## University of Nebraska - Lincoln DigitalCommons@University of Nebraska - Lincoln

Nebraska Cooperative Fish & Wildlife Research Unit -- Staff Publications Nebraska Cooperative Fish & Wildlife Research Unit

2014

### Panarchy: Theory and Application

Craig R. Allen
University of Nebraska-Lincoln, callen3@unl.edu

David G. Angeler Swedish University of Agricultural Sciences, david.angeler@slu.se

Ahjond S. Garmestani
U.S. Environmental Protection Agency, garmestani.ahjond@epa.gov

Lance H. Gunderson

Emory University, lgunder@emory.edu

C. S. Holling Resilience Center

Follow this and additional works at: http://digitalcommons.unl.edu/ncfwrustaff

Part of the Aquaculture and Fisheries Commons, Environmental Indicators and Impact
Assessment Commons, Environmental Monitoring Commons, Natural Resource Economics
Commons, Natural Resources and Conservation Commons, and the Water Resource Management
Commons

Allen, Craig R.; Angeler, David G.; Garmestani, Ahjond S.; Gunderson, Lance H.; and Holling, C. S., "Panarchy: Theory and Application" (2014). *Nebraska Cooperative Fish & Wildlife Research Unit -- Staff Publications*. 127. http://digitalcommons.unl.edu/ncfwrustaff/127

This Article is brought to you for free and open access by the Nebraska Cooperative Fish & Wildlife Research Unit at DigitalCommons@University of Nebraska - Lincoln. It has been accepted for inclusion in Nebraska Cooperative Fish & Wildlife Research Unit -- Staff Publications by an authorized administrator of DigitalCommons@University of Nebraska - Lincoln.

# Panarchy: Theory and Application

Craig R. Allen,<sup>1</sup>\* David G. Angeler,<sup>2</sup> Ahjond S. Garmestani,<sup>3</sup> Lance H. Gunderson,<sup>4</sup> and C. S. Holling<sup>5</sup>

<sup>1</sup>U.S. Geological Survey, Nebraska Cooperative Fish & Wildlife Research Unit, University of Nebraska, Lincoln, Nebraska 68583, USA; 
<sup>2</sup>Department of Aquatic Sciences and Assessment, Swedish University of Agricultural Sciences, PO Box 7050, 750 07 Uppsala, Sweden; 
<sup>3</sup>National Risk Management Research Laboratory, U.S. Environmental Protection Agency, 26 W. Martin Luther King Drive, Cincinnati, Ohio 45268, USA; 
<sup>4</sup>Department of Environmental Studies, Emory University, Atlanta, Georgia 30322, USA; 
<sup>5</sup>Resilience Center, Vancouver Island, Nanaimo, British Columbia, Canada

#### ABSTRACT

The concept of panarchy provides a framework that characterizes complex systems of people and nature as dynamically organized and structured within and across scales of space and time. It has been more than a decade since the introduction of panarchy. Over this period, its invocation in peer-reviewed literature has been steadily increasing, but its use remains primarily descriptive and abstract. Here, we discuss the use of the concept in the literature to date, highlight where the concept may

be useful, and discuss limitations to the broader applicability of panarchy theory for research in the ecological and social sciences. Finally, we forward a set of testable hypotheses to evaluate key propositions that follow from panarchy theory.

**Key words:** complex systems; discontinuities; novelty; regime; resilience; social–ecological systems; transformations.

#### Introduction

Humans build mental models of complex systems to make their structures and dynamics tractable for scientific inquiry. Multidimensional, nonlinear processes and structures characterize complex systems, including ecological, social, or coupled socialecological systems. Nevertheless, these systems are amenable to simplification. Panarchy is a conceptual model that describes the ways in which complex systems of people and nature are dynamically organized and structured across scales of space and time (Gunderson and others 1995; Gunderson and Holling 2002; Holling and others 2002). Panarchy uses a systems approach to understand ecosystem dynamics and emphasizes hierarchical structuring.

However, panarchy is different from typically envisioned hierarchies in that control is not just exerted by larger-scale, top-down processes, but can also come from small scale or bottom-up processes. Additionally, the dynamics of renewal and collapse within-scale domains, that is, adaptive cycles differ from the more static view of traditional hierarchy theory. Because of the potential for cycling within adaptive cycles to affect both smaller scales and larger scales, panarchy theory emphasizes cross-scale linkages whereby processes at one scale affect those at other scales to influence the overall dynamics of the system.

A complex system such as an ecosystem can be decomposed into structural and process elements that can be defined over a fixed range of spatial and temporal scales. A terrestrial ecosystem dominated by needle-leafed evergreens, for example, has discrete structures and processes at a number of scales. It can be described at a leaf or needle scale range (centimeters to meters in space and months to years in time); a tree scale range (multiple meters

Received 3 June 2013; accepted 6 September 2013

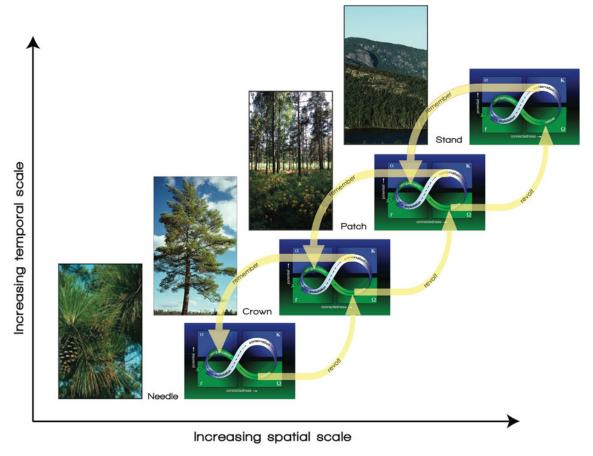
**Author Contributions:** CRA, DGA, ASG, and LHG conceived and wrote the paper. CSH conceived the paper.

