

# PROMOTING RESILIENCE

# ERIC DESJARDINS

Rotman Institute of Philosophy and Department of Philosophy, University of Western Ontario London, Ontario N6A 5B8 Canada

E-MAIL: EDESJAR3@UWO.CA

#### GILLIAN BARKER

Rotman Institute of Philosophy and Department of Philosophy, University of Western Ontario London, Ontario N6A 5B8 Canada

E-MAIL: GBARKER5@UWO.CA

# Zoë Lindo

Department of Biology, University of Western Ontario London, Ontario N6A 5B8 Canada

E-MAIL: ZLINDO@UWO.CA

# CATHERINE DIELEMAN

Department of Biology, University of Western Ontario London, Ontario N6A 5B8 Canada

E-MAIL: CDIELEM@UWO.CA

# Antoine C. Dussault

Département de Philosophie, Université de Montréal Montréal, Québec H3C 3J7 Canada

E-MAIL: ANTOINECDUSSAULT@HOTMAIL.COM

# KEYWORDS

resilience, conceptual pluralism, resilience thinking, response diversity, functional redundancy, complex adaptive systems, social-ecological systems, adaptive management

#### ABSTRACT

Broadening contingents of ecologists and environmental scientists have recently begun to promote ecological resilience both as a conceptual framework and as a practical goal. As some critics have noted, this growing interest has brought with it a multiplication of notions of ecological resilience. This paper reviews how and why the notion of ecological resilience has been adopted, used, and defended

The Quarterly Review of Biology, June 2015, Vol. 90, No. 2 Copyright © 2015 by The University of Chicago Press. All rights reserved. 0033-5770/2015/9002-0002\$15.00

in ecology since its introduction by C. S. Holling in 1973. We highlight the many faces of ecological resilience, but unlike other reviewers who see these as disunified and confused, we interpret ecological resilience as an evolving, multidimensional, theoretical concept unified by its role in guiding practical response to ecological and environmental challenges. This perspective informs a review of some of the factors often recognized as favoring resilience (structural and response diversity, functional redundancy, modularity, and spatial heterogeneity); we show how the roles and relationships of these factors can be clarified by considering them in the theoretical framework of Complex Adaptive Systems (CASs).

#### Introduction

RESILIENCE is a central notion for several biological disciplines, including physiology (Tusaie and Dyer 2004), ecology (Holling 1973; Pimm 1991; Shrader-Frechette and McCoy 1993; Brand and Jax 2007; Myers-Smith et al. 2012), and psychology (Luthar et al. 2000; Fletcher and Sarkar 2013). As one might expect, applying this notion to a diverse array of phenomena has led to conceptual divergence or pluralism. The resulting conceptual divisions are often merely linguistic, but in discussions about the usage of "resilience" in ecology they reflect deep theoretical issues. In 1973, C. S. Holling published a seminal paper titled Resilience and Stability of Ecological Systems, in which he distinguished two properties related to the capacity of ecosystems to stay "the same" over time:

One can be termed *stability*, which represents the ability of a system to return to an equilibrium state after a temporary disturbance; the more rapidly it returns and the less it fluctuates, the more stable it would be. But there is another property, termed *resilience*, that is a measure of the persistence of systems and of their ability to absorb change and disturbance and still maintain the same relationships between populations or state variables (Holling 1973:14, emphasis added).

These two properties came to be identified as "engineering resilience" and "ecological resilience" (Holling 1996), and we will look more closely at this key distinction momentarily. But the story has become more complex: recent analyses (e.g., Brand and Jax 2007; Myers-Smith et al. 2012) suggest that researchers interested in "ecological resilience" sensu Holling have recently been vigorously multiplying definitions, and conceptual pluralism is now rampant. Most commentators are critical of this proliferation. Brand and Jax

(2007), for example, allege that ecologists in this tradition have been diluting or clouding the original meaning of this important theoretical term—the lynchpin of Holling's framework—endangering "both conceptual clarity and practical relevance" (Brand and Jax 2007) and preventing theoretical progress. Although we agree that diverse aspects of "ecological resilience" have become salient since Holling's original formulation, we want to reconsider the claim that this undermines conceptual clarity and theoretical development. As our review will show, the short history of "ecological resilience" can be seen as a process of conceptual fine-tuning, adjusting the relationship of "ecological resilience" to two core ideas: first, the capacity to absorb or tolerate change and, second, the persistence of a dynamically defined state. Moreover, we will suggest that the changes that have accrued in these conceptual relationships have not impaired theoretical development, but have instead supported the development of a more comprehensive and fruitful theoretical framework called "resilience thinking." Once we look beyond the concept of ecological resilience and the set of properties it identifies, we see an organizing principle—an ideal that shaped (and was shaped by) the development of a more inclusive analytical framework geared primarily toward *practical* outcomes in Social-Ecological Systems (SESs).

We begin by presenting a review of central work on "ecological resilience" that confirms and documents the multiplication of definitions, but instead of concluding that this diversity brings confusion and dilution, we argue that these developments have been fruitful. They offer heuristics, models, methods, and goals for researchers working toward an improved understanding of linked

systems of human and nature. The promotion of "resilience" is thus better conceived as a unifying force that brings together a host of environmental, ecological, and social science disciplines in the service of overarching practical goals.

Building on this conceptual review, we then examine some of the general systemic properties influencing the resilience of SESs, which must be considered by practitioners seeking to promote resilience in these systems. We argue that resilience depends on various interdependent properties of Complex Adaptive Systems (CASs): diversity of elements and diversity in how these respond to change, functional redundancy, spatial heterogeneity, and diversity of connections between elements and processes at various scales. We will show how these aspects of complexity can apply to SESs and how they determine the capacity of SESs to adapt and transform.

# THE EVOLUTION OF "ECOLOGICAL RESILIENCE"

Let us return to Holling's initial cleavage between ecological and engineering resilience. Why did Holling find it necessary to draw this distinction? Several reasons are important here. First was a divergence between the concerns of mainstream theoretical ecologists and those of ecologists involved with the practical aspects of resource management. Theoretical ecologists were for the most part interested in engineering resilience, and had very little to say about ecological resilience. Holling (1973) attributed this tendency to the influence of classical physics in the field, which resulted in an emphasis on the quantitative instead of the qualitative, and in particular in the extensive use of one quantitative construct: a simple conception of resilience as the "ability of a system to return to an equilibrium state after a temporary disturbance; the more rapidly it returns and the less it fluctuates, the more stable it would be" (Holling 1973:14). This traditional view of ecological phenomena, which Holling saw as "less a meaningful reality than a perceptual convenience" (Holling 1973:1), embraced what Holling came to call an "equilibrium-centred view"—describing the

behavior of ecological systems in their close-to-equilibrium state. Noting that such systems are often far from equilibrium, however, Holling saw a lacuna here. He saw a need to develop a notion of stability that could better account for the changing and unpredictable behavior of ecological systems and their capacity sometimes to persist despite such apparent disorder. He argued that "[d]ifferent and useful insight might be obtained . . . by viewing the behavior of ecological systems in terms of the probability of extinction of their elements, and by shifting emphasis from the equilibrium states to the conditions for persistence" (Holling 1973, in Gunderson et al. 2010:20).

149

The boreal forest is one of Holling's favorite examples of an ecological system that is better understood through the notion of ecological resilience. The boreal forest is a dynamical system that is highly regulated by the spruce budworm and its interaction with the spruce-fir forest. Most of the time populations of budworms are relatively low, kept in check by bird predators. When dry conditions prevail for two or more years, however, bird populations drop, leading to a spruce budworm outbreak and the major destruction of its principal food source, the balsam fir (adult budworms lay their eggs on fir leaves and the larvae feed on their buds). Between outbreaks the balsam firs grow and reproduce, along with the spruce and the birch, creating very dense stands. These conditions are especially difficult for birch and spruce, and eventually the forest comes to be dominated by fir again, until the next insect outbreak. Looking at this system at a sufficiently long timescale, we thus see that the fir-dominated forest is only transiently stable. Between outbreaks, the fir is favored, but during outbreaks, the birch and the spruce are favored, because they are less susceptible to budworm grazing.

