interim years. These principles complement Ostrom's (42) findings that successful institutions allow stakeholders to participate in changing rules that affect them.

A few key institutional ingredients appear necessary to facilitate the movement of systems out of crisis through a reformation. In the review of management histories in western systems (16) these included functions of learning, engagement and trust. Kai Lee (30) calls this "social learning", by combining adaptive management frameworks within a framework of collective choice. Other authors (2, 14) describe this as social capital; comprised of the institutions, traditional knowledge, and common property systems that are the mechanisms by which people link to their environment.

SUMMARY AND CONCLUSIONS

Resilience in engineering systems is defined as a return time to a single, global equilibrium. Resilience in ecological systems is the amount of disturbance that a system can absorb without changing stability domains. Adaptive capacity is described as system robustness to changes in resilience. In ecological systems, resilience lies in the requisite variety of functional groups and the accumulated capital that provide sources for recovery. Resilience within a system is generated by destroying and renewing systems at smaller, faster scales. Ecological resilience is reestablished by the processes that contribute to system 'memory' of those involved

in regeneration and renewal that connect that system's present to its past and it to its neighbors.

Many human activities shrink ecological resilience by attempting to control variability in key ecosystem processes. This loss of resilience is often accompanied by a change in system state, signaled as a resource crisis. When a system has shifted into an undesirable stability domain, the management alternatives are to restore the system to a desirable domain, allow the system to return to a desirable domain by itself, or adapt to the changed system because changes are irreversible.

Resilience is maintained by focusing on keystone structuring processes that cross scales, on sources of renewal and reformation, and on multiple sources of capital and skills. No single mechanism can guarantee maintenance of resilience. Strategies that address requisite variety of purposes and concentrate on renewal contribute to resilience. Institutions should focus on learning, and understanding of key cross-scale interactions. Learning, trust and engagement are key components of social resilience. Social learning is facilitated by recognition of uncertainties, monitoring and evaluation by stakeholders. The most difficult issues to deal with are those whose consequences will be realized 10 to 50 years in the future over broad scales.

ACKNOWLEDGMENTS

This work was supported by a grant from the John D. and Catherine T. MacArthur Foundation, and is a contribution of the Resilience Network, a Joint Program of the University of Florida and Beijer International Institute for Ecological Economics. As always, C.S. Holling continues to provide inspiration and novelty in clearly articulating his imaginative theories. Brian Walker, Steve Carpenter, Martin Scheffer have been most helpful in educating me as to the complex dynamics of ecosystems. This work has benefited from discussions with Garry Peterson and Rusty P. Pritchard, Jr.

Visit the Annual Reviews home page at www.AnnualReviews.org

LITERATURE CITED

- Berkes F. 1995. Indigenous knowledge and resource management systems: a native Canadian case study from James Bay. In *Property Rights in a Social and Ecological Context*, ed. S Hanna, M Munasinghe, pp. 35–49. Washington, DC: Beijer Int. Inst. & World Bank
- Berkes F, Folke C. eds. 1998. *Linking Social and Ecological Systems Management Practices and Social Mechanisms for Building Resilience*. New York: Cambridge Univ. Press. 459 pp.
- Carpenter SR, Cottingham KL. 1997. Resilience and restoration of lakes. *Conservation Ecology*. Vol. 1. ([url: http://www.consecol.org](http://www.consecol.org))
- Carpenter SR, Kitchell JF, eds. 1993. *The Trophic Cascade in Lakes*. Cambridge: Cambridge Univ. Press. 385 pp.
- Carpenter SR, Ludwig D, Brock WA. 1999.

