Review

The adaptive cycle: More than a metaphor

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A B S T R A C T

The adaptive cycle and its extension to panarchy (nested adaptive cycles) has been a useful metaphor and conceptual model for understanding long-term dynamics of change in ecological and social–ecological systems. We argue that adaptive cycles are ubiquitous in complex adaptive systems because they reflect endogenously generated dynamics as a result of processes of self-organization and evolution. We synthesize work from a wide array of fields to support this claim. If dynamics of growth, conservation, collapse and renewal are endogenous dynamics of complex adaptive systems, then there ought to be signals of system change over time that reflect this. We describe a series of largely thermodynamically based indicators that have been developed for this purpose, and we add a critical and heretofore missing component–namely, that of understanding dynamics of change (adaptive cycles) at objectively identified spatial and temporal scales nested within each system, instead of solely at the system level. The explicit consideration of scales, when coupled with selective indicators, may circumvent the need for multiple indicators to capture system dynamics and will provide a richer picture of system trajectory than that offered by a single-scale analysis. We describe feasible ways in which researchers could systematically and quantitatively look for signatures of adaptive cycle dynamics at scales within ecosystems, rather than relying on metaphor and largely qualitative descriptions.

1. Introduction

The adaptive cycle and its extension to panarchy (nested adaptive cycles) was proposed as a metaphor and conceptual tool for understanding long-term dynamics of change in complex adaptive systems (CAS) like ecosystems and social–ecological systems (Gunderson and Holling, 2002). As such, the concept has had uptake by researchers from a variety of fields (Bunce et al., 2009; Burkhard et al., 2011; Randle et al., 2014; Fath et al., 2015; Kharrazi et al., 2016; Thapa et al., 2016b) despite the lack of empirical evidence demonstrating adaptive cycles in real data (though see Carpenter et al., 1999; Angeler et al., 2015). However, work from a wide array of fields, focused on an even wider array of ideas—self-organized criticality, edge of chaos, regime shifts, sustainability, resilience, punctuated equilibrium, game theory, and thermodynamics (Langton, 1990; Lindgren and Nordahl, 1994; Kauffman, 1995; Bak and Boettcher, 1997; Ulanowicz, 1997; Aronson and Plotnick, 2001; Jorgensen et al., 2007; Lockwood and Lockwood, 2008; Scheffer, 2009)—suggests that the adaptive cycle describes endogenously generated dynamics in complex adaptive systems as a result of the internal processes of self-organization and evolution over time. We propose that adaptive cycle dynamics are ubiquitous in complex adaptive systems and synthesize work from a diversity of fields to

support this claim. We discuss a subset of ecological indicators that were developed to measure dynamics of change in ecosystems, and argue that the explicit consideration of scales via the discontinuity hypothesis and panarchy, when coupled with selective indicators, may minimize the need for multiple indicators to capture system dynamics and provide a richer picture of system trajectory than that offered by a single-scale analysis. The indicators we discuss can more precisely be conceived of as indicators, goal functions, or orientors (Nielsen and Jorgensen, 2013), but for simplicities sake we use the word indicator as a more generic concept broadly representing a system signal that can change over time. Our emphasis is on feasible ways in which researchers could systematically and quantitatively look for signatures of panarchical dynamics in ecosystems, rather than relying on metaphor and largely qualitative descriptions. In short, we propose that adaptive cycles are real dynamics of real systems and not just handy conceptual metaphors, and identify the simplest indicators likely to act as a signal of adaptive cycle dynamics.

2. Adaptive cycles and panarchy

An adaptive cycle describes system movement through a 3-dimensional state space defined by system potential, connectedness, and
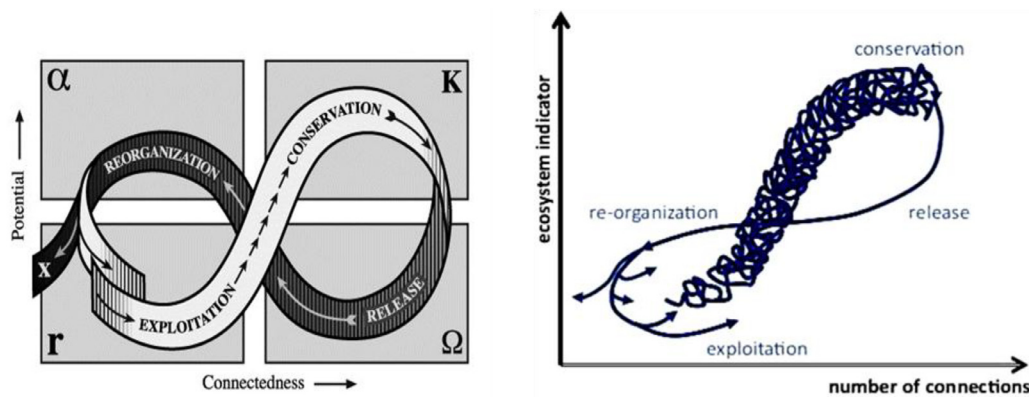

Fig. 1. Two-dimensional representation of the adaptive cycle as originally conceived on the left (Gunderson and Holling, 2002) and revised by Burkhard et al. (2011), on the right. The revised version is rotated 45° so that there is no increase in resilience at the end of the release phase, and to more realistically capture non-monotonic growth in the exploitation and conservation phases.

resilience (Fig. 1) (Holling, 1986; Gunderson and Holling, 2002).