Holling (1986) eventually introduced the concept of an "adaptive cycle" as a way of understanding this common "boom-and-bust" pattern in ecosystems and (he argued) other living systems. The adaptive cycle goes through four basic stages: growth, conservation, release (or creative destruction), and reorganization (or renewal). In the example

above, the rapid recolonization after an outbreak by pioneer and opportunist species, such as birch and spruce, corresponds to the growth phase. These events lead to the gradual accumulation of "capital." But growth reaches its limit and firs, which are especially well adapted to dense conditions, slowly become dominant. The accumulation of biomass and increase in causal connectedness that follow correspond to the *conservation* phase. As this phase advances, the forest enters what Clements (1916) would have called its mature and stable "climax" stage. But as Holling notes, the stability of this phase is paradoxically fragile, for the relations between the various species reach a fine and delicate balance, and the forest becomes "so over-connected that rapid change is triggered" (Holling 1986 in Gunderson et al. 2010:95). Events that would have little influence during the growth phase can now cause a sudden shift in the precarious balance for example, a couple of hot, dry years can result in an outbreak in an insect population. Such a shift can inaugurate the *release* phase, when the system ceases to store and maintain its "capital"—accumulated biomass and complex causal organization—but simply releases it. The connections that took years to establish and stabilize suddenly break down.

The distinction between the two notions of resilience is crucial at this stage of the narrative. As the ecosystem progresses in the conservation phase, it becomes increasingly stable (its engineering resilience increases), just as Clements had said. Yet, it also becomes fragile or vulnerable (its ecological resilience decreases). The loss of ecological resilience explains how a relatively small change can result in a complete shift in the structure of the system. As we will see in the next section, several factors can explain the fact that mature systems in their conservation phase can present a reduced capacity to absorb change.

Once released from the biomass of the forest, the carbon and nutrients can be reassimilated by the organisms that initiate a new growth phase. The period in which these organisms are becoming established, and beginning to capture the free resources, corresponds to the *reorganization* phase. Sometimes the cycle basically repeats the same stages with fidelity, as in Clements' succession theory (Clements 1916). Alternatively, instead of a mere renewal, the system can reorganize in such a way that different growth and conservation phases occur. The system could, for instance, become dominated by aspen and birch trees during the conservation phase rather than repopulating with balsam fir (Holling 1978). Indeed, the insect outbreaks discussed above leave many dead trees standing or fallen, creating the perfect conditions for intense fires that can in turn modify the regeneration process and the dominant composition of the mature forest.

Ecologists in the mid-20th century tended to emphasize mostly engineering resilience, and even sometimes conflated both forms of resilience. Eugene Odum's treatment of ecological succession offers an example of such conflation. In The Strategy of Ecosystem Development, Odum defines ecological succession as presenting three essential characteristics:

(i) It is an orderly process of community development that is reasonably directional and, therefore, predictable. (ii) It results from modification of the physical environment by the community... (iii) It culminates in a stabilized ecosystem in which maximum biomass... and symbiotic function between organisms are maintained per unit of available energy flow (Odum 1969:262).

Odum's definition of succession as a directional and predictable process culminating in stability and maximization of energy flow is largely guided by what Holling later identified as "engineering resilience." But the sentence that immediately follows suggests that Odum also identifies this form of stability with something akin to ecological resilience:

In a word, the "strategy" of succession as a short-term process is basically the same as the "strategy" of long-term evolutionary development of the biosphere—namely, increased control of, or homeostasis with, the physical environment in the sense of achieving maximum protection from its perturbations (Odum 1969:262).

This idea is further elaborated in a subsequent section, where Odum states that the process of ecosystems succession (or matura-

tion) involves the formation of "increasingly intimate associations and reciprocal adaptations between plants and animals" (p. 264), which leads to mechanisms that presumably afford the ecosystem a greater capacity to mitigate perturbations. We will see in the next section that ecologists have come to adopt an opposite viewpoint, and the delineation between ecological and engineering resilience is critical for this change of perspective. Suffice to say for the moment that, if we read the idea of "maximum protection from its perturbations" as a precursor of ecological resilience, then these passages clearly suggest that Odum, unlike Holling, interpreted the mature and stable stage of ecological succession as being resilient in both the engineering and ecological senses.

Discussions of resilience and adaptive cycles have often been justified by considering the implications of an ecosystem's capacity to reorganize into a new "regime" characterized by a different conservation state. Holling, and many after him, saw not only that ecological systems were usually to be found in states far from their theoretical equilibrium points, but also that mainstream ecology lacked the conceptual tools to "deal . . . with the reality of more than one equilibrium" (Holling 1996, in Gunderson et al. 2010:54). If ecological systems undergo transitions between alternative dynamical equilibria, then ecological theory needs an analysis of the kind of stability that prevents such transitions—an analysis that conceives stability in terms of a capacity to persist within a given dynamic equilibrium in the face of disturbance. It is worth retracing some of Holling's steps here, for his treatment of the subject has greatly influenced the way in which many other ecologists have come to conceive of ecological resilience in situations involving multiple equilibria.

Holling's 1973 paper explores the different types of behaviors a system can show, expressed in terms of patterns of movement in a state space. Although Holling notes that these models had to make several simplifying assumptions, he argued that they nevertheless constituted a useful "starting point to organize and guide understanding" (Holling 1973:6). The type of equilibrium that seemed to offer the best heuristic

was the "domain of attraction" (Holling 1973:6), i.e., a region in the state space toward which the system tends to return if displaced, but which cannot be achieved once the variables defining the system pass beyond a certain threshold. Holling argued that the empirical evidence available at the time supported the hypothesis of multiple domains of attraction. The argument appears in his graphical treatment of fecundity-density curves and functional responses, decomposed into fecundity and mortality curves. Because mortality and fecundity are not linear, they may create multiple equilibrium points:

Empirical evidence . . . suggests that realistic forms to fecundity and mortality curves will generate sinuous reproduction curves . . . with the possibility of a number of equilibrium states, some transient and some stable. These are precisely the conditions that will generate domains of attraction, with each domain separated from others by . . . thresholds (Holling 1973:12).

Holling was still walking on thin ice at this point. Despite his claim that our most realistic models would predict the existence of thresholds separating multiple attraction domains, it is nevertheless clear throughout the paper that the multistate model had yet to pass a more rigorous empirical test (see communication "Origins of Ecological Resilience" published in Gunderson et al. 2010: 425-429). This partly explains why it took another 10-15 years before a larger group of ecologists began to take interest in this notion of resilience. During the 1980s and 1990s, ecologists continued to analyze stability in terms of efficiency (e.g., Pimm 1991) and some even tried to show that there was empirical evidence invalidating the multiequilibria model (e.g., Sousa and Connell 1985). But these criticisms did not prevent many ecologists from shifting away from a simplistic equilibrium view. The multiequilibria model has since gained increasing theoretical and empirical support from the work of several other biologists and community ecologists working on assembly rules and the role of environmental change (e.g., Lewontin 1969; Sutherland 1974; Diamond 1975; May 1977; Dublin et al. 1990; Laycock

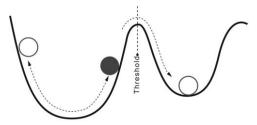
1991; Knowlton 1992; Scheffer et al. 1993), such that by the early 2000s, ample empirical evidence in favor of the multiequilibria model had made its way into the ecological literature (Beisner et al. 2003; Folke et al. 2004 provides a substantive list of examples from freshwater, marine, forest, savanna, arctic, and subarctic systems). A closely related research program was started at the same time by ecologists interested in the role of disturbances, historical contingencies, and heterogeneity in the formation of ecological communities (e.g., White 1979; Pickett and White 1985). This line of work, too, was critical of equilibrium models, but its proponents, instead of endorsing multiple equilibria, promoted a nonequilibrium interpretation of nature, emphasizing abiotic density-independent factors over the biotic density-dependent ones (see Chapter 3 in Cooper 2003 for a discussion of the nonequilibrium view).

The possibility of alternative stability domains was essential in Holling's original account of ecological resilience and remained one of the central features in other studies. Understanding the processes favoring *persistence* is not as important when things always tend to return the same state. But it becomes far more important when the system of interest has the potential to shift into a different stability domain, especially if the new domain is "less desirable" than the current one.

