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Original Contributions

Adaptive Capacity of Social-Ecological Systems: Lessons from Immune Systems

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Abstract: How do systems respond to disturbances? The capacity of a system to respond to disturbances varies for different types of disturbance regimes. We distinguish two types of responses: one that enables the system to absorb disturbances from an existing disturbance regime, and one that enables a system to reconstruct itself after a fundamental change in a disturbance regime. We use immune systems as a model for how systems can deal with disturbances, and use this model to derive insights in adaptive capacity of social-ecological systems. We identify a tension between the two types of responses where one benefits from learning and memory while the other requires fast-turnover of experience. We discuss how this may affect building up adaptive capacity of social-ecological systems.

Key words: disturbance regime, adaptive capacity, social-ecological systems, immune systems, resilience

Introduction

Social-ecological systems (SESs) are a broad class of systems, from urbanized regions to hunter gatherer societies, in which both social processes among humans as well as ecological processes are included, and where the ecological and social components interact (Berkes and Folke, 1998). SESs experience disturbances at different temporal and spatial scales. For the long-term functioning of a SES in a certain desirable configuration, the biological and social agents in the system need to be able to cope with expected and surprising disturbances. During human history, societies have experienced successes and failures in finding a fit between social and ecological systems (Diamond, 2005). Human-induced global changes increase the challenges of managing SES. Therefore, it is important to explore what determines the ability of a system to respond to change. Understanding system characteristics that contribute to the ability to cope with change is essential for defining sustainable interactions between humans and their environment. Unfortunately, the discussion of responses to change for social-ecological systems is murky. First, it is not clear how to precisely define the boundaries and components of a SES. Second, a variety of temporal and spatial scales complicate the analysis by making any analysis scale-dependent. We attempt to explore a different system, the immune system, as a model for how a system may respond to change at a variety of scales. There are obvious important differences between immune systems and SESs, but nevertheless we think that this exercise provides interesting insights for scholars interested in the interface between ecological and health sciences.

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White and Pickett (1985, p 7) define a disturbance as ''any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment.'' A disturbance regime is defined in terms of scale, frequency, predictability and severity (White and Pickett, 1997; Turner et al., 1998). Ecologists tend to focus on natural disturbances, like fire, floods, hurricanes, insect and disease outbreaks, etc. Within social-ecological systems, other types of disturbances need to be included such as abrupt changes in regulations preferences, market opportunities, and accessibility.

We will analyze how systems deal with changes in disturbance regimes. Such a regime change might be quantitative changes in scale, frequency, predictability, and severity of disturbance. However, those dimensions of a disturbance regime might remain the same, but the type of disturbance might change qualitatively. For example, a disturbance regime has changed qualitatively when disturbances of fire are replaced with disturbances of floods, or the change may be quantitative when the frequency of fires decrease and intensity increases in response to fire suppression. Global change can also cause change in disturbance regimes by altering the frequency and intensity of El-Niño events. Furthermore, globalization of economies can make small-scale farmers in developing countries sensitive to changes in prices and preferences at the global market.

In this article, we try to simplify the problem of scale by defining two levels. The first level relates to behavioral responses of an agent. A community that is exposed to regular disturbances, like tornadoes or forest fires, may develop organizational and infrastructural responses to absorb these disturbances more easily. Such a community derives adaptive capacity or, in other words, resilience (Holling, 1973). The second level relates to response of a population of agents to a disturbance over a period of generations. This might be cultural or genetic evolution. The disturbance regime that affects the communities makes a fundamental change and various communities may not be able to deal with it. However, a few communities may find ways to adapt, so that it functions in the new disturbance regime. Eventually, such transformations of cultural units of selection might be imitated by other communities. Obviously, this is not possible when the unit of selection is genetic information.

Although this article is meant to generate insights on how SESs may cope with disturbances, we will discuss the issues of adaptive capacity for immune systems in the expectation that this may provide insights for SESs. There is an important reason for this. Immune systems are typical examples of systems that are shaped by disturbance regimes. The evolved immune systems are robust in functioning in the world's diverse disease ecologies. Understanding principles that make immune systems able to deal with disturbances at different levels of scale may also help us to focus our attention in SES to particular phenomena. One important aspect of the immune system is that the system is well defined, unlike SES (although some argue differently [Butzer, 1980]), but also connected to other systems in the body (e.g., endocrine and nervous systems) in complex ways that might mirror connection in SES between biological and social parts of the system.

