Toward Principles for Enhancing the Resilience of Ecosystem Services

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Keywords
social-ecological, diversity, connectivity, learning, participation, polycentric

Abstract
Enhancing the resilience of ecosystem services (ES) that underpin human well-being is critical for meeting current and future societal needs, and requires specific governance and management policies. Using the literature, we identify seven generic policy-relevant principles for enhancing the resilience of desired ES in the face of disturbance and ongoing change in social-ecological systems (SES). These principles are (P1) maintain diversity and redundancy, (P2) manage connectivity, (P3) manage slow variables and feedbacks, (P4) foster an understanding of SES as complex adaptive systems (CAS), (P5) encourage learning and experimentation, (P6) broaden participation, and (P7) promote polycentric governance systems. We briefly define each principle, review how and when it enhances the resilience of ES, and conclude with major research gaps. In practice, the principles often co-occur and are highly interdependent. Key future needs are to better understand these interdependencies and to operationalize and apply the principles in different policy and management contexts.

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INTRODUCTION

A major challenge of the twenty-first century is ensuring an adequate and reliable flow of essential ecosystem services (ES) to meet the needs of a burgeoning world population. All social-ecological systems (SES) produce a “bundle” of ES, including provisioning (e.g., freshwater, crops, meat), regulating (e.g., flood and climate regulation), and cultural services (e.g., recreation, spiritual values) (1). Extensive and rapid global changes, including urbanization, growing human populations, rising consumption, and increased global connections, have led to a large and growing demand for provisioning services. Meeting these needs has resulted in large-scale conversion of natural ecosystems to cropland, which has eroded the capacity of ecosystems to produce other ES essential to human health and security—especially regulating services (2, 3). Furthermore, extensive anthropogenic changes to the world’s ecosystems are increasing the likelihood of large, nonlinear, and potentially irreversible changes, such as coral reef degradation (4). Such events often have substantial and sometimes catastrophic impacts on ES and human well-being (1, 5).

Enhancing the resilience of ES that underpin human social and economic well-being is therefore of substantial policy interest. Any consideration of policies for enhancing resilience requires a clear specification of “resilience of what to what”—what is desired to be resilient and to what (6). In this review, we focus on the resilience of ES, defined as the capacity of the SES to sustain a desired set of ES in the face of disturbance and ongoing changes in SES. Because different sectors of society often value, need, and demand different ES (7), decisions about which ES to sustain are inherently political. Every SES produces a variety of interacting ES at multiple scales, and it is not possible to increase the resilience of all ES simultaneously (1, 2). Although there are synergies among some services, important trade-offs exist between ES at a particular scale, as well as between ES at different scales. For instance, timber harvesting and use at a local scale affects carbon storage globally (3). To further complicate matters, the desired mix of ES will evolve with changing societal values and preferences (8), and the resilience of ES is only one among many desired outcomes of SES (e.g., human rights, democracy). The inevitable trade-offs between disparate, changing societal goals require resolution of collective action dilemmas and intergroup conflicts, a process that comes replete with power inequalities, asymmetric resource bases, and unequal outcomes (7).
Slow variable: a variable whose rate of change is slow in relation to the timescales of ES provision and management, and is therefore often considered constant.

Feedback: a mechanism, process, or signal that loops back to influence the SES component emitting the signal or initiating the mechanism or process.

we fully acknowledge the complex social, institutional, and political aspects of such decision-making processes, we do not address them here. Instead, we assume that some desired mix of ES has been legitimately agreed upon and focus on how the resilience of these ES may be enhanced, while allowing for the possibility of changes in the preferred mix of ES over time.

A growing number of studies provide insight into how the resilience of SES and the ES they produce may be enhanced (9–11). Although several studies have proposed general “rules of thumb” for enhancing resilience (12–14), there does not yet exist a definitive set of resilience-enhancing principles or a synthetic understanding of where and when they apply. On the basis of the literature, a “mock court workshop” at which proposed principles were debated, and a modified Delphi survey of leading experts in the field (Supplemental Material), we identified seven generic principles for enhancing the resilience of ES. (For all Supplemental Material follow the link on the Annual Reviews home page at http://www.annualreviews.org.)

These principles include (P1) maintain diversity and redundancy, (P2) manage connectivity, (P3) manage slow variables and feedbacks, (P4) foster an understanding of SES as complex adaptive systems (CAS), (P5) encourage learning and experimentation, (P6) broaden participation, and (P7) promote polycentric governance systems. In this review, we group these principles into those that focus on generic SES properties and processes (P1–3) and those that focus on the way SES are governed (P4–7) (Figure 1). This follows the distinction made by Jentoft et al. (15) between the system to be governed and the governance system. We also distinguish between governance and management, where governance is taken to be the social and political process of defining goals for the management of SES and resolving trade-offs, and management is defined as the actions taken to achieve these goals and includes monitoring and implementation (16).

This is not a definitive set of principles, but our hope is that this review will stimulate further discussion and refinement of a useful set of principles for enhancing resilience of ES.

This article reviews the evidence in support of each of the seven principles. Although most of the principles are also important for the actual production of ES, we focus exclusively on how they affect the resilience of ES, i.e., not the quantity of ES produced, but the ability to sustain production of ES in the face of unexpected shocks and disturbances as well as during slower ongoing change. We assume that ES are typically coproduced by the interaction of social and ecological factors (8, 17), so that, for instance, cereal crops are produced by the interplay of ecological factors (e.g., fertile soil, rainfall) with social factors (e.g., demand for crops, agricultural technology, market access).

We further assume that SES are CAS, characterized by emergent and nonlinear behavior, the capacity to self-organize and adapt on the basis of past experience, and substantial uncertainties; all of these have marked consequences for ES governance and management (18, 19).
For each principle, we give a brief definition, review the state of knowledge about the underlying mechanism by which the principle enhances resilience of ES and the conditions under which resilience may be compromised, and conclude with a summary of major research gaps. Although we have attempted to separate individual principles for the sake of analysis and presentation, they are in practice highly interconnected and interdependent. We discuss some of these connections and synergies in the concluding section.

**PRINCIPLE 1: MAINTAIN DIVERSITY AND REDUNDANCY**

Diversity does not simply refer to variety, but includes three interrelated and distinct components: variety (how many different elements), balance (how many of each element), and disparity (how different the elements are from one another) (20). In an SES context, important system elements that may exhibit diversity include genes, species, landscape patches, cultural groups, livelihood strategies, and governance institutions. Diversity in SES therefore encompasses biodiversity, spatial heterogeneity, livelihood strategies, and institutional diversity. Redundancy is closely related to diversity and is a system property that describes the replication of particular elements or pathways in a system (21). Redundancy is essentially the opposite of disparity and provides “insurance” for ES provision by allowing some system elements to compensate for the loss or failure of others.

**How Do Diversity and Redundancy Enhance the Resilience of Ecosystem Services?**

There is wide consensus from a variety of disciplines that diversity and redundancy are important for resilience because they provide options for responding to change and disturbance (11, 20, 22–24). The diversity of system elements, such as multiple species, management approaches, and institutions, provides the basis for innovation, learning, and adaptation to slower, ongoing change (see P5). In terms of resilience of ES to disturbances, response diversity and functional redundancy are particularly important. Response diversity refers to the variety of ways in which different species, actors, or SES elements respond to a disturbance, such as a fire or drought (25), whereas functional redundancy refers to the capacity of functionally similar elements to partly or fully substitute for each other (21).