\*Corresponding author; e-mail: allencr@unl.edu

Published online: 14 January 2014

and decades); to a forest scale range (kilometers and centuries) (Figure 1). At each scale, there is a characteristic pattern in structure, with different processes driving different patterns at different scales. This interaction between pattern and process within a given scale is driven by positive feedbacks. The interactions between living and non-living elements of a system within a single domain of scale, their development, growth and decay, has been described as an adaptive cycle (Holling 1986; Gunderson and Holling 2002). In an adaptive cycle (Figure 1), a system proceeds through phases of growth (r), conservation (k), release  $(\Omega)$ , and reorganization ( $\alpha$ ) (Holling 1986). The brief initial stage of development, the r stage, consists of the rapid exploitation and sequestering of resources. This is followed by a k stage of longer duration, characterized by the accumulation of capital, (system components or energies) which may eventually lead to a loss of resilience and the collapse of

the system because the system becomes more rigid. The  $\Omega$  stage of collapse is rapid and unleashes the energy accumulated and stored during the *k* phase. The  $\Omega$  phase is followed by reorganization during the  $\alpha$  phase, a relatively rapid period of assembly of system components, and is an opportunity for novel recombination. Reorganization is thought to become inevitable as capital (for example, biomass in ecosystems) builds. During the stage of reorganization a system may shift to a new regime characterized by a different set of processes and structures, or the original regime may persist. Thus, during reorganization, a system may either follow a generally predictable trajectory (Clements 1916), by simply resetting, or given the right set of circumstances, a reorganization may occur as novel processes or species are incorporated and the system assumes a structure quite different from that which previously existed (and thus the trajectory would be quite unpredictable).



**Figure 1.** A conceptual diagram showing the relationship between scales of ecological structure and the nested adaptive cycles comprising a panarchy for a pine dominated ecosystem. Four adaptive cycles, and scales of structure are shown for this system (for convenience only). Within-scale structures and processes interact across scales at key phases of the adaptive cycle. These cross-scale interactions can take place from lower to higher levels in the panarchy and vice versa (*yellow arrows*) (Color figure online).

A panarchy is a nested set of adaptive cycles operating at discrete ranges of scale (Holling and others 2002; Figure 1). The number of levels in a panarchy varies, but corresponds to dominant scales present in a system. A key component of this model is that cross-scale linkages are related to within-scale system position within the adaptive cycle. During reorganization at a given scale, conservative structures at larger scales provide a form of memory that encourages reorganization around the same structures and processes rather than a different set (that is, rather than a new regime). Similarly, during the  $\Omega$  phase at a given scale, "destructive" processes can affect larger scales (sometimes termed "revolt").

Since its publication a decade ago, the book Panarchy (Gunderson and Holling 2002) has been cited more than 2,600 times (Google Scholar, accessed August 2013), and the first journal article introducing the term (Holling 2001) has been cited more than 1,400 times (Google Scholar, accessed August 2013). Clearly, the concept has resonated with many, and is gaining traction in the scientific community. However, a challenge with panarchy theory is that the complexity of processes it emphasizes makes empirical testing difficult. This manuscript provides a synthesis of panarchy research and usage over the past decade, and reviews the evidence supporting the concept in complex systems including ecosystems, urban systems and social systems. We outline needed avenues of research, highlight where the concept may be useful, and describe limitations to its broader applicability for ecological and social sciences. Finally, we suggest ways to better operationalize the concept and offer a framework that makes hypothesis testing feasible.

#### PANARCHY IMPLICATIONS

Panarchy has been increasing in importance as a perspective for understanding ecosystems, linked social–ecological systems and governance. The concept is intrinsically linked to resilience and follows from attempts to characterize and assess resilience in complex systems. Panarchy can be utilized in both the abstract conceptual sense, and as a model of system dynamics that gives rise to concrete and testable hypotheses regarding the functioning of complex systems. As a heuristic, panarchy can help envision the organization of seemingly complicated systems, as has been explored by several authors (for example, Fraser 2003; Dorren and others 2004).

Ecosystems and social systems are characterized by bottom-up and top-down controls and thresh-

olds, multiple scales and nonlinear dynamics. Processes are generally scale specific, and a limited number of processes operating at distinct scales are responsible for the characteristic structures in time and space that define specific systems. This is important for humanity because self-organization (reinforcement between processes and structures) in complex systems such as ecosystems means they are relatively stable, that is, their variability stays within the systems' domain of attraction. Thus, we can expect reasonably predictable dynamics and the relatively constant provision of ecosystem goods and services. This conservativeness and selforganization is due in part to the positive interactions among biotic and abiotic elements. For example, animals interact with the ecological structure that provides a distribution of necessary resources such as food and space to exploit in space and time. In exploiting their environments, animals often change ecological structures in ways that are favorable for themselves. 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 (Jones and others 1994). Self-organization involves other biotic system elements as well. For example, many grasses are pyrophilic and, therefore, highly flammable (Brooks and others 2004). In the absence of fire, succession would often eliminate grasses. However, the presence of these grasses encourages fire, which subsequently favors grasses and excludes competitors (Peterson 2002).

Because complex systems are compartmentalized by scale (Garmestani and others 2009a, b), adaptive cycles and self-organization occur at discrete scales within a system. Adaptive cycles are separated from one another by their domain of scale (Gunderson and Holling 2002). This separation has several important effects. First, it means that key variables within systems should be distributed discontinuously. Second, it indicates that self-organizing interactions and processes, such as community-level interactions for organisms (for example, competition). compartmentalized Therefore, similarly sized organisms are more likely to strongly interact with each other than with others 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, in terms of ecological and evolutionary processes shaping species assemblages. This can also lead to the development of high levels of diversity within systems (O'Neill and others 1986), and results in patterns in the distribution of function whereby functional diversity is high within-scales and the same functional groups are represented by multiple species at different scales (Peterson and others 1998). This pattern adds to the resilience of ecosystems (Peterson and others 1998) and other complex systems (Garmestani and others 2006; Garcia and others 2011).