A tension may exist between both levels of adaptation (organisms and population), since organisms adapted to a certain disturbance regime may require high investments of energy or resources to keep up the defense mechanisms. This may affect the ability of the organisms to produce sufficient offspring. A broad indication is that certain organisms with a longer lifetime invest in adaptive immune systems, but populations of these organisms are less able to genetically adapt to new disturbance regimes. Organisms with a short lifetime have less need to invest in adaptive immune systems, but are more likely to adapt genetically if there is sufficient genetic variation. In this article, we will discuss these trade-offs in more detail by comparing how different types of organisms have evolved to deal with disturbances. These trade-offs in immune systems directly relates to the choice of adaptation strategy of social agents in a SES. On the one hand, one can invest in strategies to reduce the impact of a disturbance (dikes, warning systems, etc.). On the other hand, one can decide not to make these investments and react to a disturbance when it happens. Which strategy is preferable depends on the costs and benefits of the disturbance regime in the broader context of the SES.

The rest of the article is built up as follows. In section 2, an overview is given of the characteristics of systems that make them robust or resilient. Those are the elements that we will focus on in our comparative analysis of immune systems. In the third section, a brief introduction into the basic mechanisms of immune systems is provided. Then we analyze the system characteristics of section 2 to see if they also hold for immune systems. Section 5 will discuss immune systems for different levels of scale. In section 6, the problem of losing adaptive capacity due to our ''management'' of the immune system is discussed. We end with a discussion of how our insights from immune systems may be beneficial for understanding of adaptive capacity in social-ecological systems.

What Makes Systems Able to Cope with Change?

In most studies, redundancy has been mentioned as a key factor for making systems cope with changes: redundancy of components, information, tasks, connections, etc. (Kirschner and Gerhart, 1998; Csete and Doyle, 2002; Low et al., 2002; Staber and Sydow, 2002; Krakauer, 2003; Sole et al., 2003). Redundancy enables a system to maintain its function when a component is lost, and the redundant component takes over the function. This is the case for engineered, for institutional, and for biological systems. An example of an engineered system is a Boeing 777 that has about 150,000 different subsystem modules, but can continue to fly when many modules have been knocked out (Csete and Doyle, 2002). This redundancy is built in since the ability of the Boeing 777 to continue to function when modules fail is crucial. This might not be the case for products that have less of an effect on the lives of users during failures such as coffee machines, which can be developed more efficiently but with less robustness. An example of redundancy for institutions is informal and formal rules of resource management (Low et al., 2002). Lobster fisheries in Maine have developed a comprehensive set of rules to govern their use of resources, next to the existence of formal state and federal regulations on lobster fisheries (Low et al., 2002). The redundancy of genes is an example from biology. Experiments show that deleting a gene in an organism often has little phenotypic effect due to existence of duplicate genes or compensation of alternative metabolic pathways (Gu et al., 2003).

Modularity is a second key factor (Kirschner and Gerhart, 1998; Csete and Doyle, 2002; Staber and Sydow, 2002, Krakauer, 2003; Sole et al., 2003). With modularity, we mean that a system has different functional parts or modules that can evolve somewhat independently. The modules might be loosely linked with each other, but a failure in one module does not severely affect the others, as would happen if they were tightly linked. Sufficient links are required since modules might learn from the activities happening in other modules. Within social science, this is known as polycentricity. Ostrom et al. (1961) identified a polycentric metropolitan area as having many centers of decision making which were formally independent of each other, but one could learn from experimentation in the various centers (McGinnis, 1999). Modularity relates to the concept of (genomic) compartmentation in biology, which is the division of a cell's total genomic potential into partially independent subsets of expressed genes (Kirschner and Gerhart, 1998). This reduces the change of pleiotropic damage by mutation and increased phenotypic variation.