The heuristic model of a ball rolling on a landscape with one or multiple valleys has become the standard tool for conveying this idea (Figure 1). The ball represents the system, its position on the landscape is its state, and a cup represents a stability domain. The notion of engineering resilience assumes a system at or near a single global equilibrium. It describes the system's capacity to stay in its equilibrium state and is typically measured by the "return time" after perturbation. In this model, engineering resilience will essentially depend on the slope of the cup. The notion of ecological resilience, on the other hand, typically applies when a system can "fall" in two (or more) domains of attraction. It also assumes that the system is dynamical such that the position of the ball is always changing within the cup. As the system



Engineering resilience concept



Ecological resilience concept

FIGURE 1. ENGINEERING AND ECOLOGICAL RESILIENCE
REPRESENTED WITH THE HEURISTIC MODEL
OF A BALL TRAVELING ON A LANDSCAPE
WITH ONE OR MULTIPLE WELLS

See text for explanation. Reprinted with permission from Liao (2012).

moves about in a basin, a perturbation can "push" it past a certain threshold and force it into a different domain of attraction. Ecological resilience, which refers to the capacity of the system to persist within a stability domain, thus depends on a larger number of variables and on different properties of the cup. More precisely, it depends on the actual position of the system relative to the threshold, on the intensity and the direction of the disturbance, and on the width of the cup (Walker et al. 2004).

As clearly recognized by several protagonists of ecological resilience, this simple kind of picture, although very common, is somewhat misleading, for it does not take account of the fact that the shape of the surface, too, changes as the system evolves, changing the shape of the "cups" or even eliminating them or adding new ones (Gunderson 2000). For example, the conditions of existence can change drastically when a new species invades a habitat or when an important ecological functional group is seriously impacted by some disturbance. Such changes can in fact lead to the complete disappearance of a cer-

# TABLE 1 Selected definitions of "resilience"

| 1 | A measure of the persistence of systems and of their ability to absorb change and disturbance and still maintain the same relationships between populations or state variables.   | Holling (1973)  |
|---|---|---|
| 2 | The existence of more than one domain of attraction and the maintenance of that global structure through variability.   | Walker et al. (1981)  |
| 3 | The magnitude of disturbance that can be absorbed before the system changes its structure by changing the variable processes that control the behavior.   | Holling (1996); Gunderson (2000);<br>Gunderson and Holling (2002) |
| 4 | The magnitude of disturbance that can be tolerated before a socioecological system moves to a different region of a state space controlled by a different set of processes, including the degree to which the system is capable of self-organization, and how much it expresses a capacity for learning and adaptation. | Carpenter et. al (2001); Folke et al. (2002)                      |
| 5 | The capacity of a system to absorb disturbance and reorganize while undergoing change so as to still retain essentially the same function, structure, identity,   | Walker et al. (2004); Walker and Salt (2006)                      |

tain stability domain (Peterson 2002:39, Box 2-3). Another difficulty arising with the ballin-cup representation comes from the way in which cup surfaces are created from underlying mathematics. Discussions of stability domains often fail to acknowledge that the landscape with its valleys has to be directly derived from a set of differential equations that define the behavior of variables included in a model. As explained in Brock et al. (2008), deriving a three-dimensional surface for a set of variables is possible only if the functions describing the dynamical behavior of each variable meet some symmetry condition (see Brock et al. 2008:189 for details). Since these functions are defined from the details of the case at hand, nothing guarantees that this mathematical symmetry requirement is met. As a consequence, unless the right description is built into the model from the start, it is virtually impossible to make the calculations that would produce a landscape function and the cup surface is almost always two-dimensional (i.e., for one variable at the time). In sum, the metaphor of the ball evolving on a static, multidimensional landscape is useful as a heuristic tool, but it also comes with important representational and methodological limitations.

and feedbacks.

As demonstrated by the sample definitions provided in Table 1, the idea of *persistence* is pervasive in this analytical tradition (see also Shrader-Frechette and McCoy 1993). The subject of this persistence—what is persist-

ing—is, however, not always obvious. In fact, several different kinds of objects or conditions seem to play this role. On one hand, most definitions present resilience in terms of persistence of a system state. This generally means that the state variables that define the system remain within a certain range of values. In other words, "persistence" in this context means bounded variability. For example, the relative abundance of species in an ecosystem or the amount of water or nutrients flowing through it will generally fluctuate over time, but only within certain limits. On the other hand, persistence also applies to systemic properties such as integrity, identity, structure, and function, and these elements are unfortunately often left undefined and indeed poorly understood. Such vagueness is especially damaging when it comes to finding measurement criteria for resilience, a problem to which we will return later. Finally, another common element of these definitions is that the persistence of state and systemic integrity is tied to the maintenance of regulatory feedback relationships. This aspect of persistence appears in later definitions, where it adds to, but does not otherwise alter, the original concept. All three aspects of persistence complement each other: the persistence of regulatory processes results in persistence of identity, structure, and function, which in turn results in the bounded variability of state variables. This brings us to the second core dimension of ecological resilience, i.e., the capacity to absorb change. Unlike other traditions in the analysis of stability, defenders of ecological resilience assume from the start that ecological systems are always changing. Two types of change are typically discussed: change occurring within a stability domain and change involving a shift of stability domain. Discussions of engineering resilience tend to focus (implicitly) on the former, whereas people interested in ecological resilience generally look at both.

Discussions of changes occurring within a stability domain are related to *adaptability*, which is broadly defined as the capacity to adjust to changing external and internal processes. The original definition of ecological resilience did not relate the capacity to absorb change to adaptability, but this conception spread gradually after Holling (1986) introduced the notion of the adaptive cycle. However, the relationship between resilience and adaptability need not appear only within the rigid framework of the adaptive cycle. In fact, there are many situations in which a system's behavior will depart from the theoretical description of the adaptive cycle (see, for example, Holling and Gunderson 2002: 62). Adjustments can thus result from process of ecological succession, but also from the capacity of actors to learn, make choices, and modify their actions in order to maintain certain processes (Walker et al. 2004). As such, the notion of adaptability can be a crucial factor in the context of building resilient SESs, both at local and global scales. Folke et al. (2010), for example, discuss how adaptation to change in the Goulburn-Broken catchment in the Murray Darling Basin in Australia would require multilevel actions. This region has successfully developed its economy via agriculture, but the widespread clearing of native species and the intensive irrigation profoundly changed the species composition and the hydrology in the region. The water tables have risen and created a severe salinization problem. Unless adaptation occurs, this SES will likely shift into a different ecological regime, which could also mean that many inhabitants of this region would suffer economically. Provided that the threshold for salinity has not been passed, adaptation could

come from changes in the practices and values of actors in this region (Folke et al. 2010). At a more global scale, discussions of mitigation and adaptation to climate change could be seen through the same lens of adaptability. The human-Earth system is most likely undergoing profound changes, and unless we greatly reduce the amount of CO<sub>2</sub> released into the atmosphere, or find ways to increase its intake, future generations will live in a radically different world from that which past and current generations have enjoyed (IPCC 2014). The notion of adaptability is relevant here as it refers to the capacity of the human-Earth system to change and persist under conditions bounded by the current range of variability. It could be interesting to apply a generalized Darwinian framework (e.g., Hodgson 2010) in order to unify the different forms of adaptability found in SESs. Adaptation could thus be accounted for in terms of selection processes over populations (or ensembles) of interacting entities (including organisms and institutions) with different abilities to replicate and/or survive.

The second type of change, in which the system shifts from one domain to another, has always been part of the discussions on ecological resilience, but often only in a negative way, probably because a shift of domain means a lack of resilience. Within the framework of the adaptive cycle, it became common to interpret the loss of resilience in terms of stability and interconnection of elements. As mentioned earlier, this view stipulates that when the system enters the conservation phase of the adaptive cycle, its populations become increasingly stable and interdependent, such that the capacity of the system as a whole to absorb change and reorganize after a perturbation decreases. We will see in the next section that the story is not as simple as this. For now, suffice it to say that the ease with which a system shifts from one stability domain to another is generally presented as the contrary of resilience. Note that the notion of resilience per se is not evaluative, i.e., not good or bad a priori. A system can be in a resilient yet "degraded" state (e.g., a eutrophic lake; Walker and Salt 2006:78; Holling and Gunderson 2002:38). This value-neutral aspect of resilience typically goes unmentioned. In fact, we will see in a moment that resilience has become central to a broader conceptual framework commonly associated with sustainability, and it is generally presented under a more positive light.