Recognizing the suitability of panarchy theory as a heuristic of complex systems organization, many authors have investigated the linkages between adaptive cycles in social systems and ecosystems focusing on cycles of destruction and renewal (Carreiro and Zipperer 2011) and linking environmental change to social phenomenon such as migration (Warner 2011). Such analyses have tended to take a case study approach, determining if the particular case study corresponded to a panarchy framework (Downey 2010; Moen and Keskitalo 2010). Others have explored the link between system organization in terms of panarchy and the delivery of ecosystem services, a link that follows from understanding the distributions of function (Mhango and Dick 2011; Dick and others 2011). Panarchy has been used as a framework for managing change (Gotts 2007), identifying scales (Petrosillo and Zaccarelli 2010; Zaccarelli and others 2008), and identifying aspects of resilience (Angeler and others 2010; Gunderson 2010; Fraser and Stringer 2009; Fraser and others 2005), including causes of population collapse (Leuteritz and Ekbia 2008). Others have focused on theoretical aspects of panarchy, the links between resilience, regime shifts and thresholds (Angeler and others 2011; Garmestani and others 2009a, b) and collapse in systems (Kueker and Hall 2011).

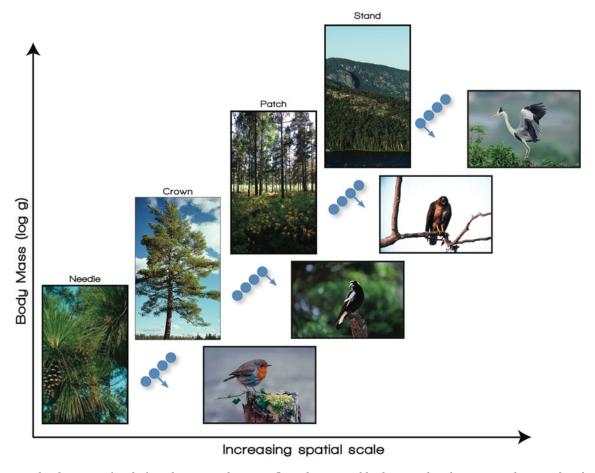
Panarchy theory has been assessed in social systems in a variety of contexts. Social scientists have evoked panarchy as a framework for understanding the linkages between social and ecological systems. Such an explicit framework helps with general understanding of the institutional and organizational change needed to enhance resilience (Brunckhorst 2002). For example, Beier and others (2009) apply the adaptive cycle model to the historical development of the Tongass National Forest, Alaska, and the extension of their findings at larger regional scales. Farrell and Twining-Ward (2004) use the panarchy model to address the manner in which tourism is conceived of for sustainability. In the Dutch Northern Frisian Woodlands, an agroecosystem dominated by dairy farmers, van Apeldoorn and others (2011) applied the panarchy model and found no alternative states in the system, but rather alternative sets of relationships within a multi-scale system.

In urban systems, a line of inquiry explicitly addressing the underlying discontinuous structure characterizes scale and discontinuities in urban systems (Bessey 2002; Garmestani and others 2005, 2007, 2008) and regional economic systems (Garmestani and others 2006). Using regional city size distributions, these empirical analyses reveal that urban systems are partitioned into discrete scales separated by thresholds (that is, they are discontinuously distributed). With respect to urban systems, small cities grew faster than average and large cities grew slower than average, which lends support to panarchy theory (Garmestani and others 2009b; Garcia and others 2011; Eason and Garmestani 2012). In firm size distributions, the distribution of functional diversity within and across scales was associated with indices of resilience (employment volatility; Garmestani and others 2006).

Legal scholars are assessing the capacity for panarchy theory to be integrated into the law, and have suggested supplementing panarchy with mechanisms from the social sciences (for example, adaptive governance) to foment sound environmental management (Garmestani and others 2009a). Other legal scholars have suggested both minor (Karkkainen 2005; Benson and Garmestani 2011) and major legal reforms (Ruhl 2012; Garmestani and Benson 2013) as the means to amalgamate the dynamic (panarchy) with the static (law). The current consensus among legal scholars is that existing law is too inflexible to accommodate resilience thinking, and therefore panarchy. Thus legal reform and new law will be required to allow for resilience-based governance.

#### From Theory to Measurement

Panarchy has been used to identify thresholds, opportunities (Van Apeldoorn and others 2011) and transformations (Evans 2008; Walker and others 2004). Identifying thresholds (Groffman and others 2006), either between regimes in a system or between ranges of scale, allows for the identification of management intervention points, those points in the adaptive cycle where a transformation may most easily be implemented. The identification of the scales of structure present in a system therefore is non-trivial and has important implications for understanding the resilience of systems. However, most research on resilience and panarchy in complex systems acknowledges scale, and the importance of cross-scale linkages, but seldom extends beyond description. The model of cross-scale resilience developed by Peterson and others (1998)



**Figure 2.** The domains of scale for adaptive cycles are reflected in animal body mass distributions. Body mass distributions of resident animals manifest panarchy in the form of aggregations in body mass distributions separated by discontinuities. Aggregations in body mass distributions correspond to the patterns of resource distribution manifest at different scales, corresponding to the influence of different adaptive cycles. *Blue dots* represent animal body mass. Representative members of each body mass aggregation are indicated (Color figure online).

provides a framework for the analysis of functions within and across scales, and discontinuity analysis provides a method for objectively identifying scales present in a system and assessing resilience (Allen and others 2005; Allen and Holling 2008).

Currently, there are several methods employed in determining discontinuities. For example the Gap Rarity Index (Restrepo and others 1997), Cluster Analysis (SAS Institute, Inc. 1999), Bayesian Classification and Regression Tree analyses (Chipman and others 1998; Bremner and Taplin 2004), and kernel density estimation (Havlicek and Carpenter 2001) have been used to evaluate discontinuities in animal body mass distributions (Figure 2). These methods are useful because they allow identifying the number of dominant scales that are present in a complex system (Allen and others 2005). As discussed above, variability in complex systems may increase near thresholds (for

example, at the edges of body mass aggregations). These methods are therefore particularly suitable for evaluating variability patterns in complex systems by examining whether species are located in the center or edges of body mass groups.

Although body mass is an important trait of animal species, the lack of sufficient body mass data for other organism groups (for example, plants) has led to a bias of discontinuity research toward a few taxa. Also, because body mass integrates processes acting at distinct evolutionary and ecological time scales, our ability to discern among the relative importance of ultimate factors generating discontinuous body mass distributions is limited. Therefore, using data independent of body mass, such as population variability, to identify discontinuities and cross-scale structure may increase the robustness of discontinuity analyses (Angeler and others 2010, 2011; Karunanithi and others 2008; Eason and others 2014).