Response diversity and functional redundancy work in combination to enhance the resilience of ES (26, 27). Most ES are produced by multiple species or SES elements, which respond differently to disturbances owing to differences in their physical traits, the timing of their contribution to ES, or the spatial scale at which they operate. This variety usually allows at least some of the elements to persist through particular disturbances and continue delivering ES (25). For example, seed dispersal in Ugandan forests is performed by mammals ranging in size from mice to chimpanzees. Although small mammals are negatively affected by localized disturbances, larger, more mobile species are not and can therefore maintain the seed-dispersal function (28). In traditional agroforestry systems, diverse tree and crop species with varying requirements for light and nutrients are planted so that harvests are discontinuous in time and failure of any one crop, owing to disease or drought, will not have catastrophic impacts on food provision (29).

In governance contexts, a variety of organizational forms (e.g., government department, nongovernmental organization, community organization) with overlapping domains of authority provide for a diversity of responses and thereby facilitate the maintenance of ES in the face of economic or political upheaval (P7) (23).

Functional redundancy and response diversity are also important in enabling adaptation to slower, ongoing change. For example, grassland plant communities can maintain a relatively consistent production of fodder biomass over long periods despite changes in environmental conditions and species.
abundances because species more suited to the new environmental conditions are able to compensate for the decline of less well-suited species (30). Similarly, investment in diverse ES-based activities (e.g., fishing, ecotourism) can enhance the resilience of associated livelihoods as it enables people to rebalance their activities when market or environmental conditions change (24). For example, a substantial number of farmers in the drier parts of South Africa and Namibia have shifted from cattle ranching to wildlife-based ecotourism in response to changed markets and ES preferences for cultural over provisioning ES (31).

Diversity among elements contributing to a particular ES can modify the effects of disturbance itself. For example, riparian vegetation consisting of a range of different height classes provides more resistance to floodwater, thereby decreasing the impact of flooding and maintaining the ES provided by the riparian ecosystem (32). Similarly, landscape diversity influences the spread and impact of disturbances through impacts on connectivity (P2). In social systems, the diversity of values and perspectives in society can guard against fads (33) that may substantially impact ES, such as a predilection for hat feathers or pet birds.

At the landscape level, spatial heterogeneity helps ensure that some landscape patches remain undisturbed and provide refuges for the maintenance of particular ES. For instance, sacred sites, such as pools, forests, or reserve grazing areas, often function as remnant sources of critical ES, such as water and fodder, during severe droughts or after wildfires (34). Remnant patches of vegetation are also important sources of propagules for recolonization of bare areas after disturbances, such as volcanic eruptions or extreme floods, provided there is sufficient connectivity to disturbed patches (P2) (35).

Furthermore, engaging user groups with diverse perspectives can improve the understanding of SES dynamics (36, 37) and can enhance resilience of ES under certain conditions (P6). Likewise, diverse management approaches can support learning and understanding of the best ways to manage SES to ensure the sustained provision of ES and to facilitate adaptation to changes in ES over time (P5) (38).

**Under What Conditions May Resilience Be Compromised?**

Resilience of ES is maintained by a combination of diversity and redundancy, and low levels of either can lead to brittleness of the SES and compromise resilience. Both diversity and redundancy tend to increase with the number of species or elements in a SES and therefore tend to be correlated (39). However, in some cases, highly diverse systems may have low redundancy with only a few species or elements able to produce a particular ES. Loss of these “keystone species” or “key actors” typically leads to loss of many other entities because the remaining species or actors are unable to compensate effectively (40, 41). For example, one keystone species in riparian ecosystems in North America is beaver. Extensive trapping of beaver in the 1500s to 1800s led to widespread reduction in wetland habitat and associated ES (42). In other cases, high redundancy may occur in combination with low diversity. In such cases, many elements contribute to particular ES, but all elements are very similar either by design (if they are human institutions or activities) or due to environmental or historical constraints. As long as disturbances remain within the natural range of variation experienced by the system, provision of ES is expected to be resilient, but the system is likely to be vulnerable to new types of disturbances (43).

By contrast, very high levels of diversity and redundancy can undermine ES productivity and resilience in the longer term (Figure 2). Both diversity and redundancy are costly in the sense that they reduce system efficiency and increase the possibility for system stagnation (44, 45). For example, high redundancy in management organizations tends to increase the administrative costs of managing ES, interdepartmental power struggles, and contradictory regulation, which can compromise the resilience of ES (46). More generally, as the number of system elements (and hence diversity and
redundancy) increases, the number of possible interactions between entities tends to increase exponentially, as does the possibility of non-linear system dynamics (47). This increased complexity may hinder the establishment of efficient, directional pathways for the processing of matter, energy, or information, and lead to an inability of the SES to adapt in the face of change and disturbance (44, 45). For instance, the diversity of interests, preferences, expected climate change impacts, and response capacity among nations has been an important contributing factor in the stalemate surrounding climate negotiations (48). Maintaining the resilience of ES therefore requires levels of diversity and redundancy that balance the danger of system brittleness (associated with low levels of diversity or redundancy) against that of system stagnation (associated with high levels of diversity and redundancy).

**Conclusion and Research Needs**

Diversity and redundancy provide options for responding to change and disturbance; these options can increase both the reliability of ES and the potential for learning and innovation. Theoretical and empirical research suggests that it is particularly response diversity in combination with functional redundancy that is important for maintaining ES in the face of disturbance. However, both diversity and redundancy are costly in terms of increasing system complexity and inefficiency, and too much of either tends to reduce the capacity for adaptation to slower ongoing change. Enhancing the resilience of ES by investing in diversity and redundancy therefore requires finding an appropriate balance between brittleness/efficiency and stagnation/inefficiency associated with low and high levels of diversity and redundancy.

The relationships between, and trade-offs among, diversity, redundancy, and resilience, and how these vary with context and scale, are important areas for future research. Although much research has been carried out on ecological diversity and redundancy, the impacts of social and economic diversity and redundancy on the resilience of ES are less well understood. Understanding the relationships between diversity, redundancy, and resilience requires the development of practical methods for measuring diversity and redundancy and for identifying critical processes or keystone entities in different SES. Identifying and managing these vulnerable points may be the most effective way to maintain the resilience of ES.

**PRINCIPLE 2: MANAGE CONNECTIVITY**

Connectivity is defined as the manner by which and extent to which resources, species, or social actors disperse, migrate, or interact across ecological and social “landscapes” (49). Landscapes may consist of components, such as patches, habitats, or social groupings. These components are referred to as nodes and the connections between them as links. Examples of links are species interactions, corridors across habitats, or communication channels between human communities. The effect of connectivity on resilience of ES depends on the structure and strength of linkages between nodes. Structure refers to the presence or absence of links between components and how
links are distributed within an SES. Strength refers to the intensity with which components are connected, determined by factors such as corridor quality among habitats, preferences of a predator for specific prey, or the frequency of interactions between social actors.

**How Does Connectivity Enhance the Resilience of Ecosystem Services?**

Connectivity in SES facilitates the exchange of material or information necessary for the functioning of ecological and social processes, and hence often directly affects the production of ES. Connectivity also affects the resilience of ES because it affects the spread of disturbances and facilitates recovery after a disturbance (50). In social systems, connectivity may affect the governance of ES, for example, by influencing the flow of information between actors (51, 52).