In order to understand the evolution of the notion of resilience in the ecological literature, we also need to look at the broader conceptual framework that grew out of the research and reflections on the capacity of systems to absorb changes and maintain integrity. After Walker and Salt (2006), we will call this framework "resilience thinking." Brand and Jax (2007) present "resilience thinking" as one more resilience concept. This reading mistakes the role of resilience thinking, but its rise to prominence has indeed had an impact on the definition of resilience. Resilience thinking advocates for a shift in the way in which we look at the ecological systems and the relationship between natural and social systems. This framework brings together a broader constellation of concepts, some of which we have already discussed (e.g., resilience, multiequilibria, threshold, scale, feedback interactions), but also including others—concepts more directly concerned with human actions and needs, such as social-ecological systems, unpredictability, uncertainty, and adaptive management. The discussion of resilience at different scales by Folke et al. (2010) is a good example of such integration. As these authors suggest, a strong emphasis on specified resilience (i.e., the promotion of the resilience of a particular aspect of a given system to a particular type of disturbance) can lead to management decisions that narrow the options for dealing with various kinds of disturbance. Such strategies then become detrimental to a more general form of resilience (i.e., the capacity to cope with any type of uncertainties). In managing for resilience, one should thus keep in mind that the best strategy will not necessarily be to adapt and try to persist in the actual stability domain, but will sometimes be to transform; to allow the system to operate under a different regime characterized by different driving processes, thresholds, and adaptabilities. An example of a deliberate transformation could involve a change in tax structures in order to promote a modification in land use. Melting Arctic ice could be the source of nondeliberate transformation in Arctic and continental ecosystems.

This broader perspective thus clearly targets more practical outcomes. Very briefly, advocates of resilience thinking do not merely propose a different understanding of stability and change in the ecological world, they also argue for a revolution in the way ecosystems should be conceived of and managed. The concept of ecological systems as evolving dynamical systems with multiple equilibria supported a critique of the common form of management where natural variability is reduced to its minimum to increase the predictability and efficiency with which humans can use ecological resources.

Once again, Holling played a central role in this movement. For example, Holling and Meffe (1996) compare the effects of traditional "command and control" approach to a pathology:

We call the result "the pathology of natural resource management" (Holling 1986; Holling 1995), a simple but far-reaching observation defined here as follows: when the range of natural variation in a system is reduced, the system loses resilience. That is, a system in which natural levels of variation have been reduced through command-and-control activities will be less resilient than an unaltered system when subsequently faced with external perturbations, either of a natural (storms, fires, floods) or human-induced (social or institutional) origin. We believe this principle applies beyond ecosystems and is particularly relevant at the intersection of ecological, social, and economic systems (Holling and Meffe 1996:330).

This type of criticism may not belong exclusively to resilience thinking, but it is characteristic of this approach for at least three reasons. First, we see clearly here that resilience is viewed not merely as a descriptive property, but as normative: a good that we should try to achieve and promote. Second, Holling and Meffe's remarks convey the idea that instead of controlling and commanding nature, we should embrace uncertainty while

at the same time trying to reduce aspects of it. Ecological systems undergo regime shifts, so we have to accept and prepare for such events. At best we can reduce the uncertainties we face not by controlling the natural systems we interact with, but by developing our own capacities to learn and adapt. "Learning by doing" is the phrase that many use to capture the essence of adaptive management, an approach defended by and developed through resilience thinking. Despite the ongoing controversies concerning the difficulties of applying adaptive management and the diversity of approaches that fall under this approach (e.g., Gregory et al. 2006; Allen and Gunderson 2011; Allen et al. 2011; McFadden et al. 2011; Tyre and Michaels 2011), this is one of the most fruitful aspects of resilience thinking. Adaptive management has made its way into conservation biology and restoration ecology, and it is increasingly adopted by several environmental policymaking agencies (e.g., Greig et al. 2008; Parks Canada Agency 2008, 2013; Great Lakes Restoration Initiative 2014). Unsurprisingly, resilience building is commonly listed as one of the overarching goals of ecological management in this literature.

The passage quoted above also contains language that clearly emphasizes the need to extend the notion of ecological resilience to create a more inclusive conception of socialecological resilience. The promotion of resilient social-ecological systems and the idea of adaptive management are frequently to be found in more recent definitions (e.g., Carpenter et al. 2001; Folke et al. 2002, 2010). Moreover, although it is not always explicitly mentioned, contributions to this literature often seem to have the aim of making resilience thinking the analytical framework for sustainability sciences. It is often in this discursive context that the human factor becomes most salient; here resilience is seen as including the capacity of human agents to learn, adjust, adapt, and transform the socialecological systems of which they are a part.

This overview of the evolution of the notion of ecological resilience should make it clear that we need to go beyond the mere description of the properties comprising resilience, and look at a much broader picture. Only then does it become apparent that what has taken place is not so much a multiplication (and disunification) of the notions of resilience, but an attempt to extend the range of this concept over a much larger domain. Such expansion is useful and important but comes with various challenges. We will raise two of them.

First, definitions of ecological resilience have mostly been qualitative and extremely abstract. This relative lack of empirical content has certainly made it easier to extend the scope of the concept, and could even perhaps help to unify applications of the concept of resilience across disciplines (e.g., in ecology and sustainability sciences). However, the abstract concept of resilience has been difficult to apply to concrete situations, and its increasingly ambitious extensions have exacerbated this difficulty. Discussions of resilience have suffered from vagueness with respect to the central notions of "absorbing" change, persistence of states, and maintenance of structure, function, integrity, and identity. As Carpenter et al. (2001) rightly emphasized, applying resilience to concrete situations requires that we answer the question "resilience of what to what?" The heuristic model of a ball rolling across a landscape does capture many important intuitions, but it only deploys the concept in another ideal situation. A fuller version of this sort of model offers a much richer mathematical treatment, defining the state of a system with variables, and finding multiple local equilibria (Beisner 2012). But these generic mathematical tools are only tools; they cannot determine which set of variables and scale best describe the system under investigation. It remains to be seen whether Carpenter et al.'s question can be satisfactorily answered for the two-headed beast that is the social-ecological system. The fact that we have only a very tenuous understanding of this new entity makes it even more difficult to operationalize and promote resilience.

Second, when talking about ecological resilience as a capacity to absorb change, we generally imagine an ecological system along with some external factors disturbing the system, such that a resilient system—one with the proper internal organization—will be

able to absorb changes imposed by the external causes. In most discussions, the main source of these external causes has been found in human activity. But depending on how inclusive we want to be about the notion of linked social-ecological systems, this internal/external distinction may simply collapse. Whether this poses a significant difficulty depends on the importance of the distinction. If we take the idea of the socialecological system seriously we may have to discard the metaphor of "absorbing change," since this metaphor implies an external source of change for the system to absorb. But we can still talk about a differential ability to persist in a stability domain and to maintain structure, functioning, and integrity. This type of reasoning may explain the new terminology adopted by Carpenter et al. (2001) and Folke et al. (2002) (see Table 1), where the notion of "absorption" has been replaced by "tolerance," a metaphor that does not implicitly presuppose an external/ internal dichotomy.

In summary, we have seen in this section how the notion of ecological resilience has evolved over the course of the past few decades along two core dimensions: first, persistence (of structure, function, identity, and integrity) and, second, capacity to absorb/ tolerate change. One of the important drivers in the evolution of this concept is the development of a broader conceptual framework, resilience thinking, that takes resilience as one of its foundational concepts and practical outcomes as among its primary objectives. This eventually led ecologists to extend the concept of ecological resilience to yield a vague but suggestive notion of socialecological resilience, and to the development of a new approach to managing and learning about ecosystems: adaptive management. These changes provide a lens through which we can better see the unificatory role of resilience in sustainability research. In the next section, we will look more closely at the factors contributing to resilience. We will see that the conceptual evolution traced here is, to a large extent, simply a reflection of the changes involved in ecologists' developing understanding of the *conditions* that affect a system's resilience.

# DETERMINANTS OF RESILIENCE: WHAT MAKES A SYSTEM (MORE OR LESS) RESILIENT?

In exploring the question above, our goal is not to make a list of necessary and sufficient conditions for resilience, but rather to present and evaluate the types of factors that have been identified as important determinants of a system's resilience. We will see that the question "What makes a system more or less resilient?" can be answered fairly briefly: complexity and adaptivity. So it will prove useful to open the discussion with a brief introduction to the important notion of the Complex Adaptive System (CAS). We can then go on to investigate which aspects of systems of this class contribute to their resilience.