System potential is concerned with the range of options available for future responses of the system; in ecosystems this can mean an accumulation of nutrients, resources, biomass, and diversity that provide a broad range of options for the future behavior of the system in response to change. Connectedness refers to the relationships between system elements and processes, and the degree to which elements are dominated by external variability, or by relationships that mediate the influence of external variability (Holling and Gunderson, 2002a). Resilience refers to the degree of disturbance a system can buffer without moving into a new regime, or basin of attraction (Holling, 1973). The stylized cycle consists of four phases defined by the four quadrants of the state space, but importantly, system movement through the phases is not rigid or predetermined. In the two front loop phases, *r* (exploitation) and *K* (conservation), there is an accumulation of resources and relationships, at first relatively rapidly but slowing as the *K* phase is reached. Systems tend to spend the most time in these phases, and the *K* phase is often understood to be on a stable attractor, or at a quasi-equilibrium in which large-scale system features such as biomass are stable over time (Hatton et al., 2015; Allhoff and Drossel, 2016). As the system moves from the *r* phase of exploitation into the conservation phase, potential and connectedness increase, but resilience shrinks because the high connectedness amongst system elements makes the system vulnerable to cascading disturbances. In the two back loop phases, omega (release) and alpha (reorganization), dynamics are rapid as the system transitions to a new phase of exploitation. The omega phase is characterized by the rapid release of accumulated resources; examples in ecosystems would be the release of nutrients and biomass when a disturbance event such as fire, drought, insectivory or intense grazing triggers a collapse (Thapa et al., 2016a). This is quickly followed by a period of reorganization, such as when soil processes capture nutrients and pioneer species begin colonization processes (Holling and Gunderson, 2002b).

Nested adaptive cycles with bi-directional cross-scale feedbacks are called a panarchy (Fig. 2). A core hypothesis of panarchy is that the key processes that structure ecosystems occur at different ranges of spatial and temporal scales, often separated by orders of magnitude. Thus, the spatio-temporal scales of pine needle turnover on a pine tree are different than the physiographic scales of the processes that drive where boreal forest occurs on earth. Research on the discontinuity hypothesis, developed to test whether systems had identifiable scales at which adaptive cycles unfold (Holling pers. comm), demonstrates that ecosystems contain scale domains, or spatio-temporal domains over which key processes, ecological structure, and resources either do not change or change monotonically (Wiens, 1989; Holling, 1992; Nash et al. 2014). Scale domains are separated by discontinuities, or scale breaks that represent a transition to a new set of structuring processes, as in the transition from photosynthesis structuring pine needles, to herbivory driving forest patch dynamics. Thus, adaptive cycles occur at each scale domain within the system, resulting in complex systems with multiple
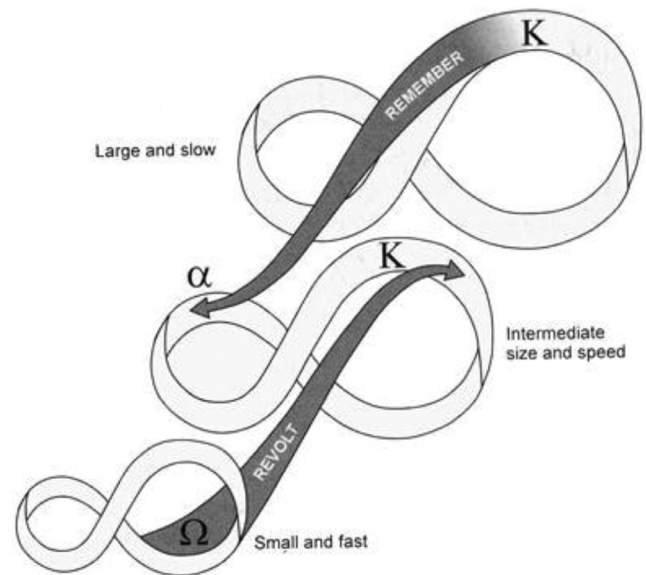

Fig. 2. The classic panarchy figure, showing three nested adaptive cycles with bi-directional cross-scale feedbacks that encompass all the spatial and temporal scales of system processes and dynamics (Gunderson and Holling, 2002).

and nested domains of scales at different phases of the adaptive cycle. At smaller and faster scale domains within a larger ecosystem, disturbances and processes of self-organization can drive cycling dynamics that are confined to those scales, while processes of renewal and regeneration depend on system memory at larger scales. Occasionally, disturbances can cascade up to larger and slower spatio-temporal scales, especially if those larger scale domains are in the conservation phase of their own adaptive cycle and smaller scale cycles approach synchrony, as the accumulation of system potential in the form of standing biomass and bound nutrients shaped by high connectance among system elements renders it more vulnerable to cascading effects up the panarchy (Gunderson and Holling, 2002).