Connectivity is particularly important in enabling recovery of disturbed SES components. For instance, coral reef recolonization following disturbance is related to the degree of connectivity between remnant patches (53). Similarly, in a disturbance experiment of macrobenthic communities, it was found that recovery was largely determined by the degree of connectivity across metacommunities (54). The importance of connectivity to the resilience of SES and the ES they produce underlies many conservation initiatives, such as the design of networks of protected areas, e.g., the Great Barrier Reef Marine Protected Area network (55). Maintaining connections to areas that serve as refuges can accelerate the restoration of disturbed areas and associated ES (50).

Connectivity between habitats enhances population viability, especially for large mammals and the ES that depend on those species (56). Reduced connectivity as a result of infrastructure, including roads and dams, has a strong effect on the viability of species’ populations (57). The Yellowstone to Yukon is one example of a regional conservation planning initiative that focuses on connecting large habitat patches by establishing or maintaining corridors to reduce the effects of reduced genetic diversity in isolated large-carnivore populations (58). Managers can mimic connectivity in fragmented landscapes through additions of species or individuals to enhance a subpopulation. More generally, network theory suggests that conserving keystone patches in the landscape, creating new patches in the vicinity of vulnerable ones, and managing highly connected patches can contribute to sustained and resilient provision of ES (59).

In social systems, it has been argued that connectivity in social networks can facilitate resilience of ES through enhanced governance opportunities. High levels of connectivity between different social groups increases information sharing and develops the trust and reciprocity necessary for collective action (P6) (52). Certain actors also serve as connectors to other landscapes, bringing outside perspectives and new ideas to local issues (P5) (51).

Network theory suggests that it is not only the presence of links and their strength that determine the resilience of ES to disturbances, but also that differences in system structure—specifically modularity and nestedness—are important (60, 61). Modularity refers to the extent to which there are subsets of densely connected nodes that are loosely connected to other subsets of nodes. Nestedness is the degree to which specialist nodes (nodes with few links) interact with subsets of generalist nodes (nodes with a lot of links). Modular ecosystems, e.g., lakes, are functionally independent locally and can prevent disturbances from spreading across space or cascading across scales (62). More generally, increased spatial heterogeneity in landscapes or between actor groups is associated with greater diversity in connections between nodes as well as with increased modularity and nestedness (51, 63). Although disturbances may still cause severe impacts in a particular node, they are less likely to spread widely in such systems (60).

**Under What Conditions May Resilience Be Compromised?**

Even though connectivity facilitates recovery following a disturbance, strongly connected systems may be less resilient to disturbances.
Modeling results show that, in highly connected systems, disturbances can propagate rapidly, leading to widespread impacts on SES and associated ES (60, 63). Pest outbreaks, disease epidemics, invasion of alien species, and even financial crises, such as the global spread of the 2008 recession triggered by the collapse of the US housing market, confirm the high risk of propagation of disturbances in strongly connected systems (64, 65). High levels of connectivity among actors can lead to synchronized behavior and unsustainable resource extraction or to strong barriers for changing unsustainable practices (49). For example, in dense social networks, information about a change in market price for timber can spread quickly and result in deforestation as multiple actors take advantage of market conditions (66). This risk is lower in less-connected systems, especially when these systems are heterogeneous (63).

In highly modular or nested systems, resilience may be jeopardized if some components become overly important compared to others (41, 67). Removal of important components, such as keystone species or highly connected patches, may trigger cascading waves of extinctions (P1). For example, models of Madagascar’s dry-forest dynamics suggest that rapid declines in pollination services could occur if small forest patches are removed from the landscape, owing to their impacts on the spatial configuration of the remaining forest area (68). In social networks, actors tend to have strong ties to other actors with similar characteristics (69). These ties can lead to modular systems with high connectivity between resource users with similar perspectives and knowledge, i.e., the “who you know is what you know” phenomenon (51). If subgroups that actively use certain ES are not engaged in management of those ES, critical knowledge of systems’ functioning and monitoring can be missed (P5) (70), and there may be a reduced potential for collective action (P6).

Conclusion and Research Needs
High levels of connectivity can facilitate ecological recovery after a disturbance and the development of the trust necessary for collective action in social systems. However, highly connected systems increase the potential for disturbances to spread and enhance the risk of homogenization of knowledge, which can lead to suboptimal management. Consequently, there is a trade-off in costs and benefits with increasing levels of connectivity, so that the resilience of ES appears to be highest in moderately connected systems, especially when heterogeneity is high.

Much remains to be understood regarding the practical applications of managing connectivity to enhance resilience of ES. Although there is a substantial body of theoretical work that evaluates how connectivity affects resilience under different conditions, few empirical studies explicitly test the relationship between connectivity and resilience of ES. One major difficulty lies in identifying and measuring connectivity. This is due to the large number of currencies for quantifying connectivity in SES (e.g., flow of energy, resources, information, interaction strengths, species movements), difficulties in defining the boundaries and agents in network representations of SES, and the dearth of longitudinal data illustrating social network dynamics. This problem is aggravated by the fact that connectivity is not a constant property: The strength and structure of links may vary over time. Another major need is to better understand which dimensions of connectivity can most effectively be manipulated to enhance the resilience of ES.

PRINCIPLE 3: MANAGE SLOW VARIABLES AND FEEDBACKS
SES consist of variables that change and interact on a range of timescales (10, 71). Slow variables determine the underlying structure of SES, whereas the dynamics of the system typically arise from interactions and feedbacks between fast variables that respond to the conditions created by the slow variables. In relation to ES, such as crop production and drinking water (which represent fast variables), slow variables include, for example, soil composition and phosphorous concentrations in lake sediments.
Slow ecological variables are often linked to regulating ES, e.g., climate regulation, flood regulation, and disease control (72). Social variables, including legal systems, values, and traditions, can also be important slow variables in relation to provisioning and cultural ES (73).

Feedbacks occur when a change in a particular variable, process or signal either reinforces (positive feedback) or dampens (negative feedback) subsequent changes of the same type. For example, introduced grasses in Hawaii promote fire, which further benefits the grasses at the expense of native shrub species, creating a self-reinforcing dynamic that is very difficult to break (74). The classic concept of economic equilibrium is based on negative feedback: Any increase in production drives down prices, which will, in turn, reduce production if it is above the optimal level of profitability (75). Monitoring is a specific form of feedback, in which information about the state or responses of the SES feeds back to actors so that they can change the way they utilize, affect, or manage a SES.

How Do Slow Variables and Feedbacks Enhance the Resilience of Ecosystem Services?

Changes in slow variables and feedbacks can lead to nonlinear changes or regime shifts in SES if certain thresholds are exceeded, with substantial impacts on the set of ES produced by the SES. Regime shifts are large, persistent, and often abrupt changes in the structure and dynamics of SES that occur when there is a reorganization of the dominant feedbacks in a system and are a common feature in CAS (76). An iconic example occurs in lakes, which can shift from a clear to a turbid water regime with marked impacts on ES, such as drinking water and water-based recreation (62). Regime shifts usually result from a combination of a shock (e.g., large rainstorm) and gradual changes in slow variables (e.g., nutrient accumulation) that erode the strength of the dominant feedbacks. When a critical threshold is crossed, a different set of feedbacks becomes dominant, and the system reorganizes, often abruptly, into a new regime with a different characteristic structure, behavior, and set of ES.