Several types of systems have been characterized as CASs: the immune system (Holland 1992), developing biological organisms (Kauffman 1993), ecosystems (Levin 1998, 2003, 2005), and societies (Lansing 2003). Our analysis focuses on the latter two categories, and on the newly identified type of system formed by their combination: the Social-Ecological System. Levin (1998), after Holland (1995), identifies the following four central properties of CASs:

*Diversity*: variety of elements within the system and within functional groups (e.g., diversity of species in a community, or within a functional ecological group such as "predator" or "decomposer").

Aggregation: the formation of aggregates (spatiotemporal inhomogeneities) and hierarchical organization through the self-organization of locally interacting elements/parts (e.g., cells aggregating into organisms, which then aggregate into communities).

*Flows*: processes that provide interconnection between elements and create an integrated whole (e.g., an ecosystem in which biotic and abiotic parts are interrelated).

Nonlinearity: the possibility for the system to follow alternative "developmental pathways" and settle into alternative (dynamic) equilibria.

Each of these properties admits of degrees. A system can be more or less aggregated, it can have many or few alternative equilibria, and it can be composed of many or few different structural elements that can be more or less interconnected by flows or processes. We will see in the following paragraphs how resilience is related to these properties.

The effect of *diversity of elements* on resilience can be seen in the backdrop of discussions about the "diversity-stability" hypothesis, according to which a system with greater diversity should be more stable. Since ecologists entertain various concepts of both stability and diversity, this hypothesis has received several interpretations (deLaplante and Picasso 2011). For example, Odum wrote in the 1950s about the increased stability of the flow of energy through trophic links for ecosystems with greater diversity of network nodes and connections. In the same decade, Hutchinson, in Homage to Santa Rosalia (1959), put forward an evolutionary argument suggesting that "the reason why there are so many species of animals is at least partly because a complex trophic organization of a community is more stable than a simple one" (Hutchinson 1959:155). The alleged reason for this stability is that a group containing many diversified species will be able to "seize new evolutionary opportunities" more easily than an undiversified group" (Hutchinson 1959:155). A few decades later, Robert May's seminal analysis in *Stability and* Complexity in Model Ecosystems (1973) challenged the hypothesis that diversity increases stability, arguing that the probability that the population size of every species will return to equilibrium after perturbation tends to decrease for ecosystems that are more species rich and more connected.

Due to more recent conceptual and empirical developments, ecologists have grown favorable to the idea that certain forms of diversity will beget stability. As argued by de-Laplante and Picasso (2011), one of the critical moves here was to show that the diversity of species may decrease the stability of individual populations, but it can at the same time contribute to the overall stability of the community or ecosystem functioning (e.g., Walker 1992; Cowling et al. 1994; Lawton and Brown 1994; Ghilarov 2000). David Tilman and John Downing were among the first ecologists to perform an experiment showing a positive relationship between species diversity and stability of ecosystem func-

tioning (Tilman and Downing 1994). Like most of the early analyses, this study interpreted the diversity-stability hypothesis in terms of engineering resilience and looked at the capacity of the plant communities to resist and recover from drought. In fact, studies interpreting this hypothesis in terms of ecological resilience appear only in the most recent round of this debate, which frames the discussion in terms of the relation between diversity and the stability of ecosystem functions and/or functioning (for a systematic presentation and analysis of recent experiments, see Loreau et al. 2002; for an overview of the social and political dimensions of this debate, see Naeem et al. 2009).

One of the key lessons from these discussions is that resilience and functional stability do not depend on species diversity alone. Very diverse systems may have low resilience if all of the elements are sensitive to changes happening in any part of the system. The property of aggregation can help in this regard. One way in which aggregation can promote resilience is by the creation of modular structure, i.e., more or less separated subsystems. Modular structures can reduce the impact of disturbance within the system (Webb and Bodin 2008). If all of the elements in a system are widely and tightly connected (i.e., a system has a nonmodular structure), then a disturbance in one region will most likely have repercussions throughout the entire system. So an intense or persistent local disturbance may result in important structural and functional changes at the system level. Research on keystone species has made extensive use of this idea. Some researchers have suggested that change in the abundance of a few well-connected species can lead to large downstream effects and ultimately to the collapse of the community (see Mills et al. 1993 for a critical analysis of the idea of keystone species). In such cases, even great diversity will not necessarily prevent a regime shift. But if the system's structure is spatiotemporally inhomogeneous and minimally connected, then the same disturbance might have a large local impact yet be less likely to propagate throughout the system.

An underappreciated factor that can contribute to modularity and resilience is spatial

heterogeneity. Spatial heterogeneity is known to contribute to the coexistence and persistence of similar species (Tilman 1994). According to the adaptive cycle theory, a system in the conservation phase will tend to lose resilience; this is partly because the process of competitive exclusion tends to eliminate all but one of the species occupying a particular niche (or very similar niches). But although it is true that competitive exclusion is to be expected in sufficiently dense and homogeneous environments, ecologists recognize that coexistence is more likely for similar species living in spatially heterogeneous environments with moderated migration between patches (Amarasekare and Nisbet 2001). Spatial heterogeneity effectively creates some modularity in the system, preventing disturbances from spreading rapidly through the system and allowing patches to be recolonized after perturbation.

The relation between modularity and resilience is not simple, however. In fact, as several conservationists have argued for quite some time now, too much modularity and patchiness may reduce resilience (Fischer and Lindenmayer 2007). This will happen, for example, if a system's capacity to adjust to change depends on the coordination and regulation of the elements present in the modules. Suppose that the regeneration of a forest depends on the presence of a predator (e.g., a species of wolf) that controls the population of large herbivore (e.g., a species of deer) feeding primarily on young leaves of some tree species that importantly define the type of forest ecosystem. As the human population becomes denser, more land is cleared and roads are built, and the forest—once homogeneous and well connected—becomes highly fragmented and patchy. The large herbivore is relatively well adapted to this change as it can still migrate from one patch to another. But suppose that the predator, for some reason, travels through the few corridors left with much less ease. Under these circumstances, chance events can take on a new importance: a disturbance (such as fire), for example, may happen to kill a large proportion of the predator population, a collection of individuals that happen to be at the wrong place at the wrong time. Without predators, the population of large herbivores will undergo uncontrolled growth, which might result in the disappearance in the understory of the seedlings and saplings of the tree species that defined the ecosystem. The change might not be apparent immediately, but over the years the mature trees will die and the forest will take on a different identity. This recognizable scenario shows that when organisms and material need to flow from one part of the system to another, too much modularity can prevent reorganization and thus play against resilience.

The discussion so far has emphasized the importance of diversity, and of some degree of both modularity and connectivity. The importance of these elements has been on the radar for a significant time now (i.e., since the introduction of the adaptive cycle model, at least), but it eventually became apparent that they are not sufficient to determine the system's resilience. The idea that "knocking down" one species might lead to radical changes in the entire ecosystem led ecologists to consider the importance of *functional* redundancy: the presence, within an ecosystem, of multiple species belonging to the same ecological group. Functional redundancy means that if one species is depleted, others are able to perform the same ecological functions, limiting the downstream effects of the initial change. Examples of this phenomenon would be a lake with multiple top predators, a forest with multiple decomposers, or an ecosystem with different species capable of fixing nitrogen. The diversity and the modularity hypotheses thus need to be amended. In order to be resilient, a system should be diverse, moderately connected, and present sufficient functional redundancy that if some members of a functional group are affected, others will maintain an adequate degree of functional integrity at the system level. Recalling that *flows* are a key feature of complex adaptive systems, we can express the idea of functional redundancy another way, noting that ecosystems can be resilient if the same functions can be realized via a multiplicity of channels.

An even more recent line of research suggests that yet another form of diversity is required for resilience to be possible. Not only do ecosystems need diversity of elements, redundancy within functional groups, spatial heterogeneity, and the capacity for systemic change, but they also require "response diversity": organisms whose traits differ in such a way that they will produce different responses to a given disturbance (Naeem and Wright 2003; Griffin et al. 2009; Mori et al. 2013). This idea is also known as the "insurance hypothesis," according to which "interspecific niche differentiation causes species to respond differently to the environment and . . . this differential response can produce compensatory dynamics among species, buffering the impact of environmental changes" (Griffin et al. 2009:79). This hypothesis identifies a form of diversity that provides a very powerful mechanism contributing to the resilience of ecological systems. Its introduction is another significant intellectual innovation in the literature on biodiversity and ecosystem functioning, and resilience theory will need to incorporate it (see especially Folke et al. 2004 and Mori et al. 2013).