Table 1. Three Core Propositions Related to the Structure of Complex Systems that Follow from Panarchy Theory

Proposition	Hypotheses	Status	References
Complex systems are discontinuously structured	Key variables are distributed discontinuously Variability increases when regimes	Tested for animal body masses, city sizes, firm sizes, aquatic communities Limited tests for lakes, models	Garmestani and others (2005, 2006), Allen and Holling (2008) Carpenter and Brock (2006)
	Variability increases with changes in scale	Limited tests with animal body mass distributions	Wardwell and Allen (2009)
	Discontinuities identify dominant scales	Limited modeling, empirical evidence	Szabó and Meszéna (2006), Angeler and Johnson (2012), Nash and others (2013)
	Functions should be distributed non-randomly with respect to scale	Limited tests, modeling	Fischer and others (2008), Wardwell and others (2008), Sundstrom and others (2012)
Complex systems undergo cycles of renewal and collanse	Cycling is apparent in a wide class of complex systems	Apparent evidence in diverse systems	Odum (1983), Diamond (2005), Angeler and others (2010)
Cross-scale linkages are critical to system structure		Evidence for contagious processes such as pest outbreaks, fire	Ludwig and others (1978)
	Function distribution across scales is critical to maintaining system dynamics and resilience	Some empirical evidence	Nyström and Folke (2001), Sundstrom and others (2012), Angeler and others (2013)

For each proposition we list hypotheses following from the propositions and the status of evidence related to the hypotheses. The references provided are not exhaustive.

Humans generally define and measure systems at scales that are tractable to humans. This means we are interested in managing and understanding systems at what we consider to be meso-scales, extents between tens of meters and thousands of meters, and frequencies between weeks and decades. Time series modeling allows us to identify the scales of temporal frequencies in complex systems, and makes it possible to track the imprints of environmental change over time (Angeler and others 2009, 2011). However, the broader application of such promising tools and more rigorous testing of facets of panarchy theory are currently limited by the general lack of standardized long-term (centuries, millennia) data. There is a clear need to create more long-term monitoring efforts, which in combination with paleontological data may allow for a better understanding of complex system dynamics.

#### TESTING PANARCHY

For panarchy theory to develop beyond a conceptual framework for envisioning complex dynamics, hypotheses that explicitly test the underlying premises are required. Panarchy theory covers many facets of complex system dynamics that are impossible to frame within a single hypothesis. Following from the theory are basic predictions regarding both the organization and dynamics of complex systems that should manifest if the propositions are true (Table 1). It presents opportunities to test specific hypotheses regarding resilience, discontinuity, novelty, structuring processes in complex systems, cross-scale phenomena, and regime shifts, among others (Table 1). Many of these manifestations have been tested empirically, some have been modeled, and some not tested at all because of data constraints.

Panarchy theory has implications for two important, interconnecting, but poorly understood phenomena: regime shifts and novelty. Given the importance of these phenomena for understanding resilience, panarchy theory has great potential to make operationalization of these phenomena explicit, ultimately improving ways for quantification and measurement.

#### Regime Changes

Regime changes occur when a system's resilience threshold is crossed and the processes responsible for a system's structure and function change and create new self-organized structures. Regime changes have received much research attention in recent years, motivated by the potentially negative consequences

for ecosystem services provisioning to humans, when a system transitions from one regime to another. Understanding of regime changes and resilience comes from studies of many ecosystems, including freshwater lakes, marine systems, forests, and wetlands (Folke and others 2004). In all of these cases, regimes and regime changes occur within specific scale ranges, but are caused by cross-scale interactions. Panarchy theory can therefore be useful for better understanding such abrupt changes in complex systems.

The management applications of panarchy theory are evident in the development of early indicators of regime shifts. Increasing variance (Carpenter and Brock 2006) and flickering (Scheffer and others 2009) are related indicators of impending ecological transition, as are some seemingly contradictory indicators such as critical slowing (Dakos and others 2008) and increased autocorrelation (Scheffer and others 2009). However, increasing variance can occur with critical slowing; we are unaware of analyses that compare the two relative to the temporal span of analysis. Carpenter and Brock (2006) suggest that certain key parameters of complex systems become more variable as they approach thresholds that occur when for example, lakes change state. It has also been shown that variability within complex systems may be non-random, and is heightened where shifts in scales of process and structure occur, that is, where discontinuities occur (Allen and Holling 2010)—and that these reflect within system cross-scale changes in structuring regimes. This suggests that it is possible to identify those variables that are most likely to exhibit increased variability prior to systemic regime shifts (refer to Novelty, below) by identifying those species already subject to heightened variability at scale breaks, which would allow more targeted and effective monitoring to determine when there is an increased probability of changing the state of a system.

At least two types of regime changes are compatible with panarchy theory, although almost all emphasis has been placed on understanding systemic regime changes. This first type of regime change occurs at a fixed spatial scale and changes the structure of the system in question. The second type of regime change occurs with changes in scale within a system, and does not lead to collapse, but rather reflects the fact that structuring processes—regimes—vary with scale. The first can occur as a system undergoes creative destruction and reorganization. The second type of regime change is a cross-scale change, manifest because changes in process and structure occur across scales

within a system. We therefore need to distinguish between regime shifts within the domain of one focal adaptive cycle (generally an ecosystem of interest) from those that can occur between domains of adaptive cycles operating at different scales, because their ecological meaning and potential implications for management are different.

With respect to the first type of regime change, systemic regime changes occur when a reorganization phase of an adaptive cycle leads to a fundamentally different type of system. A system-level regime shift can occur when the top level of a panarchy reorganizes (sometimes, but not always, rapidly) and because of the hierarchical nature of structure, the reorganization of an upper level affects lower levels. Such regime shifts are the ones typically considered in ecology, and occur, for example, when shallow lakes shift from a clear water state dominated by submerged vegetation to a degraded state with turbid waters and recurring phytoplankton blooms.

It is not the norm for the destruction cycle within an adaptive cycle to result in a regime change. The reorganization phase of the adaptive cycle is likely to simply reorganize around the same structures and processes, in which case a change in systemic structure has not occurred. The role of scale in understanding these dynamics is critical. For example, within a lake, plankton communities undergo seasonal replacement of species groups (Sommer and others 1986), suggesting repeated adaptive cycles of creative destruction within a single year at the scale of phytoplankton dynamics. This pattern is conservative and can be found across lakes with different forms of human impact (Angeler and others 2010). This highlights that phytoplankton dynamics operate in an adaptive cycle that is nested within higher levels of the entire lake's organization, and this cycling has no negative effect on the dynamics of the lake as a whole.