A third general factor is diversity in agents or links (Kirschner and Gerhart, 1998; Staber and Sydow, 2002). In complex systems, different components can become specialized in different tasks. In organizations, a diversity of connections is important for the creation of a diverse portfolio of knowledge or a shared organizational mind (Staber and Sydow, 2002). In systems with low diversity, there is less chance of creating new ideas, components, or connections. A population of organisms with the same ability to initiate an immune response will be hit hard when a harmful new disease enters the population. With genetic diversity to create new antibodies, at least a few individuals in the population might be able to resist the new disease. Tinkering, mutations, or making errors are essential to derive new components and links in a system (Kirschner and Gerhart, 1998). In a modular system, such novelty can be tested without severely disturbing other components. If the innovation is beneficial, it might be replicated. In the case of a novel disturbance such as a disease, it is essential that a system is able to generate new responses.

Immune Systems

The immune system maintains the health of the body by protecting it from invasions by harmful pathogens, such as bacteria, viruses, fungi, and parasites. The immune system tries to detect and eliminate those harmful pathogens, and also remembers successful responses to invasions and can reuse these responses if similar pathogens invade in the future. Adaptive capacity of immune systems relate to the distributed system of a highly diverse set of modules (lymphocytes) to detect harmful pathogens, where redundancy of modules lead to the possibility that pathogens can be detected (with different affinity) by different types of modules.

From comparative immunology we know that immune systems vary among organisms, but there are also striking similarities (Beck and Habicht, 1996; Cooper, 2003; Du Pasquier and Smith, 2003; Warr et al., 2003). All organisms have the ability to distinguish self from nonself.

Self-recognition is probably basic to all animal life and allows each individual to maintain its genetic integrity (Cooper, 1990). Even sponge, amoebae, and slime molds can distinguish self from nonself. Phagocytosis of foreign particles, the first line of internal defense, is also shared among animals. Phagocytic cells travel through a circulatory system, or when the organisms have no circulatory system, fluid-filled body cavity or tissues. These cells are able to detect and engulf extracellular molecules and materials, clearing the system of both debris and pathogens. Recognition is also a key process in SESs since detection of trustworthy other social agents is crucial to solve collective action problems. From experimental research, we know that the likelihood of humans to cooperate depends on the ways information about reputation is exchanged, from face-to-face communication to reputation scores in eBay and curriculum vitae (Ostrom, 2000).

In our view, the main advantage of the adaptive immune systems is the ability to match the spatial and temporal defense mechanisms to those of pathogen evolution. There are disadvantages of being a large, long-lived vertebrate host compared to small and short-lived pathogens (McDade and Worthman, 1999). Viruses and bacteria multiply rapidly, with generational intervals in the order of minutes or hours, which provide them a great opportunity for mutation and evolutionary genetic change. Long-lived vertebrates can never match the pace of pathogen evolution, but the adaptive immune system provides an appropriate evolutionary adaptation to this mismatch in scale.

The adaptive part of the vertebrate immune system consists of a class of white blood cells called lymphocytes, which circulate the body via the blood and lymph systems. Their primary function is to detect pathogens and assist in their elimination. The immune system maintains a diverse repertoire of lymphocytes with different receptors in order to eliminate different pathogens. To achieve this diversity, the immune system constantly creates new lymphocytes with new receptors. These are subject to selection processes that favor lymphocytes that bind to pathogens with high affinity. A memory of successful lymphocyte responses to pathogens is maintained to speed up future responses to those and similar pathogens.

During the first response to a new pathogen, the immune system learns to recognize it by generating new lymphocyte receptors and selecting those that are successful, as described above. This response is slow and the organism may experience illness before the infection is controlled. If the same or similar pathogens invade in the future, the immune system will respond much more quickly because it maintains a memory of successful responses from previous infections. However, there is only a limited memory capacity so memory can be lost if the body is not reinfected occasionally.

An effective immune system prevents the organism from illness, like effective environmental policies and resource governance prevents SESs from conflicts to solve collective action problems on shared resources. But like organisms experience illness for novel pathogens, SES need to experience struggle to find technological, cultural, and political solutions for new challenges. Once successful solutions are found, it is key to remember and imbed them in institutional, cultural, or technological systems. There is especially an increased interest in traditional knowledge and how different societies maintain memory about rare disturbances (Berkes and Folke, 1998).