The importance of response diversity for resilience can be understood through an example showing the insufficiency of functional redundancy alone. Imagine two lakes, each containing several different species of phytoplankton (primary producers), and both being affected by a perturbation, say a decrease in pH. The systems thus have substantial functional redundancy in primary production. In system one, however, all of the phytoplankton species are affected similarly by the increase in acidity, whereas in system two, different species respond differently, some being sensitive but others being resistant to low pH. Although system one fulfils the condition of functional redundancy, it lacks response diversity, and as a result it will lack resilience. Consequently, theories and models of resilience should be able to explain and represent the relation between response diversity and the capacity of the system to absorb change, persist, and maintain structural/functional integrity. This work is only in its infancy. Spatial heterogeneity could become important here as well, for it can create the conditions in which similar species are not equally vulnerable to a given perturbation, such that the members of a functional group that are less affected can be responsible for the maintenance of functional integrity.

The case of response diversity shows that complexity is not just a matter of structural but of functional diversity and elaboration. A key contributor to such functional complexity in CASs is *nonlinearity* and the phenomenon of historicity (or path dependence) that follows from it (Desjardins 2011, 2015). We saw in the previous section that accounts of resilience often rest on ideas of change and multiple stability domains. It would thus seem natural to take nonlinearity as a precondition for ecological resilience. Curiously enough, very few have made this an explicit criterion in their definition (but see Walker et al. 1981, listed in Table 1). We doubt that this is intentional. Yet, the irony is that they were right to omit multiequilibria as a necessary condition. Despite the importance of thinking about multiple equilibria in the historical development of the concept of resilience, and the powerful heuristic role such thinking still plays, the maturing conception of resilience captures something more fundamental than the possibility of multiple equilibria. A concern for resilience in terms of the capacity to tolerate change and persist in a certain dynamical state arises from the mere possibility of the "other," regardless of its nature. In the language of the ball-and-cup model, it is possible that there is no second cup, just a bottomless abyss. What makes resilience important is that there is a threshold, not what lies on the other side of it.

This logical point aside, discussions about resilience in SESs suggest that there are situations in which the existence of multiple stability domains is essential for resilience. We saw earlier that some researchers, in an effort to integrate resilience theory with the broader concerns of sustainability, distinguish between two capacities that reflect the important role of human agents in social-ecological systems: *adaptability* and *transformability* (Walker et al. 2004; Folke et al. 2010). These authors incorporate adaptive management into resilience theory and make explicit that self-organization in social-ecological sys-

tems involves human actions. The sort of "influence" that they have in mind when talking about adaptation is the "active promotion of resilience" via actions that contribute to the maintenance of structural and behavioral complexity (e.g., protecting biodiversity, reducing use of agricultural fertilizer, or maintaining spatial heterogeneity in a landscape). When adaptability proves extremely limited—i.e., people are unable effectively to promote resilience within the system as it currently functions-it may sometimes be necessary for human actors to take more radical innovative action. This is where multiequilibria and transformability (i.e., the capacity of actors to create a new stability domain with a different set of ecological and social conditions) come into play.

Although the emphasis on human agents and goals exhibited in these analyses could be worrisome for many conservationists, it is important to keep in mind that attempting to create new stability domains is presented as a last resort. Moreover, emphasizing transformability does not necessarily entail fabricating ecosystems according to any contemporary caprices (see Higgs 2003 and Sarkar 2011 for discussions of this type of worry in the context of restoration). The management of ecological systems need not be exclusively guided by human-centered interests; there is room in this proposal for a weaker form of anthropocentrism, one based on considered and tempered preferences and values (e.g., Norton 1984) and procedures that allow human agents to modify their preferences and values as they learn—an aim found in some of the more radical conceptions of adaptive management. Furthermore, transformability is not unique to social-ecological systems; there are numerous examples of naturally occurring regime shifts that are transformative in that they result in a modification of the landscape of possibilities that the system occupies. So although transformability could be interpreted as the antithesis of resilience at the local scale, the capacity to evolve and "invent" new ways of life can be seen as a necessary capacity for the whole biosphere to persist and support diverse life forms.

It is important to keep in mind at this point that no one has been arguing that we can or should achieve permanent resilience.

In fact, one of the messages of resilience thinking has always been to embrace change. This has implications for ecological management, but also for how we understand the world. As the adaptive cycle model suggests, the temporary loss of resilience at one scale might in fact contribute to resilience at the scale above. Remember how research on diversity and ecosystem functioning made an important contribution by suggesting that diversity contributes to the overall stability of ecosystems—not the stability of populations (Cowling et al. 1994; Lawton and Brown 1994; Tilman and Downing 1994; Ghilarov 2000). Ecological resilience theory has had a particular take on this idea. Instead of arguing that diversity can make the ecosystems stable, despite making populations unstable, resilience theory has been arguing that the ecosystem is resilient because the lower level aggregates (organisms, populations) are unstable. Take the example of cellular reproduction and death in multicellular organisms. Cells must often reproduce in order to replace the ones that die. The fine balance of death and reproduction is crucial for maintaining good functioning of organisms. Similar reasoning applies to ecosystems. The reproduction and death of individual organisms contributes to the functioning of populations and ecosystems. So change—loss of resilience of some parts—can contribute to the resilience of the whole. Again, the relation between change and resilience is not simple. Quantity and quality matter. In addition, the normative question of the "good" or "better" state(s) always haunts these discussions—as we noted at the outset, if a resilient system or state is not itself desirable, then resilience is not a good thing but a problem. We will not tackle this question in the present paper. Suffice it for the moment to emphasize that although resilience depends on systemic changes and interscale interactions, if the goal is to promote life and diversity, then not any change will do. Although loss of resilience at one level can promote it at a higher level, it is crucial not to assume that this licenses anyone to simplify ecological systems on the assumption that the resultant loss of resilience will be regained elsewhere. Clearcutting a tropical forest in order to install a monoculture that will feed a handful of species—one of the most common forms of human ecological interventions—would clearly not be promoting resilience.

# Conclusion

Our analysis has targeted two ingredients necessary for the fruitful promotion of resilience: first, definitional clarity and, second, a framework for interpreting and studying the various factors relevant for the resilience of systems. We have shown that the concept of ecological resilience has acquired several meanings since its introduction by Holling in 1973, but unlike some recent papers that emphasize the plurality and disunity of interpretations, we present this conceptual diversification as a form of evolution. Many interpretations of the concept of ecological resilience that have been formulated in the tradition initiated by Holling are variations around a central theme, namely the capacity of a system to absorb change yet maintain identity and a certain degree of integrity. Our objective, however, has not been to provide a unified view in terms of necessary and sufficient conditions. Trying to do so, we contend, would seriously misrepresent this thriving area of research. The type of unity one finds among contemporary resilience researchers is more practical than conceptual. The essence of this unity can only be seen by taking a broad perspective and asking why so many thinkers, researchers, and practitioners have been promoting resilience. As argued in the section titled Determinants of Resilience, the notion of ecological resilience was born from the recognition of two kinds of failure in ecological practice. First, as Holling and other members of the Resilience Alliance made clear from the start, traditional analyses of stability, by focusing on efficiency and by ignoring the complex and changing nature of ecosystems, were missing an important dimension of stability. Second, the promotion of ecological resilience was also motivated by management failures and the recognition of a need to invent new approaches and redefine goals and expectations. So despite the conceptual plurality surrounding the definition of resilience, we argue that these two practical aspects have to a large extent provided unity within resilience

research. Although we do think that definitional clarity is crucial in research, this does not imply that good research can only come from conceptual monism. If what unifies resilience researchers is the practical promotion of resilience, then the next task is to find the factors contributing to resilience. Here again, we advocate for a pluralist stance. For many years researchers have focused principally on the relation between diversity and stability. With time, ecologists have refined their understanding of this difficult and controversial question, and it is clear now that different species of diversity are at play. Using the conceptual framework of CASs, we showed how structural and response diversity are important, but also functional redundancy, modularity, spatial heterogeneity, and nonlinearity.