3. Evidence for adaptive cycles

These descriptions of cyclic system behavior intuitively apply to virtually any living, adaptable system, and the authors of the original panarchy volume both push back against the compulsion to see adaptive cycles everywhere, and utilize examples from a variety of economic, social, and ecological systems (Gunderson and Holling, 2002). Work on the adaptive cycle and panarchy has largely occurred within resilience science, a field focused on ways to conceptualize, study, and manage complex ecological and social–ecological systems (Resilience Alliance, www.resalliance.org). However, research in non-related fields
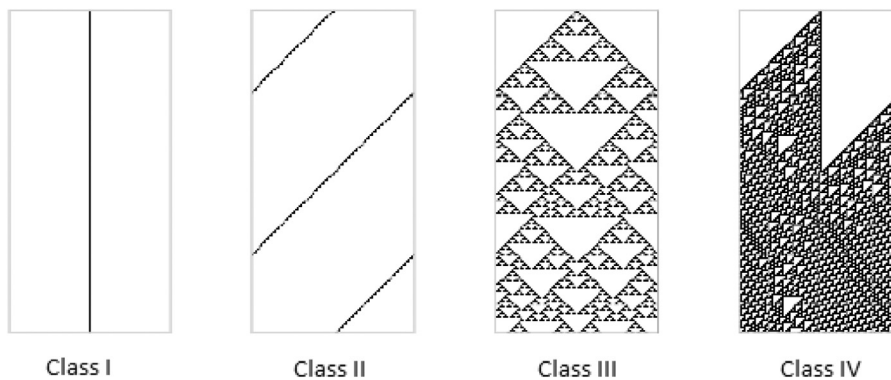
Fig. 3. The 4 classes of cellular automata end states. In Class I, evolution leads to a homogeneous state (limit points). In Class II, evolution leads to a set of separated simple stable or periodic structures (limit cycles). In Class III, evolution leads to a chaotic pattern (strange attractors). In Class IV, evolution leads to complex localized structures, sometimes long-lived (long transients) (adapted from Wolfram, 1984).

also suggests that the fundamental dynamics of system development, maturation, collapse, and reorganization captured by the adaptive cycle are endogenous dynamics of CAS's that reflect internal processes of self-organization and evolution over time.

Complex adaptive systems arise when systems are non-isolated (Jorgensen et al., 1999); that is, they import energy and export entropy, and structure and complexity emerge from processes which arise to dissipate energy, generating the essential characteristics of a complex system (Schneider and Kay, 1994). Many have argued that when systems are driven by the same 'physical principles and forces that drive self-organization in open, inorganic, far-from-equilibrium systems', such as nonequilibrium thermodynamics (Kurakin, 2010), then the patterns of emergence of structure and process should be generalizable across system types. If ecosystems and other complex adaptive systems are driven by the same fundamental rules of thermodynamics and physics then the basic phases of the adaptive cycle may be a generic feature of complex adaptive systems.

Empirical evidence to support the contention that these dynamics are endogenous to self-reinforcing, evolutionary systems comes from a range of fields. Non-equilibrium dynamics of change that are less extreme then fold-bifurcations (regime shifts), such as those of the adaptive cycle, can be difficult to model, either because data from real systems is highly labor-intensive to collect, non-linear dynamics are often intractable to mathematical resolution, and because reconciling mathematical predictions with experimental communities in a laboratory setting can be difficult (Fussmann et al., 2000). Nonetheless, simple rules and local interactions among system elements can generate non-linear dynamics that fall into a range of behavior from fully ordered and at equilibrium, to chaotic and characterized by wildly oscillating fluctuations (Fussmann et al., 2000; Becks et al., 2005). In a study of predator–prey interactions in laboratory conditions, population dynamics included chaotic behavior, as well as stable limit cycles and coexistence at equilibrium (Becks et al., 2005). Foster and Wild (1999) used a non-linear logistic diffusion sigmoid curve to map the phases of self-organization in economic systems, which mirror the adaptive cycle, while Lindgren and Nordahl (1994) found that modeling the tension between competition and cooperation in evolution in social systems creates a shifting pattern of dynamics where cooperative structures self-organize, grow, occasionally enjoy long stable periods, and then break up over time. The system is in a perpetual non-equilibrium state from the trade off between competition and cooperation, and complex and unpredictable patterns and structures emerged from an initial chaos. The patterns were cyclic and punctuated; over time a pattern emerged and stabilized until a mutation/innovation appeared that abruptly generated pattern collapse and reorganization. The cycling behavior of companies over time follows the adaptive cycle closely, as many companies jostle somewhat randomly for their niche, a small number grow explosively to a large size and dominate for sometimes decades, and then inevitably crash and fail (Beinhocker, 2006). While in ecosystems the players still standing after

a crash can reorganize and begin the process over again in competition with opportunistic invaders, usually the same company does not re-enter the playing field after failing, but is replaced by a multitude of new small start-ups, or previously subordinate companies that are competitively freed (Beinhocker, 2006).

In archaeology, Marcus (1998) developed a dynamic model of social evolution that explains the 'cycles of consolidation, expansion, and dissolution' (Parkinson and Galaty, 2007) of geopolitical states which has since been shown to fit a wide range of archaeological communities, while work by Tainter (1988) describes what can happen when the collapse phase occurs at the level of the panarchy, rather than at smaller-scale adaptive cycles (i.e. collapse of civilizations). Jain and Krishna (2002a,b) modeled evolution in a simulated ecosystem and found cyclical dynamics as a result of endogenous interactions that correspond to both punctuated equilibrium and adaptive cycle dynamics. The parameter which drove the system through the phases of growth and collapse was the changing pattern of connectance between system elements, precisely as predicted by panarchy (Gunderson and Holling, 2002).

