



*Insight*, part of a Special Feature on [Catastrophic Thresholds, Perspectives, Definitions, and Applications](#)  
**Novelty, Adaptive Capacity, and Resilience**

[Craig R. Allen](#)<sup>1</sup> and [C. S. Holling](#)<sup>2</sup>

---

**ABSTRACT.** We present a conceptual framework that explores some of the forces creating innovation and novelty in complex systems. Understanding the sources of variability and novelty may help us better understand complex systems. Understanding complex phenomena such as invasions, migration, and nomadism may provide insight into the structure of ecosystems and other complex systems, and aid our attempts to cope with and mitigate these phenomena, in the case of invasions, and better understand and or predict them. Our model is broadly applicable to ecological theory, including community ecology, resilience, restoration, and policy. Characterizing the link between landscape change and the composition of species communities may help policymakers in their decision-making processes. Understanding how variability is related to system structure, and how that generates novelty, may help us understand how resilience is generated. We suggest that there are three primary opportunities for the generation of novelty into complex systems. These sources of novelty are inherent in the cross-scale structure of complex systems, and are critical for creating adaptive capacity. Novelty originates from the inherent variability present in cross scale structures, within scale reorganization associated with adaptive cycles, and whole-scale transformations resulting from regime shifts. Although speculative, our ideas are grounded in research and observation, and they may provide insight into the evolution of complex systems.

**Key Words:** *adaptation, cross-scale, extinction, innovation, invasion, speciation*

---

## INTRODUCTION

Understanding complex phenomena such as invasion, extinction, migration, nomadism, and speciation may provide us with a better grasp of the structures of ecosystems and other complex systems as well as aid our attempts to better understand and/or predict these phenomena. All of these phenomena represent novelty. Understanding how variability is related to the structures of complex systems and how that structure helps generate novelty may help us understand how ecological resilience is generated. Understanding ecological resilience and the capability of an ecological system to absorb disturbance without collapsing and reorganizing into a different ecological state (Gunderson et al. 2010) is critical to humanity given rapid landscape and climate change. Here we present ideas that we hope provide insight into the evolution of complex behaviors and the emergence of resilience and adaptive capacities.

Ecosystems are organized by interactions among biotic and abiotic processes operating at discrete, or nearly discrete, scales (O'Neill et al. 1989). In hierarchy theory, different scales are referred to as levels of the hierarchy in an abstract sense. We use the term scale as nearly analogous with hierarchical levels and relate scales of hierarchical structure to space and time domains in ecosystems. A domain of a scale is defined as the spatial extent of a structure or process of interest and its temporal frequency. For example, forest gaps resulting from winds are relatively small in space but occur quite frequently, whereas the destruction of entire forests by hurricanes is a rare event but occurs over large spatial extents. Within scales, biotic and abiotic interactions reinforce one another, creating persistent structures and scale-specific patterns. For example, fires in longleaf pine (*Pinus palustris*) ecosystems of the southeastern USA promote the regeneration of longleaf pine, which in turn further promotes fires by dropping highly flammable leaf litter. Across scales, different patterns and processes

---

<sup>1</sup>U.S. Geological Survey, Nebraska Cooperative Fish and Wildlife Research Unit, <sup>2</sup>Department of Zoology, University of Florida

dominate and are only loosely coupled with processes at higher or lower scales (Holling 1992, Peterson et al. 1998). Together, the suite of abiotic processes interacting with biotic elements produce loosely structured hierarchical systems with emergent qualities such as resilience. Reinforcement and inhibition among interacting processes drive this organization. The partitioning of process, structure and function within and across scales provides resilience to complex systems.

The changes in structures and patterns with changes in scale in complex ecological systems provide different templates at different scales with which biota may interact. Within a scale, species strongly interact, and the result is a diversity of species' lifestyles and thus functions, while actual and potential competition among species is reduced (Peterson et al. 1998, Fischer et al. 2007, Wardwell et al. 2008). This is simply because species with similar life spans and step lengths that live in the same ecological system are more likely to come into contact with each other than with species that are considerably larger or smaller. Competition among species that exploit the same or similar resources (i.e., members of the same functional group) is reduced if resources are segregated by scale, thereby lessening the potential for competitive exclusion. In other words, species that exploit the same resource in the same or a similar manner are more likely to coexist if they are of different body sizes. Species that exploit the same resource in similar ways are members of the same functional group, and redundant function is certainly present among species, but the co-existence of 'redundant' species is facilitated when those seemingly redundant species live at different ecological scales. This produces a reinforcement of functions across scales. The function of seed dispersal, for example, is present at a wide range of scales in ecological systems, ranging from the dispersal of a few meters by ants to the dispersal across many kilometers by mammals such as tapirs. Such an arrangement of function within and across scales, regardless of origin, provides a robust response to a variety of perturbations, especially to perturbations that tend to scale up, such as insect outbreaks (Peterson et al. 1998). Changes in domains of scale are characterized by distinct scale breaks, reflecting abrupt changes in pattern and structure. Ants and tapirs live in the same environments but do not interact with the same structures, and there is not a continuous transition between the structures with which ants and tapirs

interact. Heightened variability at the species, population and community levels has been observed at those transitions between scales (Allen et al. 1999, Allen and Saunders 2002, 2006, Gunderson et al. 2007, Skillen and Maurer 2008, Wardwell and Allen 2009), as indicated by phenomena such as invasion, extinction, nomadism, and migration. We believe this reflects heightened variability at transitions between structures discernable at specific scales and that variability provides opportunities for and generates novelty.

Here, we offer a conceptual framework that addresses the forces that create novelty in complex systems. We explicitly consider the generation of novelty in ecological systems, but believe the general concepts are appropriate to other complex systems, such as societies, for which we might consider innovation as well as novelty. Although novelty and innovation are recognized as critical to adaptation, the generation thereof is rarely discussed. It is, however, critical to consider landcover and landuse change on Earth in this era of rapid climate change. We believe that the generation of novelty, and hence adaptive capacity, is critical for maintaining resilience in complex systems under stress. Therefore, we address how the generation of novelty enhances resilience. Our model is broadly applicable to ecological theory, resilience theory, community ecology, restoration, and policy. Understanding the sources of variability and novelty may help us better understand complex systems.