One of the next tasks that resilience researchers need to accomplish is to develop representational tools that make it possible to articulate clearly the relation between these factors and the realization of resilience. The model of choice for representing resilience is often the ball on a multiequilibria landscape (see the section titled Determinants of Resilience). This intuitive heuristic is effective for representing alternative regimes and helps clarify the difference between engineering and ecological resilience. Yet, like any heuristic, this model has important limitations. First, by representing the system as a ball or a point evolving on a landscape, we lose contact with many structural and behavioral elements mentioned in the previous section. As a result, it is not always clear how this heuristic is supposed to guide investigators interested in measuring and comparing the contributing factors of resilience, or managers interested in modifying those factors. Second, the heuristic can carry a spurious sense of concreteness and precision. It has been emphasized that the state of the system, its distance from a threshold, the strength of the perturbation, and the dimensions of a particular cup matter in assessing resilience (Walker et al. 2004). But the concrete factors determining these aspects of the stability domain often remain obscure. Third, even in abstract terms, this representation is unable to capture key

dimensions of ecological systems and processes. For the sake of convenience or because of mathematical constraints, landscapes are usually represented in two dimensions for a handful of variables, but of course the number of variables defining a system often goes far beyond such low numbers. Likewise, the landscapes as represented are static, yet they are after all supposed to evolve as the system undergoes various changes. In addition, as the model of nested adaptive cycles indicates, it is important to be able to talk about multiscale interaction in discussing resilience, but this crucial phenomenon remains difficult to capture with the model of the ball rolling on a landscape. It is important not to be overly critical. The resilience of a system depends on many elements of complexity, and perhaps no

model can perfectly capture all of them. We think, however, that the recent research on network modeling could complement the ballin-cup heuristics and fill in some of the lacunae noted above. More specifically, we think that network theory is a well-established framework with enormous analytical resources and potential (Newman 2003) and models of socialecological networks offer an intuitive and relevant way to represent linked systems of people and nature (Janssen et al. 2006; Cumming et al. 2010; Parrott 2010; Gonzalès and Parrott 2012; Frey and Rusch 2013). Like many others, these analyses have been mostly theoretical. It will be interesting to see what practical lessons come out of this line of inquiry, especially as more researchers assess the resilience of actual social-ecological networks.

# REFERENCES

- Allen C. R., Gunderson L. H. 2011. Pathology and failure in the design and implementation of adaptive management. Journal of Environmental Management 92:1379-1384.
- Allen C. R., Fontaine J. J., Pope K. L., Garmestani A. S. 2011. Adaptive management for a turbulent future. Journal of Environmental Management 92:1339-1345.
- Amarasekare P., Nisbet R. M. 2001. Spatial heterogeneity, source-sink dynamics, and the local coexistence of competing species. American Naturalist 158:572-584.
- Beisner B. E. 2012. The shifting states of resilience: easier to define than to measure. Ideas in Ecology and Evolution 5:57-62.
- Beisner B. E., Haydon D. T., Cuddington K. 2003. Alternative stable states in ecology. Frontiers in Ecology and the Environment 1:376-382.
- Brand F. S., Jax K. 2007. Focusing the meaning(s) of resilience: resilience as a descriptive concept and a boundary object. Ecology and Society 12:23.
- Brock W. A., Carpenter S. R., Scheffer M. 2008. Regime shifts, environmental signals, uncertainty, and policy choice. Pages 180-206 in Complexity Theory for a Sustainable Future, edited by J. Norberg and G. S. Cumming. New York: Columbia University Press.
- Carpenter S., Walker B., Anderies J. M., Abel N. 2001. From metaphor to measurement: resilience of what to what? Ecosystems 4:765-781.
- Clements F. E. 1916. Plant Succession: An Analysis of the Development of Vegetation. Washington (DC): Carnegie Institution of Washington.
- Cooper G. J. 2003. The Science of the Struggle for Existence: On the Foundations of Ecology. Cambridge (United Kingdom): Cambridge University Press.

- Cowling R. M., Mustart P. J., Laurie H., Richards M. B. 1994. Species diversity, functional diversity and functional redundancy in fynbos communities. South African Journal of Science 90:333-337.
- Cumming G. S., Bodin Ö., Ernstson H., Elmqvist T. 2010. Network analysis in conservation biogeography: challenges and opportunities. Diversity and Distributions 16:414-425.
- deLaplante K., Picasso V. 2011. The diversity-ecosystem function debate in ecology. Pages 169-200 in Philosophy of Ecology, edited by K. deLaplante, B. Brown, and K. Peacock. Oxford (United Kingdom): Elsevier.
- Desjardins E. 2011. Historicity and experimental evolution. Biology and Philosophy 26:339-364.
- Desjardins E. 2015. Historicity and ecological restoration. Biology and Philosophy 30:77-98.
- Diamond J. M. 1975. Assembly of species communities. Pages 342-444 in Ecology and Evolution of Communities, edited by M. L. Cody and J. M. Diamond. Cambridge (Massachusetts): Harvard University Press.
- Dublin H. T., Sinclair A. R. E., McGlade J. 1990. Elephants and fire as causes of multiple stable states in the Serengeti-Mara woodlands. Journal of Animal Ecology 59:1147-1164.
- Fischer J., Lindenmayer D. B. 2007. Landscape modification and habitat fragmentation: a synthesis. Global Ecology and Biogeography 16:265–280.
- Fletcher D., Sarkar M. 2013. Psychological resilience: a review and critique of definitions, concepts, and theory. European Psychologist 18:12-23.
- Folke C., Carpenter S., Elmqvist T., Gunderson L., Holling C. S., Walker B. 2002. Resilience and sustainable development: building adaptive capacity

- in a world of transformations. AMBIO: A Journal of the Human Environment 31:437–440.
- Folke C., Carpenter S., Walker B., Scheffer M., Elmqvist T., Gunderson L., Holling C. S. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. *Annual Review of Ecology, Evolution, and Systematics* 35:557–581.
- Folke C., Carpenter S. R., Walker B., Scheffer M., Chapin T., Rockström J. 2010. Resilience thinking: integrating resilience, adaptability and transformability. *Ecology and Society* 15:20.
- Frey U. J., Rusch H. 2013. Using artificial neural networks for the analysis of social-ecological systems. *Ecology and Society* 18:40.
- Ghilarov A. M. 2000. Ecosystem functioning and intrinsic value of biodiversity. Oikos 90:408–412.
- Gonzalès R., Parrott L. 2012. Network theory in the assessment of the sustainability of social-ecological systems. *Geography Compass* 6:76–88.
- Great Lakes Restoration Initiative. 2014. *Action Plan II.* http://greatlakesrestoration.us/actionplan/.
- Gregory R., Ohlson D., Arvai J. 2006. Deconstructing adaptive management: criteria for applications to environmental management. *Ecological Applica*tions 16:2411–2425.
- Greig L., Marmorek D., Murray C. 2008. Guide for Preparation of Adaptive Management Plans. Prepared by ESSA Technologies Ltd., Richmond Hill, Canada, for Fisheries and Oceans Canada, Western Arctic Area, Central and Arctic Region, Yellowknife, Canada.
- Griffin J. N., O'Gorman E. J., Emmerson M. C., Jenkins S. R., Klein A.-M., Loreau M., Symstad A. 2009. Biodiversity and the stability of ecosystem functioning. Pages 78–93 in *Biodiversity, Ecosystem Functioning, and Human Wellbeing: An Ecological and Economic Perspective*, edited by S. Naeem, D. E. Bunker, A. Hector, M. Loreau, and C. Perrings. Oxford (United Kingdom): Oxford University Press.
- Gunderson L. H. 2000. Ecological resilience—in theory and application. Annual Review of Ecology and Systematics 31:425–439.
- Gunderson L. H., Holling C. S. 2002. Panarchy: Understanding Transformations in Human and Natural Systems. Washington (DC): Island Press.
- Gunderson L. H., Allen C. R., Holling C. S. 2010.
  Foundations of Ecological Resilience. Washington (DC): Island Press.
- Higgs E. 2003. Nature By Design: People, Natural Process, and Ecological Restoration. Cambridge (Massachusetts): MIT Press.
- Hodgson G. M. 2010. Darwinian coevolution of organizations and the environment. *Ecological Economics* 69:700–706.
- Holland J. H. 1992. Complex adaptive systems. *Daedalus* 121:17–30.
- Holland J. H. 1995. Hidden Order: How Adaptation Builds Complexity. Reading (Massachusetts): Addison-Wesley.