With respect to the second type of regime change, regime changes that reflect the transition between domains of adaptive cycles (discontinuities in scaling regimes) identify a change in scale, and occur in every complex adaptive system. As one changes scale to a higher or lower level in a system one shifts from the influence of one adaptive cycle to another; the adaptive cycles are discrete and non-overlapping and characterized by different structuring processes affecting different spatial scales and occurring at different temporal frequencies (Allen and others 2005) (Figure 2). The change from one scale to another, from one adaptive cycle to another, means that the structures and

processes that interact to create adaptive cycles are different, and so changes in scale also bring about a change in the structuring regime. Thus this type of "regime change" does not reflect an active change in the status of the system or phase of an adaptive cycle, but simply reflects the fact that structure and process changes discontinuously with scale, and different "regimes" are responsible for structure at different scales. This cross-scale structure, with scales separated by discontinuities, provides the structural underpinnings for cross-scale interactions and the overall resilience of the system (Peterson and others 1998), and provides one of the few quantitative approaches available for measuring resilience (Allen and others 2005; Nash and others 2014).

#### Novelty

Novelty is the creation of new things, or new combinations (Allen and Holling 2010) via natural or human process, and innovation is the process whereby humans develop novelty. Theory and empirical analyses have shown heightened variability at the species, population and community levels at the discontinuities separating scaling regimes (Allen and others 1999; Allen and Saunders 2002, 2006; Gunderson and others 2007; Skillen and Maurer 2008; Wardwell and Allen 2009). Ecologically dynamic and unusual phenomena occur at discontinuities, and these observations may provide insight into the organization of complex systems. Increased variability at transitions between scales, measured with discontinuities in animal body sizes, has been associated with species invasions and extinctions (Allen and others 1999). That is, successful invaders and species with high extinction risk were more likely situated close to the edge of body mass aggregations (close to scale transitions). This pattern is attributed to an increased variability of resources at discontinuities between scaling regimes (O'Neill and others 1989; Allen and others 1999). From a complex systems perspective, this suggests that although 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 and others 1999; Skillen and Maurer 2008), it is an opportunity for other species that successfully invade and exploit these locations/resources. However, invasions and extinctions are not mutually exclusive, because invaders can outcompete native species of similar size if they are able to better use resources. Such competitive interactions would be less pronounced if species differ fundamentally in their size and thus resource-use patterns; that is, if they operate in different scaling regimes. It is clear that discontinuities between scaling regimes in panarchies are arenas of "experimentation," meaning that biodiversity and ecosystem processes are exposed to constant innovation and novelty. This has profound implications for resilience. It also provides confirmation of the characterization of discontinuities as scale breaks indicating cross-scale change in structuring regimes; individual, species and community turnover in time and space are indicative of both high variance and flickering.

Invasive species have subtly, or sometimes grossly, different ways of interacting with their new environments relative to native species and their addition may reflect a system in transition (Allen and others 1999). The common belief among conservation biologists is that invasive species are destructive and transformative forces that may reduce the resilience of the ecosystems they invade, eventually pushing them toward a novel, undesired state, with reduced provision of ecosystem services. However, insight from complexity approaches and panarchy theory suggests that their addition in many cases may not alter, but rather reinforce existing ecological organization and thus increase resilience (Forys and Allen 2002). Panarchy theory clearly has potential to reveal patterns of complementarity, synergism and antagonism between invasive species and the ecological organization and resilience of the ecosystems they invade. In this context, panarchy theory has also been useful to explain why invasive species can be difficult to manage. Building resilience and the creation of novelty can also occur following the emergence or loss of dominant scales in the ecological system (Allen and Holling 2010). There is recent evidence that the regional spread of an invasive species due to regional environmental change can lead to an increased number of scales in the landscape at which its biomass occurs, by adding novel structure and processes (adaptive cycles) to the invaded system. These "emergent scales" created by the addition of new species/ processes may become self-organizing, which may increase the resilience of the invasion and complicate management interventions (Angeler and others 2012).

Invasions and extinctions are perhaps the cases that best document the generation of novelty in complex systems, but there is also evidence that phenomena like nomadism and migration, with an implicitly high variability of population dynamics in space and time, are also associated with scale transitions (Allen and Holling 2010). The few examples dealing with the generation of novelty and innovation from a complex systems perspective

highlight a wealth of research opportunities that might contribute to increase our understanding of complex system dynamics and resilience. Phenomena that operate at broad spatial extents (nomadism and migration) also suggest that not only resources and other niche-based processes but also potentially other community structuring forces such as neutral dynamics (for example, stochastic demographic processes, dispersal, biogeographical history) may also be important in generating novelty. These factors will need more explicit consideration in future research.

Panarchy provides an alternative framework for integrating and analyzing data sets over wide ranges of spatial and temporal domains. It is an alternative to current models of scale invariance and emergent statistical inference. History has shown that many ecological theories (such as resilience theory) require multiple decades to test and evaluate, because that is the appropriate time scale over which many of the complex ecosystem dynamics unfold. In a changing world, in which human effects are now global and rapid, the need to understand the dynamics of complex systems, and to act upon that knowledge, is pressing. Humankind's understanding of complex systems is growing, but whether our understanding and ability to manage these systems is outpaced by our transformation of them will ultimately determine the longevity of our current regime.

#### Conclusions

Much of the treatment of the concept of panarchy currently in the literature is focused on a metaphorical use of the term, but some core concepts have been tested and others are testable with current data. Most of the existing empirical tests revolve around discontinuities and their detection in vertebrate body mass distributions. However, discontinuities have been tested for and documented in other organisms and social systems (Leaper and others 2001; Garmestani and others 2005, 2006), and the ideas underlying panarchy related to discontinuities, have been sustained. In addition, limited modeling and empirical tests have demonstrated a strong link between discontinuities and the grouping of variables they identify, and scale specific structure in the environment (Szabó and Meszéna 2006; Nash and others 2013). Relatively long-term data sets are becoming available that have allowed for novel approaches to detect discontinuities and scaling in temporal variables. These data have revealed discrete groups of species that exhibit distinct temporal frequencies, with some responding to slow environmental variables and others responding to fast variables (Angeler and Johnson 2012; Angeler and others 2013). Time series data hold much promise, but the scales of pattern and structure that can be discerned have upper bounds set by the limit of the temporal extent of the data series, and lower bounds set by the frequency of sample collection.