## **CROSS-SCALE ORGANIZATION IN COMPLEX SYSTEMS**

An ecosystem is the product of non-linear interactions among its component parts. If all parts of an ecosystem interacted equally, ecosystems would be incredibly complicated and impossible to understand. However, ecosystems are complex systems; the way in which they are organized makes them less complicated and more easily understood, at least in an abstract sense. As complex adaptive systems, ecosystems possess emergent properties such as resilience and discontinuous structures that vary across scales. This cross-scale structure has been recently described as a panarchy, a nested set of adaptive cycles with clearly differentiated structures across scales. An adaptive cycle (Holling and Gunderson 2002) describes the process of development and decay in a system (Figure 1) and

is generally “self-organizing” because positive interactions reinforce its structures. The process that adaptive cycles describe is similar to the process of succession, but the concept is important because a nested set of adaptive cycles each occurring at a specific scale comprises a panarchy. In an adaptive cycle, the initial stage of development is of short duration and consists of a rapid exploitation and garnering of resources by system components. This stage has been termed the *r* stage or function and is a period of rapid growth in pioneering or early successional species. The *r* stage is followed by the *k* stage or function, a stage of longer duration that is characterized by the accumulation of biomass or other system elements or energies as well as increasing connectivity and rigidity. Increasing connectivity and rigidity during the *k* phase leads to decreased resilience and eventual collapse. This stage of collapse, the *omega*, is rapid and unleashes the energy accumulated and stored during the *k* phase. The *omega* phase is triggered, for example, by forest fires or pest outbreaks. Collapse during the *omega* phase is followed by reorganization during the *alpha* phase, a relatively rapid period of the assembly of components, analogous to the pioneer stage in ecosystems or a system under high gain (Allen et al. 2001).

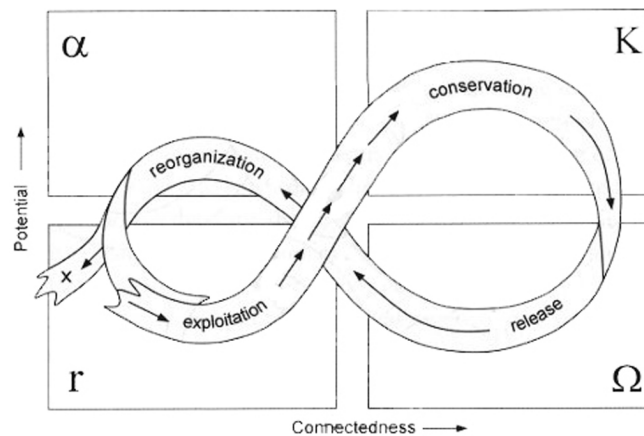
Adaptive cycles do not exist in isolation. Adaptive cycles operate over limited ranges of scale, whereas complex systems are characterized by a rich array of scales, each scale exhibiting characteristic structures and dynamics. A panarchy is a nested set of adaptive cycles (Figure 2). An ecosystem and other complex systems can be conceptualized as a panarchy. For resilience theory, it is critical to understand the scales of interest and the scale of analysis because one level of a panarchy may collapse and cascade to lower levels, but the system as a whole may be maintained. For example, at very small space and time scales, the leaves of trees exhibit an adaptive cycle with an annual periodicity; forest stands also exhibit adaptive cycles, with a decadal or greater periodicity and relatively large spatial extent. A forest fire that “resets” a forest stand starts that stand at the *omega* phase of an adaptive cycle, but it does not necessarily affect larger scale structures, such as the landscape in which the forest stand is embedded. Each adaptive cycle operates over a discrete range of scales in both time and space and is connected to adjacent levels (adaptive cycles). Resilience is a property that can exist at any scale in a panarchy.

A given level may not be very resilient, but the larger system may be. Unlike the top-down control envisioned in traditional hierarchies, connectivity between adaptive cycles in a panarchy can be from levels above or below.

## **CROSS-SCALE STRUCTURE AND DISCONTINUITIES**

The structure of complex systems is strongly self-organizing and may be quite conservative. This structure provides the core ‘memory’ of a system in that its structure is unlikely to change. The components of complex systems such as ecosystems interact to create conservative structures in time and space – interactions that are reinforced persist, whereas those that are not fade away. This is important for humans because complex systems such as ecosystems often remain apparently more or less stable; thus, we can expect reasonably predictable dynamics and the relatively constant provision of ecological goods and services. This conservativeness and self-organization is due in part to the interaction of biotic and abiotic elements. Animals interact with the ecological structure that provides a distribution of necessary resources such as food and space that they can successfully exploit in space and time. In exploiting their environments, animals often change ecological structures in ways that are favorable for themselves. For example, large herbivores can alter the dynamics of succession (and competition among grasses, bushes and trees) such that the habitat is, in some sense of the word, optimal for them. Self-organization involves other biotic system elements as well. For example, many grasses worldwide are pyrophilic and, therefore, highly flammable (Brooks et al. 2004). In the absence of fire, succession would often eliminate these grasslands from the ecosystems they occupy. However, the presence of these grasses encourages fire, which favors their spread and excludes competitors. In the absence of fire, ecosystems such as the longleaf pine savannah in the Southeastern United States rapidly transform to oak forest (Peterson 2002). Strongly interacting species have been termed keystone (Mills et al. 1993) or driver species (Walker 1995). However, we note the absence of scale in such definitions. Any keystone species (or process), because it affects a system only over a limited range of scales, is a keystone only at the scale in which it interacts (unless it has truly cross-scale impacts, which is

**Fig. 1.** The adaptive cycle. A representation of the four ecosystem functions ( $r$ ,  $k$ ,  $\omega$ ,  $\alpha$ ) and the flow of events among them. The arrows show the speed of the cycle where short, closely spaced arrows indicate a slowly changing state and long arrows indicate a rapidly changing state. The cycle reflects changes in two properties: (1) Y axis—the potential that is inherent in the accumulated resources of biomass and nutrients; (2) X axis—the degree of connectedness among controlling variables. Low connectedness is associated with diffuse elements loosely connected to each other whose behavior is dominated by outward relations and affected by outside variability. High connectedness is associated with aggregated elements whose behavior is dominated by inward relations among elements of the aggregates, relations that control or mediate the influence of external variability. The exit from the cycle indicated at the left of the Figure suggests where the potential can leak away or where a change of state into a less productive and organized system is likely. From *Panarchy: Understanding Transformations in Human and Natural Systems* L.H. Gunderson and C.S. Holling, eds. Copyright © 2001 by Island Press.