Strengthening the stabilizing feedbacks in a system can help maintain a particular SES regime and associated ES in the face of external stresses, e.g., climate change (77). For example, coral reefs can shift between regimes dominated by hard corals that provide ES (e.g., fisheries and ecotourism) and regimes dominated by seaweed. The resilience of the hard-coral regime can be enhanced by promoting the abundance of herbivores (e.g., parrot fish that graze on seaweed), as it reduces the possibility for seaweed to become established in the face of shocks such as coral-bleaching events (53). Feedbacks in the governance system can also be strengthened to enhance the resilience of hard corals by, for instance, creating governance structures that support the empowerment of reef users and provide incentives to prevent overfishing (78).

In other cases, it may be necessary to disrupt or weaken the feedbacks that keep an SES in a resilient but undesired regime. This can be particularly important in ecosystem restoration projects and to facilitate transformation of an SES into a new regime that produces a more desirable set of ES (79, 80). For example, fire suppression may lead to invasion of grasslands by trees, but restoring grasslands and associated grazing ES cannot be achieved simply by reintroducing fire (81). This is because once trees reach a certain critical size, they are not killed by fire and inhibit fires from burning. Grassland restoration often requires the physical removal of the trees to give grasses the opportunity to re-establish and enable fires to burn. Provided fires then occur frequently enough, the grassland will be maintained by fire because the fires kill small trees. Social feedbacks can similarly keep a system locked in an undesirable regime and require weakening to enable transformation. For example, in the Amudarya River basin in Central Asia, reinforcing feedbacks in the agricultural system, vested interests, and a patronage system keep the system locked in an unsustainable water management regime that cannot meet the needs of the region (82).
It has been proposed that critical thresholds in slow variables can be avoided by conserving regulating ES (83, 84). A decline in regulating services, such as erosion control and nutrient cycling, for example, contributed to desertification-related regime shifts during the Dust Bowl years in the United States, and during the 1980s and 1990s in the Sahel (1). Similarly, modifications to the water cycle through agriculture can lead to changes in the timing and flows of water, contributing to regime shifts in downstream water bodies, soil moisture regimes, and microclimates, as well as potentially reducing the long-term capacity of agricultural systems to produce food in some parts of the world (83).

**Under What Conditions May Resilience Be Compromised?**

The absence of monitoring information on changes in slow variables and feedbacks is often an important contributor to environmental degradation and loss of resilience (P5). For example, in the Goulburn Broken catchment in southeast Australia, the slow rise in groundwater tables resulting from vegetation clearing remained unknown until water tables rose above a critical threshold that led to soil salinization and significantly impacted agricultural production (85). Slow variables are often ignored in monitoring and management as attention tends to focus on fast variables that show more variability and response over short timescales and that are often easier to observe. Opportunities to learn about changes in slow variables and feedbacks are also hampered, in part, because it is difficult to detect or predict regime shifts (62). However, emerging work on early warning indicators of regime shifts based on changes in the statistical behavior (e.g., rising variance, autocorrelation) of a system as it approaches a critical threshold provides some promise of improved monitoring possibilities in the future (86).

Monitoring information alone is, however, insufficient to avoid loss of resilience of ES. Even where slow variables are acknowledged and monitored, appropriate action may not occur for a variety of reasons. For instance, although several key slow variables and feedbacks are known with respect to climate change, vested and competing interests, and lack of agreement on the appropriate responses, have hampered the implementation of a coordinated international response (48). Establishing governance structures that can effectively respond to information about changes in slow variables is therefore equally critical to preventing regime shifts that undermine the provision of desired ES.

Management interventions that obscure, remove, or ignore stabilizing feedbacks that underlie the provision of desired ES can erode the resilience of ES. For example, it has been argued that the 2005 flood in New Orleans was partially caused by human-engineered modifications to the delta system that did not permit natural sediment and flood dynamics to absorb changes in water flows (87). In other cases, policies or markets can send signals to resource users and change feedbacks; for example, spikes in commodity prices can lead to overexploitation of agricultural ecosystems (88). In such cases, introducing appropriate rules or incentives can create feedbacks that dampen the effect of such disturbances.

**Conclusion and Research Needs**

The theoretical basis for the importance of managing slow variables and feedbacks to maintain SES regimes that produce desired bundles of ES is widely acknowledged in the resilience literature. However, practical experience with identifying and managing key slow variables and feedbacks to avoid regime shifts, particularly beyond the handful of well-documented shifts, such as lake eutrophication, is currently limited. Maintaining regulating ES as a proxy for managing slow variables might be a practical way forward.

Critical research gaps relate to better understanding what regime shifts may occur in different SES and their impacts on ES. Identifying the key slow variables, feedbacks, and thresholds that trigger different regime
shifts and understanding possible cascading effects between different regime shifts are also key gaps. An important emerging area of research involves improved statistical detection of regime shifts in situations where the dynamics of the feedbacks and slow variables underlying the shifts are poorly understood. Finally, more research is needed on how to manage feedbacks to avoid regime shifts in practical SES management settings.

PRINCIPLE 4: FOSTER AN UNDERSTANDING OF SOCIAL-ECOLOGICAL SYSTEMS AS COMPLEX ADAPTIVE SYSTEMS

This principle refers to an understanding and appreciation among scientists and managers of the properties of CAS and their implications for the management of SES. Key properties include the possibility of emergent macroscale SES behavior that cannot be predicted from individual system components, the fact that SES are continually evolving and adapting in response to internal system feedbacks, and an acknowledgment of the pervasiveness of uncertainty in SES (19, 89). Understanding SES as CAS constitutes a particular mental model, or cognitive framework, used to interpret and understand the world and decide on appropriate actions (90).

How Does Understanding Social-Ecological Systems as Complex Adaptive Systems Enhance Resilience of Ecosystem Services?

Fostering an understanding of SES as CAS among actors involved in SES management is thought to enhance the resilience of ES by emphasizing holistic (rather than reductionist) approaches, the management of multiple ES and trade-offs in an integrated way, and the importance of slow variables, lags, and feedbacks in SES dynamics (P3) (16, 91). A CAS worldview also emphasizes the substantial uncertainties surrounding SES and therefore the need to continuously learn and experiment (P5) and adaptively manage uncertainty, disturbance, and surprise rather than attempt to eliminate it (11, 71). Understanding SES as CAS therefore does not directly influence the resilience of ES but affects the choice of management approaches.

Evidence for the importance of understanding SES as CAS is suggested primarily by the consequences of a lack of such understanding. Holling & Meffe (91) cite abundant empirical evidence of conventional resource management practices that optimize provision of a narrow set of ES on the basis of linear, reductionist mental models of ecosystems, which inadvertently undermine the ability of these systems to continue producing ES in the face of disturbance and change. Specific examples include the Gariep basin in South Africa (92), the Western Australia wheat belt (88), the Everglades and the Goulburn Broken catchment (12). Similarly, widespread mismanagement of fisheries (93) and forests (94) is partly attributed to forms of management based on technical, reductionist, and one-size-fits-all approaches.

Examples of transformations in ecosystem management suggest that changes in underlying mental models that acknowledge the characteristics of SES as CAS can lead to improvements in the resilience of ES. One example is the large-scale rezoning of Australia’s Great Barrier Reef, driven by increased recognition of the importance of connectivity, nonlinear change, and multiscale interactions in coral reef systems (95). The aim of the rezoning was to enhance the resilience of ecosystem functions to a range of perturbations including coral bleaching and cyclones. Recent monitoring indicates that the approach has improved the reef’s ability to provide a diversity of ES (55). In South Africa’s Kruger National Park, increased emphasis on the value of variation in maintaining biodiversity has led managers to move away from objectives that aim to keep ecosystem conditions, such as elephant populations and fire frequencies, fixed at optimal levels. Instead, elephant numbers and fires are now allowed...
to fluctuate between specified boundaries (96). This shift has reduced the human investment needed to manage ecosystems and has increased the variety of ecosystem and habitat types, as well as the opportunities for specialist species that support particular ES.