Work by early pioneers in complex system science argued that there are a limited number of system states to which systems evolve. These states strongly parallel the 4 phases of the adaptive cycle, and despite criticism that these cellular automata and Boolean network modeling efforts were too mechanical to effectively capture the dynamics of real complex systems they demonstrated that given too much or too little order, systems can be trapped in states that lead to death because they are either too static or too chaotic to support the processes necessary to sustain self-organized, persistent structural hierarchies that can adapt and evolve to changing conditions (Fig. 3) (Wolfram, 1984; Langton, 1986; Kauffman, 1993; Ulanowicz, 1997). Langton (1986) proposed that systems therefore evolve to 'edge of chaos' behavior, where they are poised at the cusp of chaos and avoid falling into the traps of frozen order or full-fledged chaos. Furthermore, evidence suggests that systems at the edge of chaos are able to maximize information, entropy rate, and adaptation (Latora et al., 2000). Ulanowicz (1997) pushed back against the claim that the edge of chaos is a point or tiny region of state space, arguing that it is more appropriately viewed as a range or region of parameter space which he calls a 'window of vitality', and subsequent work has borne this out (Zorach and Ulanowicz, 2003; Nakajima and Haruna, 2011; Benincà et al., 2015).

Edge of chaos dynamics are closely related to the theory of self-organized criticality (SOC), which argues that systems can self-organize to a region of state space that is a transition between order and chaos, where both spatial patterns and temporal frequencies exhibit power-law and/or fractal dynamics (Kauffman, 1995; Bak and Boettcher, 1997; Jørgensen et al., 1998; Pascual and Guichard, 2005; Jorgensen et al., 2007). Schneider and Kay (1994) propose that life itself is a far-from-equilibrium dissipative structure, arising to poise at the cusp between low and high entropy (order and disorder) and this tension between opposing forces is mirrored in ecology, where the tension and

trade-off between diversity and redundancy (chaos and order) plays out in evolution, community assembly, and ecological resilience (Page 2010). Studies from a broad range of fields have found edge of chaos dynamics and/or self-organized criticality in complex systems (Bonabeau, 1997; Jørgensen et al., 1998; Turchin and Ellner, 2000; Latora et al., 2000; Li, 2000; Lansing, 2003; Kurakin et al., 2007; Upadhyay, 2009; Kitzbichler et al., 2009; Kong et al., 2009; Nakajima and Haruna, 2011; Salem, 2011; Chua et al., 2012; Benincà et al., 2015), but interestingly, not all systems stay there, as some systems show such dynamics for only a range of parameter space, or for a limited duration of time, or only larger system scales stay poised at criticality (Li, 2000; Upadhyay, 2009; Medvinsky et al., 2015; Lansing et al., 2017) while smaller scales experience collapse and renewal consistent with the other system states articulated by the early pioneers.

If systems are tuned to evolve to criticality where even small events can trigger a collapse or phase transition (Bak and Paczuski, 1985; de Oliveira, 2001; Pascual and Guichard, 2005) then it is not obvious that all spatial and temporal scales of a complex adaptive system could be at a criticality point or even within a narrow range of criticality concurrently. This would generate severe instability as even small disturbances would constantly cascade up and down system scales. Instead, at ecosystem-level system scales and larger, we tend to see stable quasi-equilibrium behavior which can persist long enough that it led earlier ecologists to assume that deterministic successional behavior and equilibrium dynamics was the norm (Clements, 1936). In fact, there is robust evidence for stability in larger-scale patterns such as biomass even while community composition and abundance can be highly variable and even chaotic (Ernest and Brown, 2001; Scheffer et al., 2003; Hatton et al., 2015; Vallina et al., 2017; Sundstrom et al. 2018). Brunk (2002) argues that systems require time to rebuild the structure that allows the transmission of disturbance. In forests, for example, it takes time to regrow the biomass that becomes the fuel load which can spread fire throughout the forest, making it likely that the region of parameter space encompassing SOC for a mature system is relatively broad and *is a result of* the higher frequency of regular collapses at smaller spatial and temporal scales (recall the power law behavior of disturbance events that defines self-organized criticality) that act to prevent disturbances from cascading up to the largest scales of the system. We hypothesize that the conservation (K) phase of an adaptive cycle may well operate at SOC or the edge of chaos, but only if cycles of collapse and renewal occur with sufficient frequency at smaller spatial and temporal scales (Brunk, 2002; Gunderson and Holling, 2002). The timescales, therefore, for a power law distribution of disturbance size and frequency that include the collapse of an entire mature system will necessarily be very long, unless a system is gradually pushed out of the parameter space in which a system can maintain SOC. For example, a slow changing variable such as climate change likely shrinks the region of criticality, making it easier for disturbances to trigger a system-wide collapse. If SOC is a feature of the evolution of complex systems over time (Bolliger et al., 2003), then this suggests that younger systems, systems that experience disturbance frequency rates that prevent the generation of order and complex features, and adaptive cycles at all scale domains of the system, will show a range of evidence for the hallmarks of SOC—namely, differing degrees of power law behavior in the size distribution of disturbances and the spatial pattern of clusters of vegetation (Kefi et al., 2014). In short, we would hypothesize that within each adaptive cycle nested within a system, power law behavior and edge of chaos dynamics will increase from none in the collapse phase, to weak in the reorganization phase, and then should steadily increase to strong as the system moves through the exploitation and conservation phases (Fig. 4) (Brunk, 2002). We note that power law behavior in system features such as spatial organization or temporal frequencies of events is not mutually exclusive to asynchrony in adaptive cycle dynamics within a panarchy (Fig. 5).