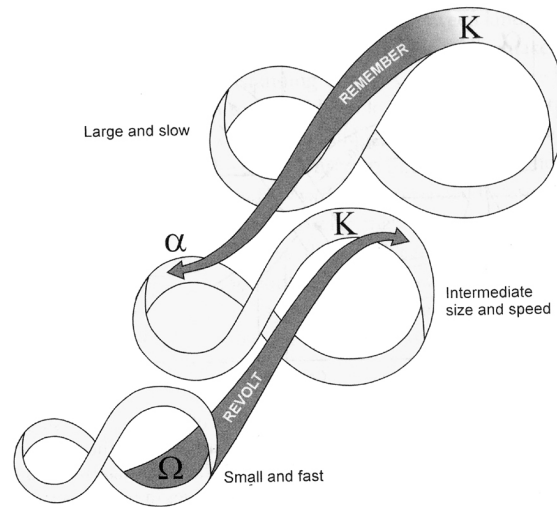


unlikely given current definitions of keystone species). Because ecosystems are characterized by a rich array of scales, there may be a rich array of keystone species present, and dominant interactions at each scale are crucial. Furthermore, a keystone or driver species often has a transient role; as system or community dynamics change, the identity of key species changes (Walker 1995, Walker et al. 1999). Self-organization is important not only for the provision of goods and services to humans but because it means that understanding ecosystems and other complex systems is at least somewhat tractable. Ecosystem structures and functions, though dynamic through time, are largely constant and educible at human time scales. The exception, of course, is when the resilience of systems is exceeded and rapid transformations occur.

Because adaptive cycles and self-organization occur at discrete scales within a system, ecosystems and other systems are characterized by

discontinuity (Garmestani et al. 2009). Discontinuities are rooted in the separation between levels of a panarchy. Different adaptive cycles and different structuring processes are separated from one another by gaps in the domains of scale that they occupy, often an order of magnitude or more (Holling and Gunderson 2002). This separation has several important effects. First, as stated above, it means that variables within systems are distributed discontinuously. Second, it indicates that self-organizing interactions and processes, such as community-level interactions for animals (including interactions such as competition), are compartmentalized by scale. Therefore, similarly sized animals are more likely to strongly interact than animals of grossly different sizes, although exceptions occur (for example, with predation). The compartmentalization of systems along an axis of scale provides rich opportunities for experimentation within levels, and this leads to the development of high levels of diversity within systems (O'Neill et al. 1986). This

**Fig. 2.** Figure 2. A panarchy. Three selected levels of a panarchy are illustrated, to emphasize the two connections that are critical in creating and sustaining adaptive capability. One is the "revolt" connection, which can cause a critical change in one cycle to cascade up to a vulnerable stage in a larger and slower one. The other is the "remember" connection, which facilitates renewal by drawing on the potential that has been accumulated and stored in a larger, slower cycle. The number of levels in a panarchy varies, is usually rather small, and corresponds to levels of scale present in a system. Excerpted from *Panarchy: Understanding Transformations in Human and Natural Systems* L. H. Gunderson and C. S. Holling, eds. Copyright © 2001 by Island Press.



results in a distributional pattern of function in which diversity is high within scales and is repeated (i.e., the function contained within is redundant) at different scales, a pattern that adds to the resilience of ecosystems (Peterson et al. 1998) and other complex systems (Garmestani et al. 2006). The presence of discrete scales of pattern and process in complex systems creates discontinuities, or scale breaks, between ranges of scales. Theory and recent empirical analysis suggest that these scale breaks generate novelty and innovation as a result of the variable dynamics at these transitions.

## VARIABILITY AT SCALE BREAKS

The body mass of vertebrates is strongly allometric with many ecological attributes of species; therefore, it is a useful proxy for the scale at which an animal interacts with its environment. Body mass distributions of vertebrates from ecosystems are discontinuous and consist of body mass aggregations of species with similar body mass

separated by gaps (discontinuities; Allen and Holling 2008). The body mass aggregations are thought to correspond with the scales of structure available in a system, and the gaps represent transitions (scale breaks) between the available ranges of scales. Discontinuities, or gaps, in variables in complex systems have been described as scale breaks where highly variable and unpredictable behavior is expected (O'Neill et al. 1989, Allen et al. 1999). Examples of high variability at scale breaks in ecosystems include the success of invasive non-indigenous species, the failure or extinction of native species and an association with migratory and nomadic species.

The association of invasive species with scale breaks has been documented in a variety of ecosystems and for both birds and mammals (Allen et al. 1999, Allen 2006). The association has been most thoroughly investigated for the Everglades ecosystem of Florida, where invasive species tend to occur at the edge of body mass aggregations. That association is significant because it links an

independent biological attribute, invasiveness, with a particular location on a body mass axis, at the edge of discontinuities. It is strengthened by the finding that declining species are also associated with scale breaks. The significance of the association is further strengthened because the analysis of successfully versus unsuccessfully introduced avian species in the Everglades demonstrates that introduction success is best predicted by distance from the edge of a discontinuity and not by intrinsic traits of species or communities. Introduced species whose body mass places them close to the edge of a body mass aggregation are more likely to become established than an introduced species whose body mass places it toward the center of an aggregation (Allen 2006). Other potential predictors of introduction success based on intrinsic or community-level hypotheses of success fail in that continental data set. It should be noted that despite a flurry of books and articles focusing on invasive species over the last 15 years, invasion biology is a discipline that is in its infancy, largely because the ability to experiment is lacking and because inference is largely based on positive cases (successful introductions or invasions). There is limited information on what species were unsuccessful in becoming established, although there are exceptions (Allen and Starr 1988). One of those exceptions is the south Florida avifauna, where we, with some surety, know the pool of unsuccessfully introduced species. The Everglades provides an additional clue to the link between ecological structure and novelty. Declining species comprise approximately 25% of the fauna in three vertebrate taxa (mammals, birds and herpetofauna; Forsy and Allen 1999), and non-indigenous species comprise a further 25%. Forsy and Allen (2002) examined historic (no non-indigenous species), current (non-indigenous and declining species included) and hypothetical future (non-indigenous species included, declining species eliminated) body mass and functional patterns for mammals, birds and herpetofauna of the Everglades. They found that neither the distribution of function nor overall body mass pattern was substantially changed by the large species turnover in their time series. Body mass pattern was conserved, and the large species turnover was primarily limited to areas of discontinuity.