The immune system of vertebrates needs to adapt to the local disease ecology the moment the organism is born. Infants are vulnerable since each pathogen is a novel pathogen. There are a number of ways the immune system and the organism adapt to novel exposures. First, antigen experience, accumulated by the mother, is transferred to newborn animals. This provides a significant passive immunity during the first months of the offspring's life when it is acquiring immunity to local pathogens. This occurs through lactation in mammals (McDade and Worthman, 1999) and through egg constituents in birds (Apanius, 1998). Invertebrates also transfer immunity to offspring (Little et al., 2003). Second, the number of lymphocytes are the highest just after birth and drop slowly to the adult level during development (Apanius, 1998; McDade and Worthman, 1999). The high diversity of lymphocytes gives the young animal the ability to test a large variety of responses to the local disease ecology. When the vertebrate is mature, the adaptive immune system is sufficiently trained to handle new pathogens in the local disease ecology. Movement to an environment with a new disease ecology might be problematic. As McDade and Worthman (1999) hypothesize, "the immune system apparently has been designed to maximize lymphocyte diversity and responsiveness early in life, thereby accelerating the somatic evolution process that minimizes the high costs of immunological inexperience and adapts each individual to the local disease ecology" (p 712). As we will discuss later in this article, SESs adapt to their disturbance regime, which may make them vulnerable to a (human-induced) change of the disturbance regime.

From an evolutionary ecology perspective, the question is how costs of immune defense are balanced between growth, reproduction, or survival of the organism (Lochmiller and Deerenberg, 2000), like environmental economists are interested in trade-offs between economic development and the costs of environmental policies. Additionally, evolutionary ecologists are interested in the specificity of the immune response (Schmid-Hempel and Ebert, 2003). Both costs and specificity are important for determining how host immune traits and pathogen infection traits evolve and potentially coevolve. In an environment where pathogens are abundant, it would be advantageous to invest in a strong immune defense mechanism, whereas, in an environment with variable food resources and few pathogens, investing in a strong immune defense may be detrimental. If a highly specific immune response is necessary in order to successfully defend, then it may not pay to mount a response unless the response will be effective. One interesting recent observation is that there may be a trade-off between different types of immune responses such that an organism cannot mount both a general and a specific response (Mallon et al., 2003).

In sum, organisms have developed a rich portfolio of (adaptive) immune and life-history responses to deal with disturbance regimes. The different types of responses seem to relate to the temporal and spatial scale with which the disturbances and organisms interact.

Scales of Adaptation

The immune system works on a variety of spatial and temporal scales. For example, on extremely small spatial and temporal scales are the molecular dynamics of the interacting antibodies, cytokines, complements, and their respective binding partners. Cytokines are molecules used for cell-to-cell communication. Antibodies and complement are molecules that bind to antigens and start the destruction of pathogen cells. For very small pathogens (i.e., viruses), the scale of molecular interactions might be of primary importance for determining the fate of an infection. These interactions take place on the order of seconds and at maximum extent within a cell or on the near surface of the cell. As the scale of the interaction is increased, we have the lymphocyte response of the immune system. This requires lymphocytes to recognize attack and signal other lymphocytes to the defense. With time, more signaling chemicals are released and more lymphocytes are recruited to the defense. Within a matter of seconds and over the course of a few days, the lymphocytes begin attacking the foreign invaders. Together, these are the molecular and cellular immune response.

Next, we have acquired immunity where antibodies are proliferated against a specific antigen. As this process continues, the antibody population becomes more specific and the concentration increases. This process can take a few weeks for a newly encountered pathogen type or can be very fast (days) for a pathogen that the organism has experienced. An important aspect of this process and scale is that of memory. In some cases, memory can last for the duration of the organism's life. So, for humans, adaptive immunity can last for decades. Evolution is the last scale and is defined by a time scale of generations of a species.

Adaptive capacity also functions at different scales within social-ecological systems. When the unit of analysis is a social agent, which may vary from an individual to a state, learning, experimentation, and memory are crucial for the resilience of the system. For example, a community that develops response mechanisms to deal with a particular disturbance regime is considered to be one social agent at one scale. Within the community, different functional components are instrumental for exploration (entrepreneurs, innovators and experimenters, visionaries), for learning (interpreters, networkers, stewards, and reinforcers), and for memory (knowledge carriers) (Folke et al., 2003, p 268). These different functional groups maintain and stimulate together the adaptive capacity of a community.

As in immune systems, not all social agents are able to adapt themselves when the disturbance regime changes. At the population level, the immune system adapts over generations as a consequence of the selection pressure of the local disturbance regime. In social-ecological systems, cultural adaptations evolve at the population level of SESs as a consequence of successes and failures of SESs to cope with disturbances.