- Management of eutrophication for lakes subject to potentially irreversible change. *Ecol. Appl.* 9:751–71
6. Conway G. 1993. Sustainable agriculture: the trade-offs with productivity, stability and equitability. In *Economics and Ecology, New Frontiers and Sustainable Development*, ed. EB Barbier, pp. 57–68. London: Chapman & Hall
 7. Craighead FC, Sr. 1971. *The Trees of South Florida*. Vol. I. *The Natural Environments and Their Succession*. Coral Gables, FL: Univ. Miami Press. 212 pp.
 8. Davis SM. 1989. Sawgrass and cattail production in relation to nutrient supply in the Everglades. In *Fresh Water Wetlands & Wildlife, 9th Annual Symposium, Savannah River Ecology Laboratory, 24–27 March, 1986*. Charleston, SC: US Dept. Energy
 9. DeAngelis DL. 1980. Energy flow, nutrient cycling and ecosystem resilience. *Ecology* 61:764–71
 10. Dublin HT, Sinclair ARE, McGlade J. 1990. Elephants and fire as causes of multiple stable states in the Serengeti-mara woodlands. *J. Anthropol. Ecol.* 59:1147–64
 11. 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
 12. Fiering MB. 1982. Alternative indices of resilience. *Water Resources Res.* 18:33–39
 13. Folke C, Berkes F. 1995. Mechanisms that link property rights to ecological systems. In *Property Rights and the Environment*, ed. S Hanna, M Munasinghe, pp. 50–62. Washington, DC: Beijer Int. Inst. & World Bank
 14. Folke C, Holling CS, Perrings C. 1996. Biological diversity, ecosystems, and the human scale. *Ecol. Appl.* 6:1018–24
 15. Grimm V, Wissel C. 1997. Babel, or the ecological stability discussions—an inventory and analysis of terminology and a guide for avoiding confusion. *Oecologia* 109:323–34
 16. Gunderson LH, Holling C, Light S, eds. 1995. *Barriers & Bridges for the Renewal of Ecosystems and Institutions*. New York: Columbia Univ. Press. 593 pp.
 17. Gunderson LH. 1994. *Vegetation: determinants of composition*. In *Everglades: The Ecosystem and Its Restoration*, ed. SM Davis, J Ogden, pp. 323–340. Delray Beach, FL: St. Lucie
 18. Gunderson LH. 1999. *Stepping Back: Assessing for Understanding in complex regional systems*. In *Bioregional Assessments: Science at the Crossroads of Management and Policy*, ed. NK Johnson, F Swanson, M Herring, S Greene, pp. 127–40. Washington, DC: Island
 19. Gunderson LH, Holling CS, Pritchard L, Peterson G. 1996. *Resilience in Ecosystems, Institutions and Societies, Propositions for a Research Agenda*. Stockholm: Beijer Inst. Discuss. Pap.
 20. Gunderson LH, Snyder JR. 1994. Fire patterns in the southern Everglades. In *Everglades: The Ecosystem and Its Restoration*, ed. SM Davis, J Ogden, pp. 291–306. Delray Beach, FL: St. Lucie
 21. Hanski I. 1995. Multiple equilibria in metapopulation dynamics. *Nature* 377:618–21
 22. Holling CS. 1973. Resilience and stability of ecological systems. *Annu. Rev. Ecol. Syst.* 4:1–23
 23. Holling CS, ed. 1978. *Adaptive Environmental Assessment and Management*. London: Wiley & Sons. 377 pp.
 24. Holling CS. 1986. The resilience of terrestrial ecosystems: local surprise and global change In *Sustainable Development of the Biosphere*, ed. WC Clark, RE Munn, pp. 292–317. Cambridge: Cambridge Univ. Press.
 25. Holling CS. 1992. Cross-scale morphology, geometry and dynamics of ecosystems. *Ecol. Mongr.* 62:447–502
 26. Holling CS. 1996. Engineering resilience vs. ecological resilience. In *Engineering Within Ecological Constraints*, ed. PC