Researchers that bridge the gap between physics and the dynamics of ecosystems or other complex adaptive systems have also argued that adaptive cycles may be generic and ubiquitous features of complex systems (Schneider and Kay, 1994; Ulanowicz, 1997; Jørgensen and Fath, 2004; Beinhocker, 2006; Kurakin, 2011). One basic tenant that has emerged is that systems accrue complexity over time as processes of self-organization generate discontinuous, hierarchical layers of structure that dissipate more energy (Schneider and Kay, 1994; Jørgensen and Fath, 2004). Furthermore, system development moves towards 'increased order, organization, and storage of usable energy in sequential phases that see first biomass, then networks, and finally information (in terms of genetic complexity) increase' (Fath et al., 2004; Jørgensen et al., 2016). Complexity and order evolve from relative simplicity and disorder under the influence of "periodic but transient setbacks in the form of organization relaxations and restructuring" (Kurakin, 2011). These authors describe detailed dynamics of change in complex adaptive systems via various applications of thermodynamics (exergy, infrared thermal measurements and electron and proton transport in autocatalytic processes) (Schneider and Kay, 1994; Jørgensen and Fath, 2004; Kurakin, 2011) that fully align with adaptive cycles and panarchy, although they place less emphasis on the stages of collapse and renewal phases, and on scaling considerations. They argue that setbacks to this trajectory of increasing complexity have occurred at all spatial and temporal scales (e.g. from a small forest fire to mass extinctions to the fall of prior civilizations), but have not changed the fundamental trajectory of increasing complexity over time; the players may come and go, but the organization of relationships tends to be preserved and evolve (Kurakin, 2011). Setbacks in this trajectory towards increased complexity are therefore temporary and of little importance. However, we argue that externalizing setbacks as temporary impediments to be overcome rather than critical for long term persistence and renewal through innovation and adaptation is problematic. Furthermore, the relative impact of 'setbacks' depends on the timescale under consideration. For example, social and economic systems at the global scale are increasingly complex (more structure and information content (Ulanowicz, 1997), but many ecological systems are at risk of simplification as anthropogenic degradations accumulate, rapid species extinctions reduces the diversity necessary for systems to retain and build complexity, and climate change drives an increased risk for system-level regime shifts. Alternate regimes can be simpler, more homogenous systems as a result of missing crucial elements that allow them to reorganize into a similar state after a disturbance. When viewed at geological timescales, it seems likely that processes of thermodynamics, self-organization, and evolution will resume the inexorable march to increasing complexity, but this may provide small comfort for humans in the 21st century.

Collectively, these theories on endogenously driven dynamics of change buttress our argument that nested adaptive cycles are generic and ubiquitous dynamics of complex adaptive systems. Furthermore, thermodynamic indicators to track system change is an active area of research; a comprehensive review of these indicators is not possible, as the literature is substantial (Ulanowicz, 1997; Fath et al., 2001, 2004; Müller, 2005; Jorgensen et al., 2007; Burkhard et al., 2011). However, Fath et al. (2001) systematically discuss ten thermodynamic indicators concerning energy uptake, use, and storage, and the manner in which they are expected to change over the course of ecosystem development. They conclude that the ten indicators are "internally consistent and complementary", and encourage using multiple indicators as each captures a different aspect of ecosystem function (Fath et al., 2001). However, there are basic ways in which their value to ecology can be enhanced, which we address here. First, these indicators have been developed to reflect dynamics of change at the system level (Fath et al., 2001; Müller, 2005), and need to be used in combination with each other to sufficiently capture the complexity of system change over time. We describe the potential of a new approach: applying the indicators *at scale domains within the system*, thus at each nested adaptive cycle. This may reduce the need to measure multiple indicators because partitioning dynamics by scale domains within the system will account for
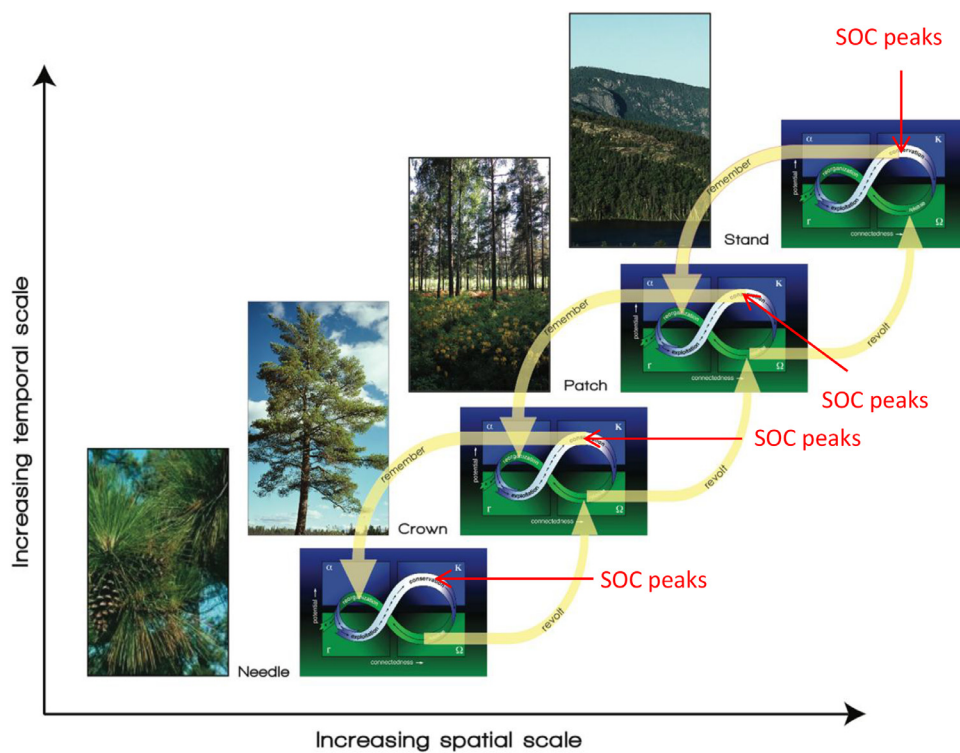
Fig. 4. A conceptual diagram of nested adaptive cycles for a pine-dominated ecosystem. Self-organized criticality should peak in the conservation phase of the adaptive cycle. Since the spatial and temporal scales increase at each level of the hierarchy, the forest system at the highest level in the panarchy should spend the most time at SOC. Adapted from Allen et al., 2014.