Hypotheses that support individual components of panarchy theory across ecological and social systems will ultimately contribute to supporting the theory as a whole. It is clear that many of the propositions and manifestations require a great deal of data of sufficient temporal span and spatial extent. Exceptional data sets from long-term monitoring programs have proven very useful to support predictions of panarchy theory that have been hitherto difficult to test (Angeler and others 2011). This calls for more long-term monitoring to test for the generality of the patterns observed so far. Time series data are present from many sites around the world, and can be tested for patterns in temporal frequencies. Body mass and abundance data are more and more commonly available. Where data are available in time spans with known regime shifts, propositions related to variance, discontinuities and regime shifts can be tested. Data that have a spatial component that crosses unique process regimes, for example, ocean data that spans regimes between warm and cold oceans, can be similarly examined. Existing data allow for the evaluation of some of the propositions following from panarchy theory through empirical analyses, but complementary and more mechanistic information regarding links between process, structure and biota of ecological systems could be obtained through specifically designed experiments. With increasing interest in the effects of anthropogenic effects on the environment, disturbance ecology can inform experimental designs for testing the influence of perturbations on ecosystems and their structure, including structural and functional attributes. Using simple ecological communities as models of complex systems (microbes, protists), such experiments could be especially useful to identify critical thresholds, where systems shift to an alternative regime.

#### ACKNOWLEDGMENTS

An earlier version of this manuscript was improved by comments from K. Nash, T. Spanbauer, and two anonymous reviewers. We also thank Bev Gunderson for graphics support. The Nebraska Cooperative Fish and Wildlife Research Unit is jointly supported by a cooperative agreement between the U.S. 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. The views expressed herein are those of the authors and do not necessarily represent those of the United States Government or U.S. EPA. We gratefully acknowledge funding from the August T. Larsson Foundation of the Swedish University of Agricultural Sciences, and the U.S. Geological Survey John Wesley Powell Center for Analysis and Synthesis.

#### REFERENCES

- Allen CR, Holling CS, Eds. 2008. Discontinuities in ecosystems and other complex systems. New York: Columbia University Press.
- Allen CR, Holling CS. 2010. Novelty, adaptive capacity, and resilience. Ecol Soc 15(3):24. http://www.ecologyandsociety.org/vol15/iss3/art24/.
- Allen CR, Saunders DA. 2002. Variability between scales: predictors of nomadism in birds of an Australian Mediterranean-climate ecosystem. Ecosystems 5:348–59.
- Allen CR, Saunders DA. 2006. Multimodel inference and the understanding of complexity, discontinuity, and nomadism. Ecosystems 9:694–9.
- Allen CR, Forys EA, Holling CS. 1999. Body mass patterns predict invasions and extinctions in transforming landscapes. Ecosystems 2:114–21.
- Allen CR, Gunderson L, Johnson AR. 2005. The use of discontinuities and functional groups to assess relative resilience in complex systems. Ecosystems 8:958–66.
- Angeler DG, Johnson RK. 2012. Temporal scales and patterns of invertebrate biodiversity dynamics in boreal lakes recovering from acidification. Ecol Appl 22:1172–86.
- Angeler DG, Viedma O, Moreno JM. 2009. Statistical performance and information content of time lag analysis and redundancy analysis in time series modeling. Ecology 90:3245–57.
- Angeler DG, Trigal C, Drakare S, Johnson RK, Goedkoop W. 2010. Identifying resilience mechanisms to recurrent ecosystem perturbations. Oecologia 164:231–41.
- Angeler DG, Drakare S, Johnson RK. 2011. Revealing the organization of complex adaptive systems through multivariate time series modeling. Ecol Soc 16(3):5. http://dx.doi.org/10.5751/ES-04175-160305.
- Angeler DG, Allen CR, Johnson RK. 2012. Insights on invasions and resilience derived from spatiotemporal discontinuities of biomass at local and regional scales. Ecol Soc 17(2):32. http://dx.doi.org/10.5751/ES-04928-170232.
- Angeler DG, Allen CR, Johnson RK. 2013. Measuring the relative resilience of subarctic lakes to global change: redundancies of functions within and across temporal scales. J Appl Ecol 50:572–84.
- Beier C, Lovecraft AL, Chapin T. 2009. Growth and collapse of a resource system: an adaptive cycle of change in public lands