- Schulze, pp. 31–43. Washington, DC: Natl. Acad.
27. Holling CS, Meffe GK. 1996. Command and control and the pathology of natural resource management. *Conserv. Biol.* 10:328–37
 28. Ives AR. 1995. Measuring resilience in stochastic-systems. *Ecol. Monogr.* 65:217–33
 29. Johnson KN, Swanson F, Herring M, Greene S. 1999. *Bioregional Assessments*. Washington, DC: Island. 398 pp.
 30. Lee KN. 1993. *Compass and Gyroscope*. Washington, DC: Island. 243 pp.
 31. Levin S. 1995. Biodiversity: interfacing populations and ecosystems. In *Ecological Perspective of Biodiversity*, ed. M Higashi, T Abe, S Kevin, Kyoto: Kyoto Univ. Press. 295 pp.
 32. Light SS, Gunderson LH, Holling CS. 1995. The Everglades: evolution of management in a turbulent ecosystem. In *Barriers and Bridges to the Renewal of Ecosystems and Institutions*, ed. LH Gunderson, CS Holling, SS Light, pp. 103–68. New York: Columbia Univ. Press
 33. Loveless CM. 1959. A study of the vegetation of the Florida Everglades. *Ecology* 40:1–9
 34. Ludwig D, Hilborn R, Walters C. 1993. Uncertainty, resource exploitation, and conservation: lessons from history. *Science* 260:17–36
 35. Ludwig D, Walker B, Holling CS. 1996. Sustainability, stability and resilience. *Conserv. Ecol.* 1:1–27
 36. Ludwig J, Tongway D, Freudenberger D, Noble J. 1997. *Landscape Ecology Function and Management Principles from Australia's Rangelands*. Collingwood, Australia: CSIRO. 158 pp.
 37. May RM. 1973. *Stability and Complexity in Model Ecosystems*. Princeton, NJ: Princeton Univ. Press. 235 pp.
 38. McClanahan TR. 1995. A coral reef ecosystem-fisheries model: impacts of fishing intensity and catch selection on reef structure and processes. *Ecol. Model.* 80:1–19
 39. Mittelbach G, Turner A, Hall D, Rettig J. 1995. Perturbation and resilience—a long-term, whole-lake study of predator extinction and reintroduction. *Ecology* 76:2347–60
 40. Neubert MG, Caswell H. 1997. Alternatives to resilience for measuring the responses of ecological-systems to perturbations. *Ecology* 78:653–65
 41. O'Neill RV, DeAngelis DL, Waide JB, Allen TFH. 1986. *A Hierarchical Concept of Ecosystems. Monogr. Pop. Biol.* Vol. 23, Princeton, NJ: Princeton Univ. Press. 254 pp.
 42. Ostrom E. 1995. Designing complexity to govern complexity. In *Property Rights and the Environment*, ed. S Hanna, M Munasinghe, pp. 245–75. Washington, DC: Beijer Intl. Inst. & World Bank
 43. Peterson G, Allen C, Holling CS. 1998. Ecological resilience, biodiversity, and scale. *Ecosystems* 1:6–18
 44. Pimm SL. 1991. *The Balance of Nature?* Chicago: Univ. Chicago Press. 434 pp.
 45. Scheffer M. 1998. *Ecology of Shallow Lakes*. London: Chapman & Hall. 357 pp.
 46. Scheffer M, Hosper SH, Meijer ML, Moss B. 1993. Alternative equilibria in shallow lakes. *Trends Evol. Ecol.* 8:275–79
 47. Sinclair ARE, ed. 1995. *Serengeti II: Dynamics, Management, and Conservation of an Ecosystem*. Chicago: Univ. Chicago Press. 665 pp.
 48. Sinclair ARE, Olsen PD, Redhead TD. 1990. Can predators regulate small mammal populations? Evidence from house mouse outbreaks in Australia. *Oikos* 59:382–92
 49. Sousa WP, Connell JH. 1983. On the evidence needed to judge ecological stability or persistence. *Am. Nat.* 121:789–825
 50. Steward KK, Ornes WH. 1975. The autecology of sawgrass in the Florida Everglades. *Ecology* 56:162–71

51. Tilman D, Downing JA. 1994. Biodiversity and stability in grasslands. *Nature* 367:363–65
52. Tilman D, Wedin D, Knops J. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* 379:718–20
53. Wade DD, Ewel JJ, Hofstetter R. 1980. *Fire in South Florida Ecosystems*. Asheville, NC:SE For. Exp. Stat., US Dep. Agri., For. Serv.
54. Waide JB, Webster JR. 1976. Engineering systems analysis: applicability to ecosystems. In *Systems Analysis and Simulation in Ecology*, ed. BC Patton, pp. 329–71. New York: Academic
55. Walker B. 1995. Conserving biological diversity through ecosystem resilience. *Conserv. Biol.* 9:747–52
56. Walker B, Kinzig A, Langridge J. 1999. Plant attribute diversity, resilience and ecosystem function: the nature and significance of dominant and minor species. *Ecosystems* 2:95–113
57. Walker BH. 1981. Is succession a viable concept in African savanna ecosystems? In *Forest Succession: Concepts and Application*, ed. DC West, HH Shugart, DB Botkin, pp. 431–47. New York: Springer-Verlag
58. Walker BH. 1992. Biological diversity and ecological redundancy. *Conserv. Biol.* 6:18–23
59. Walker BH, Langridge JL, Mcfarlane F. 1997. Resilience of an Australian savanna grassland to selective and nonselective perturbations. *Aust. J. Ecol.* 22:125–35
60. Walker BH, Ludwig D, Holling CS, Penterman RM. 1981. Stability of semi-arid savanna grazing systems. *J. Ecol.* 69:473–98
61. Walters CJ. 1986. *Adaptive Management of Renewable Resources*. New York: McGraw Hill. 374 pp.
62. Weaver J, Paquet PC, Ruggiero L. 1996. Resilience and conservation of large carnivores in the Rocky mountains. *Conserv. Biol.* 10:964–976
63. Young M, McCay BJ. 1995. Building equity, stewardship and resilience into market-based property rights systems. In *Property Rights and the Environment*, ed. S Hanna, M Munasinghe, pp. 210–33. Washington, DC: Beijer Int. Inst. & World Bank