Species invasions and extinctions represent turnover in animal community composition, but there is other documented variability at scale breaks in animal communities. Migration and nomadism

represent unpredictable or annual turnover in community composition and are also novel and poorly understood behaviors, in an evolutionary sense. Both allow the exploitation of resources at a level that could not otherwise be achieved, at least not without some other novel approach to secure resources that vary so strongly in both time and space. In Mediterranean-climate Australia, near the city of Adelaide, the climate is highly variable, and the avifauna has among the highest, perhaps the highest, incidence of nomadism in the world. There, nomadism is best predicted by a combination of body mass, nectivory and proximity to discontinuity. Birds that are bigger, feed on nectar and have body masses that place them closest to discontinuities are most likely to be nomadic (Allen and Saunders 2002, 2006, but see Woinarski 2006). Similarly, migrant birds have body masses that tend to place them close to discontinuities in body mass distributions. Weeks and Allen (unpublished data) investigated the relationship between migrant species and body mass distributions for the migrant bird species that breed in South Carolina, USA, but that annually depart for the winter. They did the same for species that migrate to Costa Rica (La Selva) during the winter but that breed elsewhere. They found that in both South Carolina and Costa Rica, migrants tend to have body masses proximate to discontinuities. Interestingly, the South Carolina migrants that winter in Costa Rica, which have body masses close to scale breaks in the body mass distribution of South Carolina resident birds, are not close to scale breaks in the body mass distribution of Costa Rica birds. (South Carolina migrants are a small subset of the migrant species present in Costa Rica.) Analysis of migrant South African birds also suggests an association with discontinuities (Alai 2010). This suggests that their existence near discontinuities and their variable resources represent an unexploited, but risky, opportunity. It may be overly risky to exploit 'at the edge' on both the wintering and summering grounds.

## **NOVELTY AND INNOVATION**

Novelty and innovation are required for systems to remain dynamic and functioning. Without innovation and novelty, systems may become over-connected and dynamically locked, and the capital therein may be unavailable (Gunderson and Holling 2002). Novelty and innovation are required to keep existing complex systems resilient and to create new structures and dynamics following system crashes.

This is true in all complex systems, and the importance of novelty is recognized as much (if not more) in the management and business world as it is in scientific fields.

Speaking of management hierarchies, Pierce and Delbecq (1977) described the organizational elements required for innovation. One of those elements is differentiation, which is necessary for the initiation of innovation. We find differentiation present in ecological systems in many forms, genotypically, phenotypically and functionally, and this is paralleled in social and social-ecological systems. Decentralization is another important element described by Pierce and Delbecq. It is a key component of complex systems and is related to Pierce and Delbecq's concept of stratification, which we interpret as levels within a hierarchy. Pierce and Delbecq (1977) also discuss contextual attributes of innovation, specifically environmental uncertainty, larger size and age. Larger hierarchies have more opportunities for innovation, and older hierarchies are less open to innovation. Clearly, novelty is important for the maintenance and health of a wide variety of systems—ecological, social, cultural, and combinations thereof. Novelty and innovation are needed to maintain not only maintenance functions, but also the adaptive capacity of systems and to allow complex systems the latitude to 'explore' alternative structures and dynamics, that is, to evolve. Below, we describe the generation of novelty as related to the structure of discontinuous, panarchically organized complex adaptive systems.

## **TYPES OF NOVELTY**

The generation of novelty and innovation is a characteristic of dynamic complex systems. It is generated at all levels. For example, in biological systems, it is generated at the genetic level through random processes of mutation, at the species level through the selective processes of evolution, at the community level as a result of assortment and changes in the species pool, and at the ecosystem level as a result of changes in key driving processes and self-organizing (reinforcing) interactions.

There are fundamental similarities around which the concept of novelty can be organized. We organize novelty into three types: background, incremental and punctuated. These are discussed below. All three types of novelty generation can be

either locally or globally novel. Locally novel additions are novel to that particular system. For example, the addition of an invasive species to an ecosystem adds novelty to that system, but the invasive species was in existence prior to its invasion of a new ecosystem. On the other hand, globally novel additions did not previously exist and are new not only to the particular system within which they are generated or added but are also new to the globe. Speciation within a system represents the addition of global novelty.

## **Background**

Novelty is generated as a result of the normal dynamics of complex systems. In terms of a panarchy with a discontinuous structure, novelty is generated at the edge of scale breaks (at the transitions between domains of scale) as a result of the highly variable distribution and occurrence of resources in space and time, which in turn is reflected in the high variability in biotic components of the system (e.g., Allen et al. 1999, Skillen and Maurer 2008). This generation of novelty creates options for systems, is critical in maintaining adaptive capacity, and serves as a reservoir of potential functions that may be required following transformations or as normal system dynamics evolve. In the thermodynamics and gain literature, this has been termed internal complexification because it builds upon extant structures (Tainter 1990, Tainter et al. 2003). Such novelty is at the heart of resilience.

## **Incremental**

Self-organizing processes among the biotic and abiotic elements of complex systems, such as ecosystems, add complexity over time. Some of that complexity is added during the r and k stages of an adaptive cycle in the form of new connections, new functions and new arrangements of elements. However, new levels (new adaptive cycles) can also be added during r stages. The addition of new layers to a hierarchy adds new scales of opportunity for elements of complex systems such as species or firms. In a thermodynamic sense, the emergence of a new layer of structure in a hierarchy results from self-organization with a steep thermodynamic gradient, termed external complexification because it results partially from an external gradient (Tainter et al. 2003). The addition of new levels of adaptive

cycles may make a complex system more resilient and thus less prone to cross-scale collapse (i.e., the collapse of all levels of a panarchy at once, including the top level, termed a regime shift or a flip to an alternative state)(Allen et al. 2005).

### **Punctuated**

When the resilience of a complex system is exceeded, a system may collapse, and all levels of a panarchy may experience the omega phase simultaneously (Gunderson and Holling 2002). Novelty may be added to or introduced to a system during reorganization. Here the novelty added (for example, new animals to a community or ecosystem) may be local or global. While this type of transformation and novelty generation is not likely to spawn globally novel elements, it does provide opportunities for globally novel arrangements of elements. The addition of novelty in a punctuated manner may also occur within adaptive cycles, when individual cycles enter the omega – alpha phases, and this may also build overall resilience over time and in response to changing conditions.