- governance and forest management in Alaska. Ecol Soc 14(2):5. http://www.ecologyandsociety.org/vol14/iss2/art5/.
- Benson MH, Garmestani AS. 2011. Embracing panarchy, building resilience and integrating adaptive management through a rebirth of the National Environmental Policy Act. J Environ Manag 92:1420–7.
- Bessey KM. 2002. Structure and dynamics in an urban landscape: toward a multiscale view. Ecosystems 5:360–75.
- Bremner AP, Taplin RH. 2004. Performance of localized regression tree splitting criteria on data with discontinuities. Aust N Z J Stat 46:367–81.
- Brooks ML, D'Antonio CM, Richardson DM, Grace JB, Keeley JE, DiTomaso JM, Hobbs RJ, Pellant M, Pyke D. 2004. Effects of invasive alien plants on fire regimes. Bioscience 54:677–88.
- Brunckhorst DJ. 2002. Institutions to sustain ecological and social systems. Ecol Manag Restor 3:108–16.
- Carpenter SR, Brock WA. 2006. Rising variance: a leading indicator of ecological transition. Ecol Lett 9:311–18.
- Carreiro MM, Zipperer WC. 2011. Co-adapting societal and ecological interactions following large disturbances in urban park woodlands. Aust Ecol 36:904–15.
- Chipman HA, George EI, McCulloch RE. 1998. Bayesian CART model search. J Am Stat Assoc 93:935–48.
- Clements FE. 1916. Plant succession: an analysis of the development of vegetation. Washington, DC: Carnegie Institution of Washington.
- Dakos V, Scheffer M, van Nes EH, Brovkin V, Petoukhov V, Held H. 2008. Slowing down as an early warning signal for abrupt climate change. PNAS 105:14308–12.
- Diamond JM. 2005. Collapse: how societies choose to fail or succeed. New York: Penguin Books.
- Dick JM, Smith RI, Scott ME. 2011. Ecosystem services and associated concepts. Environmetrics 22:598–607.
- Dorren LKA, Berger F, Imeson AC, Maier B, Rey F. 2004. Integrity, stability and management of protected forests in the European Alps. For Ecol Manage 195:165–76.
- Downey SS. 2010. Can properties of labor-exchange networks explain the resilience of swidden agriculture? Ecol Soc 15(4):15. http://www.ecologyandsociety.org/vol15/iss4/art15/.
- Eason T, Garmestani AS. 2012. Cross-scale dynamics of a regional urban system through time. Region et Developement 36-2012.
- Eason T, Garmestani AS, Cabezas H. 2014. Managing for resilience: early detection of catastrophic shifts in ecological systems. Clean Technol Environ Policy. doi:10.1007/s10098-013-0687-2.
- Evans GR. 2008. Transformation from "Carbon Valley" to a "Post-Carbon Society" in a climate change hot spot: the coalfields of the Hunter Valley, New South Wales, Australia. Ecol Soc 13(1):39. http://www.ecologyandsociety.org/vol13/iss1/art39/.
- Farrell BH, Twining-Ward L. 2004. Reconceptualizing tourism. Ann Tour Res 31:274–95.
- Fischer J, Lindenmayer DB, Montague-Drake R. 2008. The role of landscape texture in conservation biogeography: a case study on birds in south-eastern Australia. Divers Distrib 14:38–46.
- Folke C, Carpenter SR, Walker BH, Scheffer M, Elmqvist T, Gunderson LH, Holling CS. 2004. Regime shifts, resilience and biodiversity in ecosystem management. Ann Rev Ecol Evol Syst 35:557–81.

- Forys EA, Allen CR. 2002. Functional group change within and across scales following invasions and extinctions in the Everglades ecosystem. Ecosystems 5:339–47.
- Fraser EDG. 2003. Social vulnerability and ecological fragility: building bridges between social and natural sciences using the Irish Potato Famine as a case study. Conserv Ecol 7(2):9. http://www.consecol.org/vol7/iss2/art9/.
- Fraser EDG, Stringer LC. 2009. Explaining agricultural collapse: macro-forces, micro-crises and the emergence of land use vulnerability in southern Romania. Glob Environ Change 19:45–53.
- Fraser EDG, Mabee W, Figge F. 2005. A framework for assessing the vulnerability of food systems to future shocks. Futures 37:465–79
- Garcia JH, Garmestani AS, Karunanithi AT. 2011. Threshold transitions in a regional urban system. J Econ Behav Organ 78:152–9.
- Garmestani AS, Benson MH. 2013. A framework for resilience-based governance of social–ecological systems. Ecol Soc 18(1):9. http://www.ecologyandsociety.org/vol18/iss1/art9/.
- Garmestani AS, Allen CR, Bessey KM. 2005. Time series analysis of clusters in city size distributions. Urban Stud 42:1507–15.
- Garmestani AS, Allen CR, Mittelstaedt JD, Stow CA, Ward WA. 2006. Firm size diversity, functional richness and resilience. Environ Dev Econ 11:533–51.
- Garmestani AS, Allen CR, Gallagher CM, Mittelstaedt JD. 2007. Departures from Gibrat's law, discontinuities and city size distributions. Urban Stud 44:1997–2007.
- Garmestani AS, Allen CR, Gallagher CM. 2008. Power laws, discontinuities and regional city size distributions. J Econ Behav Organ 68:209–16.
- Garmestani AS, Allen CR, Cabezas H. 2009a. Panarchy, adaptive management and governance: policy options for building resilience. Neb Law Rev 87:1036–54.
- Garmestani AS, Allen CR, Gunderson L. 2009b. Panarchy: discontinuities reveal similarities in the dynamic system structure of ecological and social systems. Ecol Soc 14 (1):15. http://www.ecologyandsociety.org/vol14/iss1/art15/.
- Gotts NM. 2007. Resilience, panarchy, and world-systems analysis. Ecol Soc 12(1):24. http://www.ecologyandsociety.org/vol12/iss1/art24/.
- Groffman P, Baron J, Blett T, Gold A, Goodman I, Gunderson L, Levinson B, Palmer M, Paerl H, Peterson G, Rejeski D, Reynolds J, Turner M, Weathers K, Wiens J. 2006. Ecological thresholds: the key to successful environmental management or an important concept with no practical application? Ecosystems 9:1–13.
- Gunderson L. 2010. Ecological and human community resilience in response to natural disasters. Ecol Soc 15(2):18. http://www.ecologyandsociety.org/vol15/iss2/art18/.
- Gunderson LH, Holling CS, Eds. 2002. Panarchy: understanding transformations in human and natural systems. Washington, DC: Island Press.
- Gunderson LH, Light SS, Holling CS, Eds. 1995. Barriers and bridges to the renewal of ecosystems and institutions. New York: Columbia University Press.
- Gunderson L, Allen CR, Wardwell D. 2007. Temporal scaling in complex systems: resonant frequencies and biotic variability.
  In: Bissonette JA, Storch I, Eds. Temporal dimensions in landscape ecology: wildlife responses to variable resources.
  New York: Springer. p. 78–89.