Understanding SES as CAS can be facilitated by a number of analytical frameworks and tools. These include the Millennium Ecosystem Assessment conceptual framework (1) and the adaptive cycle (71). Methodologies such as scenario planning (a structured process of exploring and evaluating future complexity and uncertainty) have proven particularly powerful and have been used successfully in a wide range of SES settings, including tropical forest communities, lakeshore management in the United States, and political change in South Africa (97, 98).

**Under What Conditions May Resilience Be Compromised?**

Presenting the concept of complexity in ways that do not create a sense of bewilderment remains a key challenge in practical ecosystem management settings. Complexity can be understood in a number of ways, some of which do not reflect an appreciation of the fundamental properties of CAS. For example, complexity is sometimes taken to mean all dimensions of a system that are not yet understood (89). Viewing complexity simply as the unknown tends to overwhelm managers and lead to gridlock and stagnation. When combined with more traditional views about the need for reducing uncertainty before taking action, such interpretations may lead managers to invest heavily in monitoring and data collection, rather than encourage the use of adaptive approaches that allow for uncertainty (38).

Management based on an understanding of SES as CAS often challenges existing institutional arrangements and worldviews, and may face substantial opposition (19). It implies a more integrated approach that is difficult to address across governance units that are usually separate (e.g., water and land). In addition, it often implies a change in management paradigm from a focus on causality and control, to a focus on coping with change and uncertainty, which may be difficult to operationalize in contexts that focus on accountability and meeting targets (16). At the same time, it remains unclear to what extent the motivation for managers to engage in adaptive learning approaches is founded explicitly on an understanding of CAS. In practice, an understanding of SES as CAS is likely to co-emerge and be reinforced by learning-focused approaches such as adaptive management (P5).

**Conclusion and Research Needs**

There is some empirical evidence to suggest that understanding of SES as CAS can facilitate the management of SES in ways that enhance the resilient provision of ES, mainly through the choice of management approaches that allow for uncertainty, variability, and change. Much of this evidence comes from examples in which a lack of such understanding has eroded the resilience of ES. However, it remains unclear to what extent an understanding of SES as CAS underlies the adoption of adaptive management approaches as well as the importance of such understanding for the resilience of ES.

There are several key research gaps with respect to the role of understanding SES as CAS in enhancing the resilience of ES. First, there is a need to better define what this understanding is and a need to understand the degree to which a greater understanding of SES as CAS leads to management choices that enhance the resilience of ES. Second, there is a need to determine how to best invest efforts in fostering the understanding of SES as CAS, and whether there are aspects of this understanding that are more important than others in enhancing resilience of ES. A third key gap is to better understand what tools and processes (e.g., scenario planning, participatory approaches, adaptive management) are most...
**Learning**: the process of modifying existing or acquiring new knowledge, behaviors, skills, values, or preferences at individual, group, or societal levels

**PRINCIPLE 5: ENCOURAGE LEARNING AND EXPERIMENTATION**

The term learning has been used loosely in the resilience literature, which has been criticized for conflating the concepts of social learning and organizational (or loop) learning (99). We define learning as the process of modifying existing or acquiring new knowledge, behaviors, skills, values, or preferences. Learning is inherently located at the individual level, but also goes beyond the individual to become situated within wider groups, organizations, or communities of practice, where it is referred to as social learning (99). Social learning occurs through social interactions (e.g., conversations between actors within social networks) and can take place through intentional, facilitated processes (100); or it can be an emergent outcome (101). Participation (P6) is therefore a key enabler of social learning.

**How Do Learning and Experimentation Enhance Resilience of Ecosystem Services?**

Learning has been considered fundamental to building resilience and dealing with uncertainty in SES since at least the late 1970s (38, 71). The need for learning is based on the assumptions that knowledge is always incomplete and that uncertainty, change, and surprise are inevitable in complex SES. Hence, there is a constant need to revise existing knowledge to enable adaptation to evolution and change in SES, as well as to maintain ES in the face of disturbance and change (11, 12).

Various traditional practices underpin the generation, accumulation, and transmission of knowledge and institutions for responding to and managing ecological surprises (102). These include practices such as multiple-species and landscape patchiness management, which enable comparison and learning about responses of different species or vegetation communities. Traditional learning-based approaches also include mechanisms for cultural internalization of new practices and the adaptation of worldviews and cultural values. For example, in the traditional caribou-hunting Cree society, an event of extreme overhunting that resulted in the disappearance of caribou in the early 1900s triggered the development of a more conservationist approach that became encoded in the ethical and cultural beliefs of the Cree (102).

In contemporary settings, experimentation and monitoring are widely used tools for facilitated learning in natural resource management. Monitoring provides information about changes in SES and ES, whereas experimentation involves the active manipulation of particular SES processes and structures to observe and compare outcomes (38). Although monitoring and experimentation have often been carried out by specialist agencies and universities, there is growing recognition of the importance of broader participation in the learning process by all parties involved in SES governance and management (P6) (103). Monitoring and experimentation are central to adaptive management and adaptive comanagement (38, 104), which typically involve a series of management experiments that support learning about SES responses to management actions or disturbances. The participatory nature of adaptive management and comanagement enables sharing and reflecting on experiences, ideas, and values with others, which builds trust and relationships and facilitates social learning as well as collective action (P6) (101).

Learning can occur at different levels (105, 106), which contribute in different ways to enhancing resilience of ES. Single-loop learning comprises a change in skills, practices, or actions to meet existing goals and expectations; this learning focuses on the question, Are we doing things right? In contrast, double-loop learning actively questions the assumptions that underlie action by asking, Are we doing the right things? For example, a study of US community-based forestry organizations found that collaborative monitoring activities led to
single-loop learning (recommendations for optimal treatment of invasive weed species that threaten forests) and double-loop learning (realization of the impact of salvaging timber) (107). Triple-loop learning involves a more deep-seated questioning of values and norms that underlie institutions and actions by asking, How do we know what the right thing to do is? Triple-loop learning can result in the restructuring of beliefs and values, underlies transformations in worldviews, and may prompt changes in ecosystem governance and management approaches (16, 108).

More generally, evidence suggests that learning can contribute to improved governance processes that affect the resilience of ES. For example, participatory learning processes can help actors learn about each other’s mental models (P4), which builds social capital, in turn supporting institutional change and conflict resolution (109, 110). Sendzimir et al. (111) found that learning processes led to a paradigm shift in how to manage the Tisza River basin in Europe—from a conventional command-and-control paradigm to one based on living with water. This encompasses integrated solutions for a multifunctional landscape that combine flood protection with restoration of ecological conditions in rivers, which contrasts with earlier engineering-based approaches.

**Under What Conditions May Resilience Be Compromised?**

Evidence in support of learning and experimentation does not indicate what type of learning is most appropriate and under what conditions; however, it is clear that the design of the learning process is crucial. Experience suggests that, to be effective, the process of monitoring and learning needs to be collaborative and long-term as well as able to withstand the impact of short-term politics and objectives (112, 113). Power dynamics in particular can influence how learning takes place, including who is learning, the linkages between learners, what type of learning takes place, whose knowledge is included and integrated or discarded, and what is monitored (114, 115). Powerful stakeholders can dominate poorly implemented learning processes and assert the standing and influence of their own knowledge, thereby co-opting or misrepresenting other voices within communities (116). For example, power concentrated in the national government can stifle the potential contribution of learning and innovation at the local scale (117).