### **NOVELTY AND RESILIENCE AND ADAPTIVE CAPACITY**

Adding levels to a panarchy (or other incremental novelty), the generation of novelty at scale breaks (background), and punctuated novelty may all build resilience in systems. The novelty generated at scale breaks, and as importantly, the potential for the generation of novelty at scale breaks, builds adaptive capacity in complex systems. Jain and Krishna (2002) documented how dormant innovations in complex graph networks can take over system dynamics at times when other dominant elements become weak (i.e., when the resilience of the system is diminished). Having a constant source of innovation and novelty is clearly important for systems, both following transformations and during their normal dynamics, if a system is not to become over-connected and over-capitalized. Without a continual source of novelty, complex systems such as ecosystems cannot be adaptive or dynamic. Scale breaks are a key source for such innovation. It should be noted, however, that innovation and novelty may be destructive forces as well. Invasive species, for example, can alter basic process and structure in ecosystems and be a source of collapse and transformation. Thus,

innovation and novelty may be a double-edged sword in some circumstances. In ecosystems, for example, in addition to being a cause of major extinctions, 'innovation' is also the prime source of recovery (Jain and Krishna 2002).

### **THE GENERATION OF NOVELTY AT SCALE BREAKS**

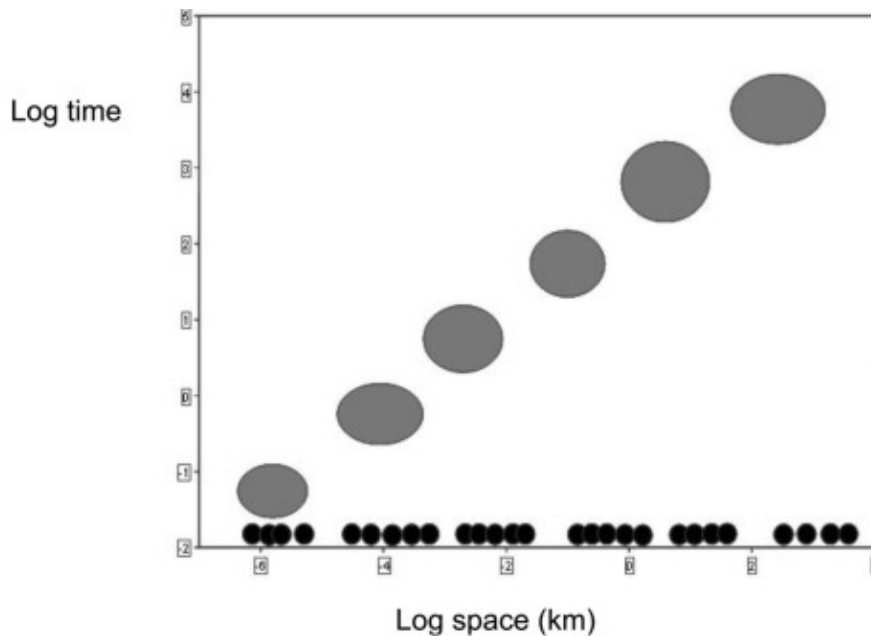
The novelty generated at scale breaks, those regions between adaptive cycles in a panarchy, is critical for complex systems. Furthermore, these regions may represent 'novelty pumps,' regions of the actual and potential production of innovation and novelty. As discussed above, highly variable phenomena are associated with discontinuities in animal body mass distributions. Body mass distributions reflect the scales of available structures in an ecosystem, which in turn reflect the panarchical structure of the system (Figure 3). Thus, discontinuities in body mass patterns reflect the location of scale breaks in ecological structure. A similar structure is also present in other complex systems, such as regional urban systems (Garmestani et al. 2005) and regional economic systems (Garmestani et al. 2006).

Phenomena such as invasion, extinction, nomadism, and migration in animal communities reflect high variability, but also represent the creation or insertion of novelty. Invasive species have subtly or grossly different ways of interacting with their new environments, as compared to native species, and their addition may reflect a system in transition (Allen et al. 1999). Their addition may not alter, but rather reinforce existing ecological organization (Forys and Allen 2002) and thus build resilience, or they may be destructive and transformative forces.

We assert that the generation of novelty at scale breaks results from a high variability in resources (Figure 4; O'Neill et al. 1989, Allen et al. 1999). While high variation in resource abundance and location in space and time is a hardship for some species (see, for example, the propensity of declining species to have body masses proximate to discontinuities (Allen et al. 1999, Skillen and Maurer 2008)), it is an opportunity for other species that successfully invade and exploit these locations/resource or that develop novel and innovative behaviors (Figure 5). However, a strategy that focuses on resources that are highly predictable, especially when the structure of a system is dynamic and when the location of scale breaks may shift over



**Fig. 3.** Discontinuous body mass distributions (black circles on x-axis representing animal body masses along a body mass axis) reflect the levels of scale (grey circular regions, representing space-time domains of structures) available in a given system, which in turn reflect the underlying panarchy. The x axis represents both spatial scale of processes and a body mass axis for species inhabiting the system.



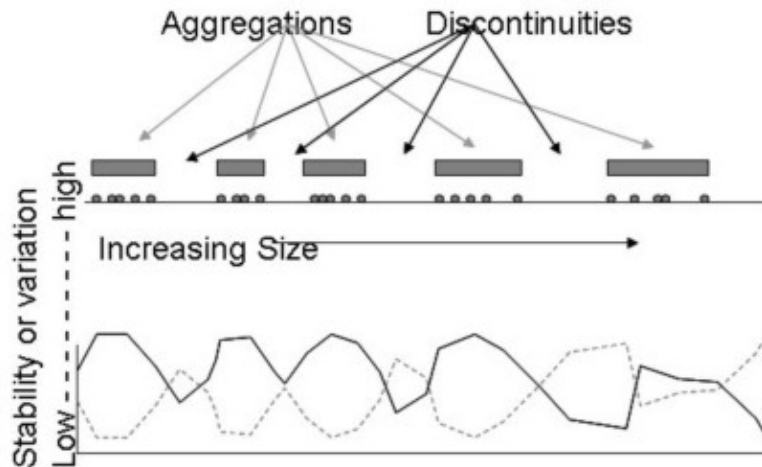
time, is likely not an optimal long-term strategy. However, it is the best strategy when the stable resources far from a discontinuity are effectively sequestered by others and niches are saturated.