Losing Adaptive Capacity

The developmental environment can greatly influence the ability of an individual to develop a functional and robust immune system. When the developmental environment changes from what was experienced during the evolutionary history of the organisms, problems can arise that may lead to a loss of adaptive capacity. Three such influences are the prevalence of pollutants in the environment, changes in nutrition, and exposure (or lack of exposure) to pathogens and parasites when young. Much of this research is correlative, such that causal mechanisms are not known, but in the case of pollutants, there is some good experimental evidence that chemicals that mimic hormones are capable of producing developmental abnormalities at very low doses (Hayes et al., 2002). With regards to pollutants, heavy metals and endocrine disrupting chemicals are thought to be most important. Nutrition also plays a role in maintaining immune function because the antibody response is known to be metabolically expensive.

A history of exposure to pathogens and parasites is thought to help the body develop a strong immune system. The role of pathogen exposure on the immune system has been termed ''The Hygiene Hypothesis.'' The hygiene hypothesis started as an observation that children who grew up in rural areas were less likely to develop allergy and asthma (Kilpelainen et al., 2000; Von Ehrenstein et al., 2000). It is thought that exposure to pathogens and parasites in early childhood causes a change in cytokines (Yazdanbakhsh et al., 2002; Liu and Murphy, 2003). Curtain cytokines are correlated to the occurrence of allergy and asthma. Therefore, early priming of the immune system through constant disturbance by antigens sets up an immune system that is more capable of responding appropriately to future disturbances.

This hypothesis is relevant to the current discussion on SES because it states that a lack of disturbance when young (pathogen exposure) causes a poorly functioning immune system to develop. This is based on the observation that children that grow up on farms and in a day-care environment (presumably where pathogen exposure is high) are less likely to develop allergies and asthma when adults (Kilpelainen et al., 2000; Von Ehrenstein et al., 2000; Liu and Murphy, 2003). This is an appealing idea because SESs are often characterized by disturbance regimes. Therefore, a possible response to a lower frequency of disturbances is a reduction of the extent that a social or an ecological system can cope with future variability and disturbance. A typical example is fire suppression in many forests and rangelands. Originally, these ecosystems were adapted to a high frequency of small fires. Human intervention reduced the frequency of fires and, as a result, fuel has been built up in forests leading to large, intensive and destructive fires (Holling, 1986). In rangelands, fires prevent shrubs from out competing grass, but fire suppression by pastoralists (to avoid the short-term loss of grass biomass), leads to long-term shrub encroachment (Carpenter et al., 2001). Like the hygiene hypothesis, human intervention in SES may change disturbance regimes to meet short goals but make the system more vulnerable to disturbances in the long term.

The increased used of drugs has led to problems of resistance development (Trape et al., 1998; Tenover, 2001). By using drugs, we may provide the immune systems with some help to handle invasions of a selected set of harmful pathogens. Unfortunately, the role of mutations and the ability of bacteria to exchange genetic information was underestimated (Tenover, 2001). Furthermore, drugs are used too often, even when not necessary, and the creation of selective pressure by intense use of drugs in hospital settings leads to the proliferation of drug-resistant bacteria. Drugs were meant to be additional tools to fight against invasions, but the overuse of drugs made the enemy only stronger.

Like immune systems, social-ecological systems can lose adaptive capacity by suppressing disturbances. The well-known example is the suppressions of fire that lead to an accumulation of fuel on the forest floor and an accumulation of tree biomass (Holling, 1986). Also, a lack of fire leads to suppression and elimination of fire-resistant species through competition from other species because there is a cost to being fire resistant. In addition, when a fire eventually occurs, it will be hot and intensive, affecting soil conditions and the capacity of the forest to recover. This causes the system to change from a forest (large woody vegetation) to a nonforest (grass and shrub) system. Management of SESs can reduce the risk of system change to an undesirable state by tolerating small crises (fires or an immune response) in order to prevent a large crisis (ecosystem conversion or bacterial resistance).