Experimentation applied at the wrong scale (for example, over short timescales or limited spatial scales) can lead to inappropriate management decisions or fail to provide an adequate basis for decision making (101). By its nature, experimentation in SES is risky and requires leadership, trust, networks, and resources. When a community’s social capital is so eroded that the community cannot afford to make mistakes, social capital might have to be built up or provided from other scales before experimentation can be considered (118). The learning process also needs to guard against maladaptive or dysfunctional learning, which threatens the system’s function or may require processes of unlearning. Institutional conditions are important in this respect as they act as barriers as well as facilitators of learning at different levels (114).

**Conclusion and Research Needs**

A long-held assumption in SES management is that learning and experimentation are important for understanding SES and provide an important (though not sufficient) basis for adapting management to ensure continued provision of ES in the face of disturbance and change. However, the evidence in support of learning and experimentation does not indicate what type of learning works and under what conditions. We know, however, that learning can play a key role in changing worldviews (P4) and that the design of learning processes, particularly the participatory aspects (P6), is crucial to guard against maladaptive learning and domination of the learning process by powerful subgroups.

There are numerous research gaps and challenges with respect to how learning promotes
Participation: active engagement of relevant stakeholders in SES management and governance

resilience of ES. First, there is a need for greater conceptual clarity on what loop learning and social learning are, as well as on how each contributes to the resilience of ES. Second, there is a need to better understand the conditions and institutions that support learning to inform the design of learning processes in practice. A third gap relates to how different types of knowledge can be integrated at the same scale and across scales to facilitate learning. Other key challenges include the influence and negotiation of power asymmetries in the learning process and developing methods to monitor and evaluate whether learning has taken place in a given setting.

PRINCIPLE 6: BROADEN PARTICIPATION

Participation refers to the active engagement of relevant stakeholders in the management and governance process (119). Participation can range from simply informing stakeholders to complete devolution of power (120) and can occur in different stages of a management process: from identifying problems and goals to implementing policy, monitoring results, and evaluating outcomes. The resilience literature generally considers participation for pragmatic rather than ideological (e.g., human rights) reasons, focusing on stakeholders with an active interest in the management of ES or with relevant local or scientific knowledge (101).

How Does Participation Enhance Resilience of Ecosystem Services?

Participation appears central to facilitating the collective action required to respond to disturbance and changes in SES and ES (121, 122). The participation of a diversity of stakeholders in SES management is suggested to improve legitimacy, facilitate monitoring and enforcement, promote understanding of system dynamics, and improve a management system’s capacity to detect and interpret shocks and disturbances (123, 124). Demonstrated outcomes of participatory processes include increased levels of cooperation between actors, increased transparency through greater sharing of information, and increased capacity to feed information directly into management decisions (103, 125). These factors are often necessary (but not sufficient) for responding to changes in SES through adaptation of management practices and institutions, and therefore contribute to maintaining the resilience of ES.

Participation can be particularly important in strengthening the link between information gathering and decision making. This link is considered vital for ongoing learning (P5) and effective decision making. Evidence from the Philippines and elsewhere suggests that participatory approaches tend to increase the comprehension and perceived validity of information and its use in decision making (125, 126). Evidence from China indicates that participation in monitoring can promote learning processes that create opportunities for consensus building, collective sense making, and action (127). In Ecuador and elsewhere, evidence points to a shift in perceptions and attitudes as a positive outcome of participatory monitoring (103). A shift in perceptions and attitudes can lead to a questioning of existing institutions and decision making, which may facilitate a transition to more appropriate governance arrangements that enhance the resilience of ES (P4) (16).

Participation of a variety of actors, including those with nonscientific or experiential knowledge, is thought to promote understanding of SES dynamics by providing a range of ecological, social, and political perspectives that may not be gleaned through more traditional scientific processes (114, 123). To what extent such greater understanding is actually achieved, and if and how it enhances the resilience of ES beyond increasing the capacity for collective action, is linked to gaps in our understanding of learning (P5) and difficult to establish from the existing literature.

Under What Conditions May Resilience Be Compromised?

Although ample evidence suggests that participation can contribute to enhanced resilience
of ES, this will not occur in all cases but depends on the participants, the process, and the social environment (119). Participatory strategies that fail to build social capital, or fail to effectively link to natural systems, can degrade the resilience of ES. For example, Büscher & Schoon (128) show how transfrontier conservation areas, promoted as “peace parks,” often lead to competition and conflict between stakeholders instead of the envisioned collaboration and mutual understanding needed for successful conservation efforts. Similarly, participation of groups focused on short-term gains rather than long-term resilience can degrade rather than enhance the resilience of ES. Who participates and what they contribute are context specific and need to be continually revised throughout the policy process or adaptive management cycle (119).

The success of participation further depends on the institutional setting in which it takes place. For example, weak forms of comanagement that promote the devolution of responsibility to local resource users without the authority to act to protect resources may degrade rather than enhance the resilience of ES. In Chilean fisheries and elsewhere, formalized comanagement agreements undermined previously strong local resource management institutions (70). The agreements added a layer of formal management structure between resource users and the resource, weakening local capacity to respond to changes in the resource base. A similar situation has been reported in Canada where government-driven participatory strategies, overlaid on unrecognized indigenous rights, hastened resource extraction as a way of asserting government over indigenous sovereignty (129).

**Conclusion and Research Needs**

The role of participation in ecosystem management is well accepted (104, 122). Participation appears to function mainly as a facilitating mechanism that promotes the capacity for learning (P5) and collective action in response to SES change. However, evidence highlighting the importance of participation is equally matched with evidence demonstrating situations in which participation may undermine the resilience of ES. A nuanced understanding of who participates, under what conditions participation is appropriate, and how participation takes place is therefore essential. The participation of stakeholders should not be accepted as beneficial to resilience of ES in all cases.

A key research challenge is to better understand how participatory processes support resilience under different conditions, such as different institutional settings, resource-poor versus resource-rich contexts, and urban versus rural systems. Second, we lack an understanding of the most effective processes for participation, including who should be involved and who decides on this, as well as of the timing, approaches, and tools for participative processes in different contexts. Third, there are very few empirical studies that demonstrate the outcomes of participatory processes for resilience of ES. Key gaps relate to the identification of indicators or other metrics to evaluate both the outcomes of participatory tools and processes and also the implications of these for ES resilience.

**PRINCIPLE 7: PROMOTE POLYCENTRIC GOVERNANCE SYSTEMS**

Polycentricity refers to a governance system with multiple governing authorities at differing scales (23). Governance is defined as the exercise of deliberation and decision making among groups of people who have various sources of authority to act and may be practiced through a variety of organizational forms (e.g., bureaucratic department, watershed council, nonprofit organization). In polycentric systems, each governance unit has independence within a specified geographic area and domain of authority, and each unit may link with others horizontally on common issues and be nested within broader governance units vertically. One of the key principles of polycentricity is to match governance levels to the scale of the problem (130).
It is thus particularly relevant to resources like ES that have strong multiscale aspects.