some of the issues that necessitate the use of multiple indicators. It will also provide a sensible way to address the importance of the collapse and reorganization phases at smaller scales in maintaining system dynamics in the conservation stage at larger spatial and temporal scales. The literature on these indicators has not dealt substantively with the collapse and renewal phases (Ulanowicz, 1997; Fath et al., 2004; Coscieme et al., 2013), perhaps because the emphasis has been exclusively on system-level dynamics, where collapse is fairly rare. Finally, the indicators are not easily used by general ecologists or land managers. They are intimidating in their language, their complexity, and their daunting data requirements (Müller, 2005). We discuss a subset of indicators that have varying degrees of feasibility—we feel it is important to discuss, for example, ascendency, despite its difficulty of use because it is one of the more comprehensive and well developed thermodynamic indicators. However, our ultimate objective is to focus on indicators that simplify tracking dynamics of change within an ecosystem by explicitly accounting for hierarchy and scales, and are feasible for ecologists to use as a tool because they lower the bar for the volume and detail of data required.

4. Ecological indicators for tracking system change–potential signals of adaptive cycle dynamics

The following indicators are ultimately all thermodynamic in origin, in that they track flows and storage of energy in the system (Schneider and Kay, 1994; Ulanowicz, 1997; Fath and Cabezas, 2004; Mayer et al., 2006; Karunanithi et al., 2008). We discuss them for their potential utility in tracking adaptive cycle dynamics of change in ecosystems, when considered in the context of a system being comprised of a nested adaptive cycles operating at distinct spatial and temporal scales (a panarchy). Many of these indicators have been tested on ecosystems, sometimes by comparing successional stages within or across the seasons (Bastianoni and Marchettini, 1997; Lu et al., 2015), or comparing systems with different degrees of degradation by processes like lake eutrophication (Patrício et al., 2004; Ludovisi, 2006) but few indicators have been evaluated by researchers for their performance during the release and reorganization phases, over long temporal spans, or at multiple scales.
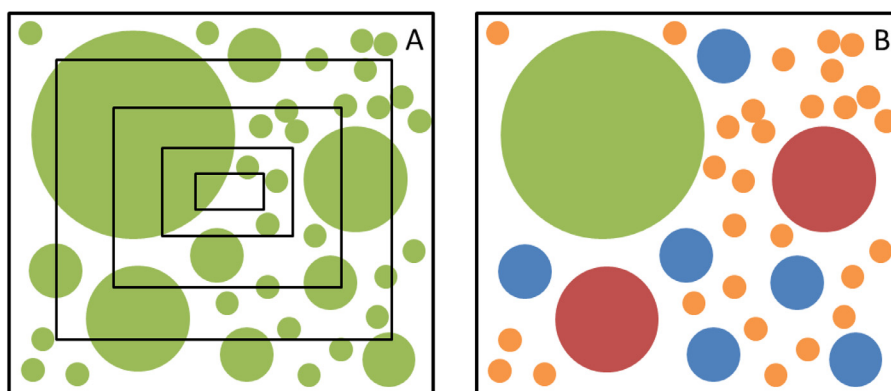

Fig. 5. In this simplified representation of vegetation patch size, patch size distribution fits a power law regardless of the size of the observation window (A), as is characteristic of self-organized criticality. This is not mutually exclusive to B, where patches operating at different spatial and temporal scales (patch color (or patch pattern in the black and white version) represents spatial and temporal scale at which it operates) can be in different phases of the adaptive cycle, and thus may not be at self-organized criticality.