Adaptive Capacity of Social-Ecological Systems

The previous examples in immunology make us aware that there is a potential conflict between adaptation to a particular disturbance regime and the adaptive capacity to respond to a change in disturbance regimes. If a society is confronted with a stable or predictable disturbance regime, it may develop adaptive capacity to reduce the impacts of specific disturbances. In fact, SESs which exist over a long period have often been adapted to a particular disturbance regime [Janssen et al., in review]. Colding et al. (2003) report several examples of such adaptations. The first example is the adaptation of traditional agriculture in Polynesia with cyclones. These cyclones are unpredictable, severe disturbances. In Samoa, cyclonic storms are relatively frequent (40 cyclones in the last 160 years, with severe cyclones at intervals of 20–30 years). The agricultural system is embedded in a sophisticated institutional structure that organizes community response to periodic environmental disasters. Adaptations are crop diversity, cooperation in planting and restoration after cyclones, and emergency food storage. In other areas of Polynesia, where the cyclones decrease in frequency, the agricultural system has been transformed into monocultures of cash crops. In the event of a severe cyclone, those islands are not able to recover without outside help, but rely on outside subsidies for survival. The change in agricultural system caused by access to global markets has led some islands to transform to monocultures, but at the cost of losing their adaptation to cyclone events. For islands with a high intensity of cyclones, the benefits of adapting to the global market do not (yet) outweigh the costs of losing their traditional agricultural system that is adapted to the particular disturbance regime of cyclones.

A similar story can be given for Bangladesh. Char-dwellers, live on chars that are islands made up of sediment deposits. These chars might be washed away in floods, and periodically a household needs to move. They have built adaptations to the disturbance regime by crop diversity, erosion-buffering, and flexible property rights systems. Moreover, the agricultural system is dependent on periodic flooding. Due to top-down flood control measures imposed by the central government, like building dikes, the river morphology changes the locations of flooding. This leads to frequent movement in water supply for agriculture. The question is whether the people of Bangladesh can derive new adaptive capacity to the changed disturbance regime caused by changed river morphology, or whether the disturbance regime has changed so much that a transformation of the SES is required to continue living in Bangladesh.

Carlson and Doyle (2002) discuss the notion of systems being robust but fragile. This refers to systems that are adapted to certain disturbance regimes, but can be fragile to new types or frequency of disturbance. Perhaps, there is a trade-off between specialized adaptation and adaptive capacity to regime changes, which would be in line with evolutionary biology where selection (adaptation) reduces additive genetic variance. And the response to selection depends on additive genetic variance. If we study dynamic systems, we do not only need to take into account disturbance regimes, but also how disturbance regimes may change, and how systems may deal with such changes.

If a system is confronted with a stable disturbance regime, it might build up mechanisms to cope with these disturbances. Since the disturbance regime is stable, it might be worthwhile to invest in learning and memory. Many studies are performed in ecology documenting how ecosystems have adapted to certain types of disturbance regimes (Pickett and White, 1985). We argue that this is common in SESs that have developed under stable patterns of disturbance.

Less well-studied are systems in which the disturbance regime changes significantly. From evolution, we know that when the environment changes drastically, a large amount of species may become extinct, providing new open niches for other species to invade. Maybe species do not specialize in building adaptive capacity to regime shifts, but some species are generalists, using many different resources, while others specialize on a small subset of available resources. Moreover, some species are characterized as a ‘‘metapopulation,’’ where local populations frequently go extinct and are recolonized by other populations. Species of metapopulations are often adapted from quick reproduction in newly occupied habitats and dispersal among habitat patches. This process itself could be seen as an SES that is adapted to severe changes in the disturbance regime.

Conclusions

Due to human-induced changes of the environment, changes in disturbance regimes are to be expected, like shifts in climate regimes, disease ecologies, and technology. How can social-ecological systems be able to adapt to such regime changes without severe human suffering? From immune systems, we can learn that systems that successfully deal with change in the disease ecology do not focus on learning and remembering adaptive responses to current local disturbance regimes in periods of rapid change. Instead, there is a need to maintain a high diversity of possible responses or be able to generate a high diversity of possible responses, in order to adapt at the population level. Therefore, it is crucial to maintain institutional diversity and institutional innovation. The current globalization trend leads to harmonization and standardization of institutions, and this reduces the ability to adapt to future changes in disturbance regimes. Globalization, however, may also lead to an opportunity to acquire new or underutilized institutional diversity, memory, redundancy, and modularity. Hence, it is crucial to understand, identify, and maintain the diversity of institutions for ecosystem management (Folke et al., 2003; Ostrom, 2005).

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