- Holling C. S. 1973. Resilience and stability of ecological systems. Annual Review of Ecology and Systematics 4:1–23.
- Holling C. S. 1978. Adaptive Environmental Assessment and Management. Chichester (United Kingdom): Wiley.
- Holling C. S. 1986. The resilience of terrestrial ecosystems; local surprise and global change. Pages 292–317 in Sustainable Development of the Biosphere, edited by W. C. Clark and R. E. Munn. Cambridge (United Kingdom): Cambridge University Press.
- Holling C. S. 1996. Engineering resilience versus ecological resilience. Pages 31–44 in *Engineering Within Ecological Constraints*, edited by P. Schulze. Washington (DC): National Academy Press.
- Holling C. S., Gunderson L. H. 2002. Resilience and adaptive cycles. Pages 25–62 in *Panarchy: Under-standing Transformations in Human and Natural Sys*tems, edited by L. H. Gunderson and C. S. Holling. Washington (DC): Island Press.
- Holling C. S., Meffe G. K. 1996. Command and control and the pathology of natural resource management. *Conservation Biology* 10:328–337.
- Hutchinson G. E. 1959. Homage to Santa Rosalia or why are there so many kinds of animals? *American Naturalist* 93:145–159.
- Intergovernmental Panel on Climate Change (IPCC). 2014. Summary for policymakers. Pages 1–32 in Climate Change 2014: Impacts, Adaptation, and Vulnerability, Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge (United Kingdom): Cambridge University Press.
- Janssen M. A., Bodin Ö., Anderies J. M., Elmqvist T., Ernstson H., McAllister R. R. J., Olsson P., Ryan P. 2006. Toward a network perspective of the study of resilience in social-ecological systems. *Ecology* and Society, 11:15.
- Kauffman S. 1993. The Origins of Order: Self-Organization and Selection in Evolution. Oxford (United Kingdom): Oxford University Press.
- Knowlton N. 1992. Thresholds and multiple stable states in coral reef community dynamics. American Zoologist 32:674–682.
- Lansing J. S. 2003. Complex adaptive systems. Annual Review of Anthropology 32:183–204.
- Lawton J. H., Brown V. K. 1994. Redundancy in ecosystems. Pages 255–270 in *Biodiversity and Ecosystem Function*, edited by E.-D. Schulze and H. A. Mooney. Berlin (Germany): Springer.
- Laycock W. A. 1991. Stable states and thresholds of range condition on North American rangelands: a viewpoint. *Journal of Range Management* 44:427–433.
- Levin S. A. 1998. Ecosystems and the biosphere as complex adaptive systems. *Ecosystems* 1:431–436.
- Levin S. A. 2003. Complex adaptive systems: explor-

- ing the known, the unknown and the unknowable. *Bulletin of the American Mathematical Society* 40:3–19.
- Levin S. A. 2005. Self-organization and the emergence of complexity in ecological systems. *BioScience* 55:1075–1079.
- Lewontin R. C. 1969. The meaning of stability. *Brookhaven Symposia in Biology* 22:13–23.
- Liao K.-H. 2012. A theory on urban resilience to floods—a basis for alternative planning practices. *Ecology and Society* 17:48.
- Loreau M., Naeem S., Inchausti P. 2002. Biodiversity and Ecosystem Functioning: Synthesis and Perspectives. Oxford (United Kingdom): Oxford University Press.
- Luthar S. S., Cicchetti D., Becker B. 2000. The construct of resilience: a critical evaluation and guidelines for future work. *Child Development* 71:543–562.
- May R. M. 1973. Stability and Complexity in Model Ecosystems. Princeton (New Jersey): Princeton University Press.
- May R. M. 1977. Thresholds and breakpoints in ecosystems with a multiplicity of states. *Nature* 269:471–477.
- McFadden J. E., Hiller T. L., Tyre A. J. 2011. Evaluating the efficacy of adaptive management approaches: is there a formula for success? *Journal of Environmental Management* 92:1354–1359.
- Mills L. S., Soulé M. E., Doak D. F. 1993. The keystone-species concept in ecology and conservation. *BioScience* 43:219–224.
- Mori A. S., Furukawa T., Sasaki T. 2013. Response diversity determines the resilience of ecosystems to environmental change. *Biological Reviews* 88:349–364.
- Myers-Smith I. H., Trefry S. A., Swarbrick V. J. 2012. Resilience: easy to use but hard to define. *Ideas in Ecology and Evolution* 5:44–53.
- Naeem S., Wright J. P. 2003. Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmountable problem. *Ecology Letters* 6:567–579.
- Naeem S., Bunker D. E., Hector A., Loreau M., Perrings C. 2009. Biodiversity, Ecosystem Functioning, and Human Wellbeing: An Ecological and Economic Perspective. Oxford (United Kingdom): Oxford University Press.
- Newman M. E. J. 2003. The structure and function of complex networks. *SIAM Review* 45:167–256.
- Norton B. G. 1984. Environmental ethics and weak anthropocentrism. *Environmental Ethics* 6:131–148.
- Odum E. P. 1969. The strategy of ecosystem development. *Science* 164:262–270.
- Parks Canada Agency. 2013. Banff National Park of Canada. *Elk Management in Banff National Park*. http://www.pc.gc.ca/eng/pn-np/ab/banff/plan/faune-wildlife/gestion-wapiti-management.aspx.
- Parks Canada Agency and the Canadian Parks Council. 2008. *Principles and Guidelines for Ecological Restoration in Canada's Protected Natural Areas*. http://www.pc.gc.ca/docs/pc/guide/resteco/index\_e.asp.

Parrott L. 2010. Measuring ecological complexity. Ecological Indicators 10:1069–1076.

165

- Peterson G. 2002. Loss of an alternative state? Box 2-3, page 39 in *Panarchy: Understanding Transformations in Human and Natural Systems*, edited by L. H. Gunderson and C. S. Holling. Washington (DC): Island Press.
- Pickett S. T. A., White P. S. 1985. *The Ecology of Natural Disturbance and Patch Dynamics*. Orlando (Florida): Academic Press.
- Pimm S. L. 1991. The Balance of Nature?: Ecological Issues in the Conservation of Species and Communities. Chicago (Illinois): University of Chicago Press.
- Sarkar S. 2011. Habitat reconstruction: moving beyond historical fidelity. Pages 327–361 in *Philosophy of Ecology*, edited by K. deLaplante, B. Brown, and K. A. Peacock. Amsterdam (The Netherlands): Elsevier.
- Scheffer M., Hosper S. H., Meijer M. L., Moss B., Jeppesen E. 1993. Alternative equilibria in shallow lakes. Trends in Ecology and Evolution 8:275–279.
- Shrader-Frechette K. S., McCoy E. D. 1993. Method in Ecology: Strategies for Conservation. Cambridge (United Kingdom): Cambridge University Press.
- Sousa W. P., Connell J. H. 1985. Further comments on the evidence for multiple stable points in natural communities. *American Naturalist* 125:612–615.
- Sutherland J. P. 1974. Multiple stable points in natural communities. American Naturalist 108:859–873.
- Tilman D. 1994. Competition and biodiversity in spatially structured habitats. *Ecology* 75:2–16.
- Tilman D., Downing J. A. 1994. Biodiversity and stability in grasslands. *Nature* 367:363–365.
- Tusaie K., Dyer J. 2004. Resilience: a historical review of the construct. *Holistic Nursing Practice* 18:3–10.
- Tyre A. J., Michaels S. 2011. Confronting socially generated uncertainty in adaptive management. *Journal of Environmental Management* 92:1365–1370.
- Walker B., Holling C. S., Carpenter S. R., Kinzig A. 2004. Resilience, adaptability and transformability in social-ecological systems. *Ecology and Society* 9:5.
- Walker B. H. 1992. Biodiversity and ecological redundancy. Conservation Biology 6:18–23.
- Walker B. H., Salt D. 2006. Resilience Thinking: Sustaining Ecosystems and People in a Changing World. Washington (DC): Island Press.
- Walker B. H., Ludwig D., Holling C. S., Peterman R. M. 1981. Stability of semi-arid savanna grazing systems. *Journal of Ecology* 69:473–498.
- Webb C., Bodin Ö. 2008. A network perspective on modularity and control of flow in robust systems. Pages 85–118 in *Complexity Theory for a Sustainable Future*, edited by J. Norberg and G. S. Cumming. New York: Columbia University Press.
- White P. S. 1979. Pattern, process, and natural disturbance in vegetation. *Botanical Journal* 45:229–299.

Handling Editor: James D. Thomson