**How Does Polycentricity Enhance Resilience of Ecosystem Services?**

Although there is an absence of studies on the role of polycentric governance in the resilient provision of ES, there are many examples of how elements of polycentricity enhance the capacity of SES to sustain desired ES. Polycentric structures confer modularity and functional redundancy that can preserve key SES elements in the face of disturbance and change (P1, P2). For example, broader levels of governance can step in when lower levels collapse and fail. The US federal government’s capacity to protect endangered species in cases where local efforts prove ineffectual is one example (131). By contrast, where institutional failure occurs at the national and international levels, local-level conservation actions can provide functional redundancy by protecting species through assisted migration and other place-based actions (132).

Polycentric systems also provide opportunities for enhanced learning and experimentation (P5), as well as broader levels of participation (P6) in governance. Governance at multiple smaller scales enhances opportunities for participation and creates natural experiments for testing different policies (23, 52). One example is the collaboration between local and state governance units in the lobster fisheries of Maine (133), where local communities have crafted multiple individualized context-specific rules, often building on innovations from neighboring groups. Other examples include the interplay between local *ejidos*, the state, and the national government in Mexican forest governance (134); the importance of nested cross-scale linkages with higher levels of governance in the Seri fisheries of the Gulf of California (135); and comanagement of protected areas (136).

Polycentricity helps capitalize on scale-specific knowledge (e.g., traditional and local knowledge) to aid learning through sharing of information, experience, and knowledge across scales (101). Local levels with more direct linkage to resource provision and use provide the basis for experimentation and institutional diversity from which successes can be shared with others. This is particularly evident in local and regional water governance where polycentric governance structures facilitate participation by a broad range of governance actors, experimentation, and the incorporation of local, traditional, and scientific knowledge (137).

**Under What Conditions May Resilience Be Compromised?**

Polycentric governance raises three key challenges, which, if not resolved, may lead to degradation of ES at one or more scales. The first is that of scale mismatch (130). ES are produced at a wide range of scales, from local provision of food to global climate regulation. Matching governance levels to the scales of different ES may call for an impractically large number of governance arrangements. However, where a mismatch exists between the scale of governance and a particular ES, lack of understanding, enforcement, and resources at the appropriate scale may lead to failures, as, for example, in the lack of institutions governing global marine fisheries (93).

A second challenge is that of negotiating trade-offs between various ES users (3, 7). Trade-offs may occur when impacts are incurred by those not affecting or benefiting from an ES, or between conflicting goals and needs among users of current or potential ES. In such cases, a polycentric approach may lead to degradation of ES at some scales if powerful elites can externalize trade-offs from their area of interest (e.g., constituency). An example of this phenomenon is the trade-off between domestic energy security and mitigating climate change when countries determine oil and gas development policies at a national level but do not account for the impacts of these policies beyond their borders (138).

Trade-offs between and across both scales and user groups link to a third challenge: the process of resolving conflict and making
collective decisions over how to allocate trade-offs. One of the largest problems in SES governance arises from who bears the costs and who benefits from enhancing resilience in favor of particular ES (7, 121). Polycentric governance systems enable those dissatisfied with the political process at one scale to go “scale shopping” for a more favorable political venue in which to frame a specific issue, as when local nongovernmental organizations dissatisfied with their national government’s policies advocate for international regimes over the same issue (139).

Evidence further suggests that polycentric governance structures are most effective in securing resilience of ES in cases where groups have open communication, accountability for actions, and time to work together to build trust and social capital (121). An example is the traditional management of provisioning services in the Chisasibi First Nation of Cree (101). Where the conditions of open communication, accountability, and trust are not met, as in the management of the Everglades for a variety of regulating services, polycentric governance is less, or not, effective (71).

Polycentric approaches are just one tool of governance. Under some situations, particularly short timescales or crises where coordination across scales impedes necessary action, there may be other tools (including top-down coercion or market approaches) that alone may accomplish specific goals more effectively than through a polycentric system (140, 141).

Conclusion and Research Needs

Polycentricity contributes to the resilience of ES by providing a governance structure that facilitates other key resilience-enhancing principles, especially redundancy (P1), modularity (P2), learning and experimentation (P5), and participation (P6). However, simply establishing polycentric institutions is insufficient; the social processes enabling polycentric governance are essential to its success. These social processes include building trust and social capital, maintaining or developing strong leadership, and bridging scales through the use of explicit strategies (52, 123). In addition, coordination among scales and governance units, and negotiating trade-offs among ES users at different scales, is critical to effective polycentric governance.

Key knowledge gaps with respect to polycentricity and its role in enhancing resilience of ES revolve around the implementation of polycentric governance and monitoring progress over time. Specifically, to what extent can polycentricity be designed? And what are the key indicators for measuring polycentricity? There is also a need to better understand how polycentricity functions in different contexts and whether it is appropriate in all systems. In cases where polycentricity has failed, there is a need to better understand the mechanisms of failure: Is it due to the polycentric structures themselves, poor implementation of polycentric principles, or some other cause? Comparative analysis of different polycentric systems could greatly advance our understanding in this respect.

CONCLUSION

Ensuring an adequate and reliable flow of essential ES to meet the needs of the twenty-first century is an enormous challenge (1, 4). In a world undergoing rapid social-ecological change, enhancing the resilience of key ES to increasing levels of disturbance and underlying system change can make an important contribution to meeting this challenge. Although a definitive set of principles for enhancing the resilience of SES and the ES they produce does not yet exist, our review suggests that there is sufficient knowledge about a preliminary set of principles to provide practical guidance for enhancing the resilience of ES. At the same time, this review supports the conclusions of Ostrom (142) that there are no panaceas for environmental governance. None of the principles are universally beneficial, and all require a nuanced understanding of how, when, and where they apply, as well as how they interact with or depend on other principles. Context matters, and ensuring the enhanced resilience of ES depends
as much on how the individual principles are applied as on achieving an appropriate combination of principles.

We found evidence for the importance of all seven principles presented in this review, albeit none of the principles are fully established or understood. The roles of connectivity (P2), slow variables and feedbacks (P3), and participation (P6) in enhancing the resilience of ES are fairly well understood, and there is substantial evidence for their importance. While there is also substantial evidence for the importance of diversity (P1) and polycentricity (P7), the most important mechanisms by which these principles act to enhance the resilience of ES are less well understood, possibly because these principles are so multifaceted. In the case of understanding SES as CAS (P4) and learning (P5), both the evidence about the importance of these principles and the mechanisms by which they enhance the resilience of ES remain somewhat unclear, partly owing to a lack of conceptual clarity on what understanding CAS and learning actually are in the context of ES governance. Additional research is needed to clarify these two concepts, as well as to gain a clearer understanding of the most important ways in which diversity and polycentricity contribute to the resilience of ES.

This review also highlights the interdependence among different principles: Applying any one principle in isolation will rarely lead to enhanced resilience of ES. For instance, polycentric governance and effective learning both depend on the social capital and trust developed through participation, whereas connectivity may not enhance resilience in the absence of diversity among nodes. A preliminary conclusion from our review is that effective participation (P6) is a precondition for the successful application of learning (P5) and polycentric governance (P7), while diversity and redundancy (P1) act in combination with connectivity (P2) to increase resilience of ES. Understanding SES as CAS (P4) may be a precondition for all the principles, or at least may substantially enhance their effectiveness, but there is little clear evidence for this. Managing slow variables and feedbacks (P3) appears to be a more independent principle, although it has clear links to learning (P5), diversity (P1), connectivity (P2), and understanding SES as CAS (P4). Better understanding of the interdependencies among principles is a critical area for future research.