CONTENTS

PREFACE: A Millennial View of Ecology and Systematics, and ARES at Age 30, <i>Richard F. Johnston</i>	1
THE KINSHIP THEORY OF GENOMIC IMPRINTING, <i>David Haig</i>	9
CENOZOIC MAMMALIAN HERBIVORES FROM THE AMERICAS: Reconstructing Ancient Diets and Terrestrial Communities, <i>Bruce J. MacFadden</i>	33
CONSERVATION ISSUES IN NEW ZEALAND, <i>John Craig, Sandra Anderson, Mick Clout, Bob Creese, Neil Mitchell, John Ogden, Mere Roberts, Graham Ussher</i>	61
THE EVOLUTION OF PREDATOR-PREY INTERACTIONS: Theory and Evidence, <i>Peter A. Abrams</i>	79
THE ECOLOGY AND PHYSIOLOGY OF VIVIPAROUS AND RECALCITRANT SEEDS, <i>Elizabeth Farnsworth</i>	107
INBREEDING DEPRESSION IN CONSERVATION BIOLOGY, <i>Philip W. Hedrick, Steven T. Kalinowski</i>	139
AFRICAN CICHLID FISHES: Model Systems for Evolutionary Biology, <i>Irv Kornfield, Peter F. Smith</i>	163
SHRUB INVASIONS OF NORTH AMERICAN SEMIARID GRASSLANDS, <i>O. W. Van Auken</i>	197
THE GRASSES: A Case Study in Macroevolution, <i>Elizabeth A. Kellogg</i>	217
THE ECOLOGY OF TROPICAL ASIAN RIVERS AND STREAMS IN RELATION TO BIODIVERSITY CONSERVATION, <i>David Dudgeon</i>	239
HARVESTER ANTS (POGONOMYRMEX SPP.): Their Community and Ecosystem Influences, <i>James A. MacMahon, John F. Mull, Thomas O. Crist</i>	265
ORIGINS, EVOLUTION, AND DIVERSIFICATION OF ZOOPLANKTON, <i>Susan Rigby, Clare V. Milsom</i>	293
EVOLUTIONARY PHYSIOLOGY, <i>Martin E. Feder, Albert F. Bennett, Raymond B. Huey</i>	315
MECHANISMS OF MAINTENANCE OF SPECIES DIVERSITY, <i>Peter Chesson</i>	343
TEMPORAL VARIATION IN FITNESS COMPONENTS AND POPULATION DYNAMICS OF LARGE HERBIVORES, <i>J.-M. Gaillard, M. Festa-Bianchet, N. G. Yoccoz, A. Loison, C. Toïgo</i>	367
IMPACTS OF AIRBORNE POLLUTANTS ON SOIL FAUNA, <i>Josef Rusek, Valin G. Marshall</i>	395

ECOLOGICAL RESILIENCE - IN THEORY AND APPLICATION, <i>Lance H. Gunderson</i>	425
QUASI-REPLICATION AND THE CONTRACT OF ERROR: Lessons from Sex Ratios, Heritabilities and Fluctuating Asymmetry, <i>A. Richard Palmer</i>	441
INVASION OF COASTAL MARINE COMMUNITIES IN NORTH AMERICA: Apparent Patterns, Processes, and , <i>Gregory M. Ruiz, Paul W. Fofonoff, James T. Carlton, Marjorie J. Wonham, Anson H. Hines</i>	481
DIVERSIFICATION OF RAINFOREST FAUNAS: An Integrated Molecular Approach, <i>C. Moritz, J. L. Patton, C. J. Schneider, T. B. Smith</i>	533
THE EVOLUTIONARY ECOLOGY OF TOLERANCE TO CONSUMER DAMAGE, <i>Kirk A. Stowe, Robert J. Marquis, Cris G. Hochwender, Ellen L. Simms</i>	565