4.1. Emergy

Emergy and the maximum empower principle was developed by Odum (1996) as a way to quantify all of the material and energy inputs of a system into one standardized unit that represents the original cost in terms of solar radiation (Cai et al., 2004; Nielsen and Jorgensen, 2013); thus the term 'embodied energy', or emergy. For example, the emergy inputs into a managed forest may include the sun, evapotranspiration, runoff, human labor, and litter (Lu et al., 2006). Emergy captures the pathway by which a system has reached its current state (Bastianoni and Marchettini, 1997). It is expected to increase with ecological succession because the energy pathway to produce a more complex organism is necessarily longer (Burkhard et al., 2011), but by itself is uninformative with regards to how a system uses its emergy inputs (Burkhard et al., 2011; Coscieme et al., 2013), and requires a formidable amount of information (Brown and Ulgiati, 2010). As a result, practitioners have developed emergy/exergy ratios to better understand the state of a system or how emergy is distributed across a system's structure, further increasing the data demands (Bastianoni and Marchettini, 1997; Bastianoni et al., 2006; Lu et al., 2015), but a similar pattern of increase during succession is supported. Calculating emergy at scale domains within an ecosystem could perhaps alleviate the need for more data-intensive emergy/exergy metrics because of the relationship between size of organism and complexity (Ludovisi, 2006).

4.2. Eco-exergy

Eco-exergy measures the amount of work a biological system can perform, or the difference in entropy between a system at equilibrium and its actual state (Fath et al., 2004). There are two primary hypotheses regarding the change in exergy over the course of ecosystem development. The first focuses on the maximization of total amount of exergy dissipated, and has been argued to be the functional equivalent of maximizing entropy production (Lin et al., 2018) so will be discussed in Section 4.3. The second hypothesis focuses on the maximization of exergy storage (Fath et al., 2004). Since ecosystems operate far from equilibrium, measuring ecosystem exergy storage reflects the total amount of energy stored in organic structures (Ludovisi, 2009). Eco-exergy equations take into account information/structure and concentration, and indirectly account for the manner in which biological matter is distributed among ecosystem compartments, typically by using carbon as the energy currency and genetic complexity as the information (Ulanowicz, 1997; Scharler, 2012; Lu et al., 2015). More biomass of more complex organisms will cause eco-exergy to rise (Fath and Cabezas, 2004). Both theory and empirical data support the hypothesis that exergy storage increases throughout ecosystem development, first from increases in biomass, then increases in network connections and cycling of materials, and finally from an increase in genetic complexity (Marques and Jorgensen, 2002; Fath et al., 2004; Jorgensen and Fath, 2004; Jorgensen et al., 2007). This does not incorporate the backloop stages of the adaptive cycle, where release and renewal should decrease exergy storage.

The detailed data required to calculate eco-exergy for an equilibrium system (used for comparison and necessary for the calculation) as well as the system of interest is daunting. Eco-exergy by itself is disconnected from a broader understanding of resilience, as the extinction of lower-order species with less genetic complexity and an increase in abundance of higher-order organisms with more complexity can drive an increase in exergy (Fath and Cabezas, 2004), but will also reduce functional redundancy and future adaptive capacity. From the perspective of the adaptive cycle, an increase in eco-exergy in this scenario would equate to reduced resilience and reduced potential, thus when eco-exergy is calculated at the system level, it does not sufficiently capture critical system features. Various combinations of eco-exergy and emergy exist to address the limitations of each individual indicator (Bastianoni et al., 2006; Coscieme et al., 2013; Lu et al., 2015), but this

also increases the information/data demands of the analysis. However, were eco-exergy to be calculated for each scale domain of the complete nested set of adaptive cycles, it would partition eco-exergy by the complexity of organisms because organisms such as mice, found at smaller and faster scales, are necessarily simpler than organisms that operate at longer and larger scales, such as wolves. Understanding changes in eco-exergy at scales may provide a sufficiently nuanced view of change that it reduces the need for multiple indicators to adequately capture system change and development through time.

4.3. Entropy production

Maximum entropy production proposes that non-equilibrium systems will evolve to steady states at which entropy production is maximized (Schneider and Kay, 1994; Fath et al., 2004; Kleidon, 2010; Skene, 2017). It is considered the equivalent of maximum exergy dissipation for a given fixed temperature (Kleidon, 2010; Lin et al., 2018) (though see Ludovisi et al., 2012), and has been explored using a variety of formulations, making it difficult to understand how broadly applicable the principle is across ecosystem types and stages of development (Meysman and Bruers, 2010). Theory suggests it is valid as a local principle of behavior, but not necessarily for the non-local case, or over longer time scales (Martyushev, 2013; Skene, 2017). Both modeling and empirical data support this argument with the caveat that the asymptote of local maximum entropy will be constrained by other levels of organization and a given environmental context (Quijano and Lin, 2015; Skene, 2017). It has also been demonstrated that maximum entropy production occurs as a function of the stage of system development, and peaks during the early to mid-stages of successional development (Fath et al., 2004; Ludovisi et al., 2005, 2012; Maes et al., 2011), which translates in the adaptive cycle to somewhere in the exploitation phase.