Mutations and other novelty that occur as background have little chance of success in the center of an aggregation, far from discontinuities and scale breaks. At the center of an aggregation, resources are stable and thoroughly exploited and competition is intense. However, at discontinuities, the high fluctuation in resources is more likely to lead to the success of random mutations. Over time, species or strategies successful at the edge may migrate into the center of an aggregation, where resources are more stable and secure (Figure 6). This is analogous to the Taxon Cycle in biogeography (Wilson 1961). Many of the major innovations in the history of life, such as the spread of novel metabolic activities in the first billion years of Earth's history, the spread of photosynthesis, the development of multi-cellular organisms, and the spread of life to terrestrial ecosystems, all share

basic similarities. In each case, innovation was constructed through an evolutionary triad of challenge, potential and opportunity. Each of these conditions is met within a panarchy, specifically at the discontinuities that define regions between levels (scale breaks).

Evolutionary innovation is the acquisition of novel morphologies and/or behaviors that open new niches, providing new ways to successfully exploit the environment. In ecosystems, an extreme case of the generation of novelty is represented by speciation. Scale breaks may offer the opportunity for parapatric or sympatric speciation. However, the isolation is not due to linear distance per se, as in parapatric speciation (Knapp and Mallet 2003), any more than it is geographic barriers. Rather, it is isolation driven by the interaction with the environment at different ranges of scale. This may strike some as unlikely. However, consider an extreme mammal example: least shrews (*Cryptotis parva*) and moose (*Alces alces*) in a boreal ecosystem. Clearly, these animals are sympatric, yet

**Fig. 4.** The relationship between discontinuities, variability and stability. Body size distributions of animals are characterized by aggregations and discontinuities (upper graphic, circles representing species). Aggregations reflect domains of scale and discontinuities reflect scale breaks. Within domains of scale, resource variation is low (lower graphic, dotted line), and at scale breaks resource variation is high. Stability (solid line) is inversely related to variability and is high within scales and low at scale breaks.

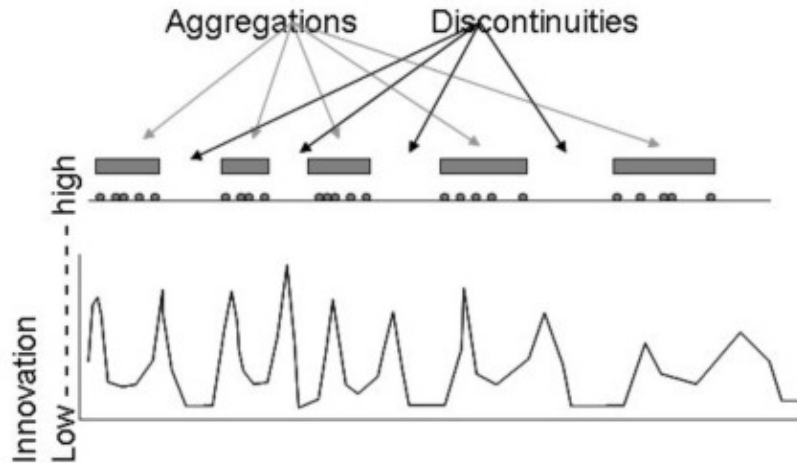


they have little (if any) interaction. The life span of a least shrew is less than two years, and that of a moose is more than twenty. The resources and structure that a shrew interacts with during the process of its life are, we believe, viewed as noise to the moose. Similarly, the structures and processes that a moose interacts with are slow relative to the life span and step size of a shrew and, therefore, they are simply background to the shrew. Sympatric speciation would not lead to such extreme size divergence quickly. However, scale-dependent isolation would likely lead to increasing size divergence between closely related species. Life at discontinuities means constant adaptation to fluctuating resources. The high variability inherent at scale breaks, and more stable opportunities for resource acquisition at higher or lower scales, provides ample opportunity for differentiation of lineages within a species (by habitat, by scale, by resource, or by a combination thereof). Because species at discontinuities are at the edge of an available range of scale, it is perhaps possible for these species to shift between scales (Allen and Saunders 2002). This provides an opportunity for sympatric speciation based on scale. Furthermore, the biological variability witnessed at the

population and community level at scale breaks hints of potential individual phenotypic and genotypic variability.

Despite a substantial volume of papers on speciation from field, laboratory and theoretical perspectives, the process leading to the creation of new species remains poorly understood (Sepkoski 1998). While sympatric speciation is (may be) controversial for some (Via 2001), habitat choice has been shown to produce assortative mating and sympatric speciation under disruptive selection (Rice 1984, Kondrashov and Mina 1986, Rice and Salt 1990), including selection on traits associated with competition or predation (Schluter 1996, Via 2001). Sympatric speciation can arise from reproductive isolation associated with adaptation to alternative resources or habitats (Turelli et al. 2001). Scale segregation may produce ecological speciation by isolating two populations based on their scale of habitat use; this may be sympatric or parapatric. The rebound of species diversity (increased speciation rates) following mass extinctions (Sepkoski 1998) suggests that incipient species are always present but the 'success' of species is greater following such events. Thus, a novelty pump, as it were, may be

**Fig. 5.** Novelty and innovation mirror discontinuities and resource variability in complex systems, and are high at the edge of discontinuities.



extremely important in providing a source following such events. Niche construction (lineages modifying their environments to construct their own ecological role and consequently construct niches for other species) seems to be especially important following mass extinctions. Why? Panarchy theory provides a possible explanation. We cannot consider species as passive elements within an ecosystem or landscape, but rather as critical engineers of their environment. Species interact in an often reinforcing manner with abiotic structure and process, traveling upon a shared trajectory, where a change by either the biotic or by the abiotic elements is equally important. Thus, mass extinctions either cause or reflect systems that have been transformed. The large loss of species means a disruption in self-organizing processes that are responsible for structure in complex systems. The loss of elements responsible for self-organizing processes with abiotic elements leads to the generation of new inter-relationships, new self-organizing processes, and thus keystone (or niche-building) species.