- Havlicek T, Carpenter SR. 2001. Pelagic size distributions in lakes: are they discontinuous? Limnol Oceanogr 46:1021–33.
- Holling CS. 1986. Resilience of ecosystems: local surprise and global change. In: Clark WC, Munn RE, Eds. Sustainable development of the biosphere. Cambridge: Cambridge University Press. p. 292–317.
- Holling CS. 2001. Understanding the complexity of economic, ecological, and social systems. Ecosystems 4:390–405.
- Holling CS, Gunderson LH, Peterson GD. 2002. Sustainability and panarchies. In: Gunderson LH, Holling CS, Eds. Panarchy: understanding transformations in human and natural systems. Washington, DC: Island Press. p. 63–102.
- Jones CG, Lawton JH, Shachak M. 1994. Organisms as ecosystem engineers. Oikos 69:373–6.
- Karkkainen BC. 2005. Panarchy and adaptive change: around the loop and back again. Minn J Law Sci Technol 7:59–77.
- Karunanithi AT, Cabezas H, Frieden R, Pawlowski C. 2008. Detection and assessment of ecosystem regime shifts from Fisher information. Ecol Soc 13(1):22. http://www.ecologyandsociety.org/vol13/iss1/art22/.
- Kueker GD, Hall TD. 2011. Resilience and community in the age of world-system collapse. Nat Cult 6:18–40.
- Leaper R, Raffaelli D, Emes C, Manly B. 2001. Constraints on body-size distributions: an experimental test of the habitat architecture hypothesis. J Anim Ecol 70:248–59.
- Leuteritz TEJ, Ekbia HR. 2008. Not all roads lead to resilience: a complex systems approach to the comparative analysis of tortoises in arid ecosystems. Ecol Soc 13(1):1. http://www.ecologyandsociety.org/vol13/iss1/art1/.
- Ludwig D, Jones D, Holling CS. 1978. Qualitative analysis of insect outbreak systems: the spruce budworm and forest. J Anim Ecol 47:315–32.
- Mhango J, Dick J. 2011. Analysis of fertilizer subsidy programs and ecosystem services in Malawi. Renew Agric Food Syst 26:200–7.
- Moen J, Keskitalo ECH. 2010. Interlocking panarchies in multiuse boreal forests in Sweden. Ecol Soc 15(3):17. http://www.ecologyandsociety.org/vol15/iss3/art17/.
- Nash KL, Graham NAJ, Wilson SK, Bellwood DR. 2013. Cross-scale habitat structure drives fish body size distributions on coral reefs. Ecosystems 16:478–90.
- Nash KL, Allen CR, Angeler DG, Barichievy C, Eason T, Garmestani AS, Graham NAJ, Granholm D, Knutson M, Nelson RJ, Nyström M, Stow CA, Sundstrom SM. 2014. Discontinuites, cross-scale patterns and the organization of ecosystems. Ecology. doi:10.1890/13-1315.1.
- Nyström M, Folke C. 2001. Spatial resilience of coral reefs. Ecosystems 4:406–17.
- O'Neill RV, DeAngelis DL, Wade JB, Allen TFH. 1986. A hierarchical concept of ecosystems. Princeton: Princeton University Press.
- O'Neill RV, Johnson AR, King AW. 1989. A hierarchical framework for the analysis of scale. Landsc Ecol 3:193–205.
- Odum HT. 1983. Systems ecology: an introduction. New York: Wiley.

- Peterson GD. 2002. Estimating resilience across landscapes. Conserv Ecol 6(1):17. http://www.consecol.org/vol6/iss1/art17/.
- Peterson GD, Allen CR, Holling CS. 1998. Ecological resilience, biodiversity and scale. Ecosystems 1:6–18.
- Petrosillo I, Zaccarelli N. 2010. Multi-scale vulnerability of natural capital in a panarchy of social–ecological landscapes. Ecol Complex 7:359–67.
- Restrepo C, LM Renjifo, Marples P. 1997. Frugivorous birds in fragmented neotropical montane forests: landscape pattern and body mass distribution. In: Laurance WF, Bierregaard RO, Eds. Tropical forest remnants: ecology, management and conservation of fragmented communities. Chicago: University of Chicago Press. p. 171–89.
- Ruhl JB. 2012. Panarchy and the law. Ecol Soc 17(3):31. doi:10. 5751/ES-05109-170331.
- SAS Institute, Inc. 1999. SAS user's guide: statistics. Version 5. Cary, NC, USA.
- Scheffer M, Bascompte J, Brock WA, Brovkin V, Carpenter SR, Dakos V, Held H, van Nes EH, Rietkerk M, Sugihara G. 2009. Early-warning signals for critical transitions. Nature 461:53–9.
- Skillen JJ, Maurer BA. 2008. The ecological significance of discontinuities in body mass distributions. In: Allen CR, Holling CS, editors. Discontinuities in ecosystems and other complex systems. New York: Columbia University Press. p. 193–218.
- Sommer UZ, Gliwicz M, Lampert W, Duncan A. 1986. PEG-model of seasonal succession of planktonic events in freshwaters. Archiv fuer Hydrobiologie 106:433–71.
- Sundstrom SM, Allen CR, Barichievy C. 2012. Species, functional groups, and thresholds in ecological resilience. Conserv Biol 26:305–314.
- Szabó P, Meszéna G. 2006. Spatial ecological hierarchies: coexistence on heterogeneous landscapes via scale niche diversification. Ecosystems 9:1009–16.
- Van Apeldoorn DF, Kok K, Sonneveld MPW, Veldkamp TA. 2011. Panarchy rules: rethinking resilience of agroecosystems, evidence from Dutch dairy-farming. Ecol Soc 16(1):39. http://www.ecologyandsociety.org/vol16/iss1/art39/.
- Walker B, Holling CS, Carpenter SR, Kinzig A. 2004. Resilience, adaptability and transformability in social–ecological systems. Ecol Soc 9(2):5. http://www.ecologyandsociety.org/vol9/iss2/art5/.
- Wardwell D, Allen CR. 2009. Variability in population abundance is associated with thresholds between scaling regimes. Ecol Soc 14(2):42. http://www.ecologyandsociety.org/vol14/iss2/art42/.
- Wardwell DA, Allen CR, Peterson GD, Tyre AJ. 2008. A test of the cross-scale resilience model: functional richness in Mediterranean-climate ecosystems. Ecol Complex 5:165–182.
- Warner K. 2011. Environmental change and migration: methodological considerations from ground-breaking global survey. Popul Environ 33:3–27.
- Zaccarelli N, Petrosillo I, Zurlini G, Hans Riitters K. 2008. Source/sink patterns of disturbance and cross-scale mismatches in a panarchy of social–ecological landscapes. Ecol Soc 13(1):26. http://www.ecologyandsociety.org/vol13/iss1/art26/.