Our review emphasizes the paucity of empirical evidence supporting the different principles. This can be attributed to conceptual difficulties regarding many principles; operational difficulties in measuring the impacts of the principles on resilience of ES (6); more generally, the nature of SES as CAS; and the relatively recent focus on ES and resilience research. The complex interactions in SES make it challenging to isolate a particular system property or principle (e.g., diversity) and establish its connection to the resilience of ES (71). Even if the effect of a particular principle is known, the fact that SES evolve and change over time implies that causal links may change (89). Furthermore, the relevant system processes often happen over long timescales, which make it difficult to assess the effect of a principle within the time frame of a typical empirical study or management experiment (62). The indicators needed to monitor long-term, nonlinear, and variable change are generally not well developed and in some cases may require nontraditional methods and ways of thinking in their assessment. Much of the evidence in support of the principles is confined to a few well-developed, local-scale case studies, and this evidence is often drawn from experience with adaptive governance, which is a broad approach to managing SES that encompasses multiple principles. Isolating the contribution of individual principles is very difficult, and in fact, the separation between principles may be more of an analytical construct than a reflection of individual, separable factors operating within an SES.

There is a pressing need for a better understanding of how the principles can be operationalized and applied in different contexts. This is particularly challenging, given that the principles are interdependent and to some extent emergent. To what extent can, and should,
we design for them? And how do we best do so?

Comparative case studies as envisaged by the new international Programme on Ecosystem Change and Society (143) could provide a powerful basis for generating an understanding of the importance of different principles and combinations of principles for the resilience of ES under different conditions, as well as for piloting different approaches to their application. To some extent, the replication of case studies across space can substitute for the long time dimensions needed to understand changes in ES as factors, such as diversity or learning, are increased or reduced (144). Furthermore, a multiscale design can help broaden our understanding of the principles to larger scales, particularly the regional scale, and help determine how the resilience of ES at the regional scale depends on resilience at local and global scales.

Comprehensive frameworks that provide a basis for detailed, comparative, multiscale SES studies have been developed (1, 142) and provide a useful starting point. A stepped evidence-based approach in which one gradually builds knowledge of a complex system while learning about what works under specific circumstances may also be a useful way forward (92).

We highlight one final challenge: generalization. Much resilience science to date has either been incredibly general or very specific. To be useful, especially for addressing the pressing social-ecological problems society faces, we need a better understanding of the middle ground between these extremes: an understanding that enables sensitivity to context but is not entirely context dependent. This review has attempted to provide a useful step in that direction.

**SUMMARY POINTS**

We reviewed seven generic principles for enhancing the resilience of ES, i.e., the capacity of SES to sustain a desired set of ES in the face of disturbance and ongoing change. In practice, these principles are often highly interdependent and co-occur. Although some principles are better established than others, there is evidence that all are important. More research is needed to better understand the principles and how they can be operationalized and applied in different contexts. These principles include

1. **Maintain diversity and redundancy:** Response diversity in combination with functional redundancy is particularly important for maintaining ES in the face of disturbance. In general, ES produced by SES with high levels of diversity and redundancy tend to be more resilient than ES associated with low-diversity and low-redundancy systems. However, very high levels of diversity or redundancy come at the cost of increasing complexity and inefficiency, which tend to reduce the capacity for adaptation to slower, ongoing change.

2. **Manage connectivity:** Connectivity can enhance resilience by providing links to sources of ecosystem recovery after a disturbance or providing new information and building trust in social networks. However, if connectivity is too high, a localized disturbance can spread throughout the system or knowledge can become overly homogenized.

3. **Manage slow variables and feedbacks:** Managing slow variables and feedbacks is important for maintaining SES regimes that underlie the production of desired ES. However, there are substantial practical difficulties in identifying possible regime shifts and their consequences for ES, as well as the key slow variables that may trigger such shifts. Maintaining key regulating services as proxies for important slow variables may be a practical way forward.
4. Foster an understanding of complex adaptive systems: Fostering an understanding of SES as CAS may increase the resilience of ES by emphasizing the need for more integrated approaches, the importance of continual learning, and the pervasiveness of uncertainty in the management of SES. However, empirical evidence is limited. In practice, understanding SES as CAS co-occurs and co-emerges with approaches that emphasize learning, experimentation, and participation.

5. Encourage learning and experimentation: Learning about social-ecological dynamics through experimentation and monitoring is essential for enabling adaptation in response to changes in SES and ES. Learning at societal levels requires trust and appropriate relationships and institutions to flourish. The optimal ways in which learning for resilience might be facilitated are currently unclear and require further research.

6. Broaden participation: Participation is important for building trust and relationships; it facilitates the learning and collective action needed to respond to change and disturbance in SES. However, a nuanced understanding is needed of who participates, under which conditions participation is appropriate, and how participation takes place.

7. Promote polycentric governance systems: Polycentricity provides a governance structure that enables other key resilience-enhancing principles, especially learning and experimentation, participation, modularity, and redundancy. Coordination among governance units, negotiation of trade-offs between users, and social capital and trust are essential for effective polycentric arrangements.

**FUTURE ISSUES**

Our review suggests the following key areas for future research and application:

1. Improved conceptual clarity and a mechanistic understanding are needed of the individual principles, the conditions under which they apply, and the interconnections among principles.

2. Comparative studies and meta-analyses could help to better understand the principles, their interactions, and the conditions under which they apply. Improved frameworks that provide a common understanding of the key features of SES would greatly assist in developing such studies.

3. Traditional evidence-based approaches are difficult to apply in the context of CAS and need to be complemented by new approaches and tools to study the dynamics of SES.

4. A better understanding of how to operationalize and apply the principles in different contexts is needed. The most important needs are understanding how the principles can be applied in collaboration with key stakeholders, and developing better measures to evaluate success.

5. To operationalize the principles, there is a critical need to understand and develop institutional arrangements and governance systems that facilitate the emergence and application of the principles, and provide a balance between control and flexibility.
DISCLOSURE STATEMENT

The authors of this article are members of the Resilience Alliance Young Scientists (RAYS) network. Dr. Martin Robards directs a program for the Wildlife Conservation Society and is on the Board of two other environmental nongovernmental organizations. The other coauthors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

We acknowledge the legendary Ralf Yorque Jr. for her continued ability to inspire us during the inevitable surprises that this project entailed. Colleagues who acted as cross-examiners in the mock court workshop gave hugely valuable input on the first iteration of this review: Elinor Ostrom, Katrina Brown, Frances Westley, Per Olsson, Mike Jones, Line Gordon, Marty Anderies, and Christo Fabricius. We also thank RAYS members who acted as devil’s advocates and discussants at this workshop: Victor Galaz, Terry Iverson, John Parker, Beatrice Crona, and Jacopo Baggio. We greatly appreciate the inputs of panelists at the Resilience Propositions on Trial panel, held at the Resilience 2011 Conference. We thank the Resilience Alliance surprises group for the original inspiration for this paper. R.B. was supported by a Branco Weiss Society in Science Fellowship and a fellowship from the Stellenbosch Institute for Advanced Study (STIAS) while coordinating the article. M.S. was supported by a Branco Weiss Society in Science Fellowship and acknowledges the Project Besatzfisch funded by the German Ministry of Education and Research in the Program for Social-Ecological Research (grant 01UU0907). G.C. acknowledges a Rhodes University postdoctoral fellowship. V.D. is supported by a European Research Council grant awarded to Marten Scheffer and by a Marie Curie fellowship. L.S. thanks Ebba och Sven Schwartz Stiftelse for support.

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