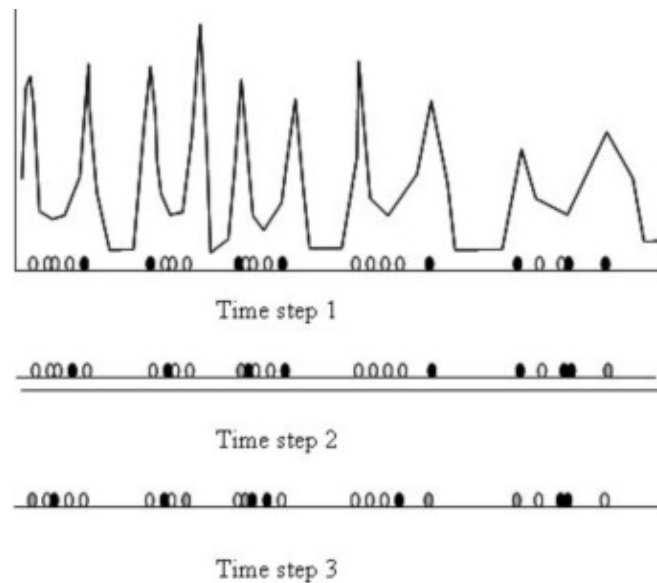
## APPLICATIONS

At the molecular, community, ecosystem, and other levels, novelty is constantly created and extinguished. Scale breaks provide a robust pump for the generation of novelty, and thus a key source of adaptive potential following transformation, and adaptation to changing conditions such as rapid climate change.

Global climate change results in rapid transformations in the organization of the complex systems that we inhabit, we create, and we rely upon. The novelty pump inherent in the structure of complex panarchies is necessary for adaptation to changing environments (for example, species undergoing long-range migration or nomadic movements may be better able to cope with global climate change).

Species in the center of aggregations may have 'built' niches that are stable. Given the conservative nature of the structure of body mass distributions (Havelcik and Carpenter 2001, Forsy and Allen 2002) and the high degree of resilience in many systems, this is adaptive for most circumstances. It is analogous to the K phase of the adaptive cycle. However, when the resilience of a system is exceeded and it transforms during other transformative events at one or more scales, this strategy is apt to be 'brittle' and vulnerable to

**Fig. 6.** The novelty cycle in discontinuous panarchical systems is analogous to the taxon cycle described by Wilson (1961). Variability in resources (line above the x axis that represents the discontinuous body mass distribution of species) is highest at scale breaks, as in Figure 5. In time step one, novel behaviors or species (black) are added at scale breaks. As time progresses (time step two) the novel behaviors or species have ‘migrated’ towards the center of body mass aggregations where resources are less variable. By step three, this migration has completed. In time steps two and three new novelty is being introduced at the edges (grey). This diagram does not show the increased extinction rates also expected to be associated with scale breaks.



failure. On the other hand, the novel strategies generated at scale breaks are likely to become dominant during such systemic crises.

Continuously pumping out novel solutions to current or potential challenges ensures a maximization of energy/resource use within a system without reorganizing the system. It also allows the system to be dynamic both in its internal structure and connectivity and in its relationship with other systems. Most of the novel solutions created by mutation and other sources do not have a challenge to respond to, and thus are conceived of as failures. However, when challenges arise, it is critical to have a solution available. Thus, generation of novelty at scale breaks helps ensure that the evolutionary potential of both species and systems is maintained.

Responses to this article can be read online at:  
<http://www.ecologyandsociety.org/vol15/iss3/art24/responses/>

#### **Acknowledgments:**

*The Nebraska Cooperative Fish and Wildlife Research Unit is jointly supported by a cooperative agreement between the United States Geological Survey, the Nebraska Game and Parks Commission, the University of Nebraska - Lincoln, the United States Fish and Wildlife Service and the Wildlife Management Institute. Support was provided to CRA by the James S. McDonnell Foundation 21st Century Research Award/Studying Complex Systems. An earlier version of this manuscript was improved by comments from T.F.H. Allen and two anonymous reviewers.*

## LITERATURE CITED

- Alai, A.** 2010. *The textural discontinuity hypothesis and its relation to nomadism, migration, decline, and competition*. Thesis, University of Nebraska, Lincoln, Nebraska, USA. *In press*.
- Allen, C. R.** 2006. Predictors of introduction success in the South Florida avifauna. *Biological Invasions* 8:491-500.
- Allen, C. R., E. A. Forsys, and C. S. Holling.** 1999. Body mass patterns predict invasions and extinctions in transforming landscapes. *Ecosystems* 2:114-121.
- Allen, C. R., L. Gunderson, and A. R. Johnson.** 2005. The use of discontinuities and functional groups to assess relative resilience in complex systems. *Ecosystems* 8:958-966.
- Allen, C. R. and C. S. Holling.** 2008. *Discontinuities in ecosystems and other complex systems*. University of Columbia Press, New York, New York, USA.
- Allen, C. R., and D. A. Saunders.** 2002. Variability between scales: predictors of nomadism in birds of an Australian Mediterranean-climate ecosystem. *Ecosystems* 5:348-359.
- Allen, C. R., and D. A. Saunders.** 2006. Multi-model inference and the understanding of complexity, discontinuity and nomadism. *Ecosystems* 9:694-699.
- Allen, T. F. H., and T. B. Starr.** 1988. *Hierarchy: perspectives for ecological complexity*. University of Chicago Press, Chicago, Illinois, USA.
- Allen, T. F. H., J. A. Tainter, J. C. Pires, and T. W. Hoekstra.** 2001. Dagnet ecology, "just the facts Ma'am: the privilege of science in a post-modern world. *BioScience* 51:475-485.
- Brooks, M. L., C. M. D'Antonio, D. M. Richardson, J. B. Grace, J. E. Keeley, J. M. DiTomaso, R. J. Hobbs, M. Pellant, and D. Pyke.** 2004. Effects of invasive alien plants on fire regimes. *Bioscience* 54:677-688.
- Fischer, J., D. B. Lindenmayer, S. P. Blomberg, R. Montague-Drake, A. Felton, and J. Stein.** 2007. Functional richness and relative resilience of bird communities in regions with different land use intensities. *Ecosystems* 10:964-974.
- Forsys, E. A., and C. R. Allen.** 1999. Biological invasions and deletions: community change in south Florida. *Biological Conservation* 87:341-347.
- Forsys, E. A., and C. R. Allen.** 2002. Functional group change within and across scales following invasions and extinctions in the Everglades ecosystem. *Ecosystems* 5:339-347.
- Garmestani, A. S., C. R. Allen, and K. M. Bessey.** 2005. Time series analysis of clusters in city size distributions. *Urban Studies* 42:1507-1515.
- Garmestani, A. S., C. R. Allen, and L. Gunderson.** 2009. Panarchy: discontinuities reveal similarities in the dynamic system structure of ecological and social systems. *Ecology and Society* 14(1): 15. [online] URL: <http://www.ecologyandsociety.org/vol14/iss1/art15/>.
- Garmestani, A. S., C. R. Allen, J. D. Mittelstaedt, C. A. Stow, and W. A. Ward.** 2006. Firm size diversity, functional richness and resilience. *Environment and Development Economics* 11: 533-551.
- Gunderson, L., C. R. Allen, and C. S. Holling.** 2010. *Foundations of ecological resilience*. Island Press, New York, New York, USA.
- Gunderson, L., C. R. Allen, and D. Wardwell.** 2007. Temporal scaling in complex systems: resonant frequencies and biotic variability. Pages 78-89 in J. A. Bissonette, and I. Storch, editors. *Temporal dimensions in landscape ecology: wildlife responses to variable resources*. Springer, New York, New York, USA.
- Gunderson, L. H., and C. S. Holling.** 2002. *Panarchy: understanding transformations in human and natural systems*. Island Press, Washington, D.C., USA.
- Havlicek, T. D., and S. R. Carpenter.** 2001. Pelagic species size distributions in lakes: are they discontinuous? *Limnology and Oceanography* 46 :1021-1033.
- Holling, C. S.** 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. *Ecological Monographs* 62:447-502.

**Holling, C. S., and L. H. Gunderson.** 2002. Resilience and adaptive cycles. Pages 25-62 in L. H. Gunderson, and C. S. Holling, editors. *Panarchy: understanding transformations in human and natural systems*. Island Press, Washington, D.C., USA.

**Jain, S., and S. Krishna.** 2002. Large extinctions in an evolutionary model: the role of innovation and keystone species. *Proceedings of the National Academy of Science* 99:2055-2060

**Knapp, S., and J. Mallet.** 2003. Refuting refugia? *Science* 300:71-72.

**Kondrashov, A. S., and M. V. Mia.** 1986. Sympatric speciation: when is it possible? *Biological Journal of the Linnean Society* 27:201-223.

**Mills, L. S., M. E. Soulé, and D. F. Doak.** 1993. The keystone-species concept in ecology and conservation. *Bioscience* 43:219-224.

**O'Neill, R. V., D. L. DeAngelis, J. B. Waide, and T. F. H. Allen.** 1986. *A hierarchical concept of ecosystems*. Monographs in Population Biology 23, Princeton University Press, New Jersey, USA.

**O'Neill, R. V., A. R. Johnson, and A. W. King.** 1989. A hierarchical framework for the analysis of scale. *Landscape Ecology* 3:193-205.

**Peterson, G. D.** 2002. Estimating resilience across landscapes. *Conservation Ecology* 6(1): 17. [online] URL: <http://www.consecol.org/vol6/iss1/art17/>

**Peterson, G., C. R. Allen, and C. S. Holling.** 1998. Ecological resilience, biodiversity and scale. *Ecosystems* 1:6-18.

**Pierce, J. L., and A. L. Delbecq.** 1977. Organizational structure, individual attitudes and innovation. *The Academy of Management Review* 2:27-37.

**Rice, W. R.** 1984. Disruptive selection on habitat preference and the evolution of reproductive isolation: a simulation study. *Evolution* 38:1251-1260.

**Rice, W. R., and G. Salt.** 1990. The evolution of reproductive isolation as a correlated character under sympatric conditions: experimental evidence. *Evolution* 44:1140-1152.

**Schluter, D.** 1996. Ecological causes of adaptive radiation. *American Naturalist* 148:S40-S64.

**Sepkiski, J. J., Jr.** 1998. Rates of speciation in the fossil record. *Philosophical Transactions of the Royal Society of London B* 353:315-326.

**Skillen, J. J., and B. A. Maurer.** 2008. The ecological significance of discontinuities in body mass distributions. Pages 193 – 218 in Allen, C. R. and C. S. Holling, editors. *Discontinuities in ecosystems and other complex systems*. Columbia University Press, New York, New York, USA.

**Tainter, J. A.** 1990. *The collapse of complex societies*. Cambridge University Press, Cambridge, UK.

**Tainter, J. A., T. F. H. Allen, A. Little, and T. W. Hoekstra.** 2003. Resource transitions and energy gain: contexts of organization. *Conservation Ecology* 7(3): 4. [online] URL: <http://www.consecol.org/vol7/iss3/art4/>.

**Turelli, M., N. H. Barton, and J. A. Coyne.** 2001. Theory and speciation. *TRENDS in ecology and evolution* 16:330-343.

**Via, S.** 2001. Sympatric speciation in animals: the ugly duckling grows up. *TRENDS in Ecology and Evolution* 16:381-390.

**Walker, B.** 1995. Conserving biological diversity through ecosystem resilience. *Conservation Biology* 9:747-752.

**Walker, B, A. Kinzig, and J. Langridge.** 1999. Plant attribute diversity, resilience, and ecosystem function: the nature and significance of dominant and minor species. *Ecosystems* 2:95-113.

**Wardwell, D., and C. R. Allen.** 2009. Variability in population abundance is associated with thresholds between scaling regimes. *Ecology and Society* 14(2): 42. [online] URL: <http://www.ecologyandsociety.org/vol14/iss2/art42/>.

**Wardwell, D., C. R. Allen, G. D. Peterson, and A. D. Tyre.** 2008. A test of the cross-scale resilience model: functional richness in Mediterranean-climate ecosystems. *Ecological Complexity* **5**:165-182.

**Wilson, E. O.** 1961. The nature of the taxon cycle in the Melanesian ant fauna. *American Naturalist* **95**:169-193.

**Woinarski, J. C. Z.** 2006. Predictors of nomadism in Australian birds: a re-analysis of Allen and Saunders (2002). *Ecosystems* **9**:689-693.