Few of the researchers directly consider entropy production at scales or levels of organization within the system (though see Dewar, 2010; Skene, 2017), though many do so indirectly by incorporating information on the structural complexity of biota such as considerations of body size, r versus K species, or complexity of a food web (Ludovisi et al., 2005; Ludovisi, 2006, 2009; Meysman and Bruers, 2010). Some of these indicators address the efficiency of the system in terms of maximizing storage of exergy per unit entropy produced and find that it increases both over the course of successional development and across lakes in different development states in a consistent manner (Ludovisi et al., 2005; Ludovisi, 2006). In other words, as a system matures, more exergy is stored per entropy produced because of the increased complexity of species along the successional gradient. However, HYPERLINK \l "bib104" Meysman and Bruers (2010) found that food webs as a whole behave differently than individual trophic compartments, suggesting that the scale at which entropy production is evaluated matters. Much of the research on entropy production has used shallow lake systems and calculated biological entropy production as a function of phytoplankton photosynthesis, as phytoplankton directly convert incoming solar radiation via photosynthesis (Ludovisi, 2006). Data on both species presence, size, and abundance is therefore readily available from aquatic sampling. Such data is far less available for terrestrial systems, which as a result have been analyzed via exergy dissipation in the form of radiation (Lin et al., 2011), and will be discussed in Section 4.4. It is possible that calculating entropy production across objectively identified scale domains would allow for a finer understanding of the pattern of maximal entropy production over time and across scales and provide a clearer expectation for the relationship between entropy production, or an entropy production/exergy storage ratio, and the stages of exploitation, conservation, release, and renewal in ecosystem dynamics over time.

4.4. Infrared

Infrared is a thermodynamic metric proposed by Schneider and Kay (1994) as a test of their proposition that complex systems such as ecosystems should increase their total dissipation over time and become more complex, whereas simple or degraded systems should dissipate less energy. They argue that "more mature systems should degrade incoming solar radiation into lower quality exergy", resulting in lower reradiated temperatures (lower airborne infrared thermal measurements). However, as Fath et al. (2004) point out, "ecosystems are complex adaptive systems, and as such one would expect the thermodynamic properties of the ecosystem to change during development". It is now understood that while more mature systems dissipate more exergy than less mature or degraded systems, exergy dissipation eventually plateaus while system maturation continues and is reflected in other thermodynamic metrics (Aoki, 1995; Fath et al., 2004; Ludovisi, 2014; Stoy et al., 2014).

Measuring infrared has primarily been explored in terrestrial systems as a viable way to measure exergy dissipation and the degree of self-organization across different stages of ecological development. Recent refinements suggest that canopy surface temperature is highly correlated with exergy dissipation/entropy production, and easier to measure (Lin et al., 2011, 2016, 2018; Lin, 2015). As with the other indicators, understanding infrared/canopy surface temperature in terms of nested adaptive cycles may address some of the shortcomings; while Schneider and Kay's (1994) hypothesis that maturing ecosystems will continually increase total dissipation as expressed by infrared may only be correct for the renewal and exploitation phases of the adaptive cycle, tracking changes in infrared within scale domains could be an effective signal of ecosystem change over time because it would account for the differing spatial and temporal scales at which processes of exergy dissipation play out. Furthermore, tracking changes in infrared/ canopy surface temperature at scales directly incorporates the differences in structural information between short-lived, high-turnover vegetative species and longer-lived species.

4.5. Ascendency

Ascendency theory (Ulanowicz, 1997) quantifies change in system dynamics by using information theory to measure growth and structure in food webs, where growth is an increase in system activity or total system throughput, and structure is the mutual information contained in the trophic flow. In the absence of major perturbations, ecosystems are expected to increase in ascendency over time (Ulanowicz, 1986; Ulanowicz et al., 2006). Ascendency, when coupled with overhead, which captures system redundancies and the material for adaptive capacity, is a process of growth and maturation in ecosystems that fully parallels panarchy. In fact, Ulanowicz (1997) used ascendency theory to test the adaptive cycle and concluded that they are fundamentally telling the same story. However, panarchy explicitly addresses the notion of cycling dynamics occurring at multiple domains of scale, and via the discontinuity hypothesis provides a method for detecting scale domains (Holling, 1992), whereas ascendency theory only touches on feedbacks across levels in the hierarchy and does not explicitly model or account for them. Furthermore, it fails to substantively treat collapse and renewal as integral and necessary processes that are both unavoidable and critical for system resilience and persistence; the stages of maturation only briefly acknowledge that there are 'temporary setbacks', and downplay the possibility of collapse occurring at large scales when a system has reached senescence (Holling's K phase). Failing to treat collapse and renewal as integral, endogenously-driven processes that are critical for system resilience at larger spatiotemporal scales constrains its ability to explain and predict future behavior. Relegating collapse and renewal to minor roles can also influence research choices that in turn can lead to misleading results; for example, Matutinovic et al. (2016) trim their data to exclude major disturbances.

Although Ulanowicz's (1997) rigorous and quantitative ascendency theory captures system development, the data demands of fully realized food webs are intense and only provide a snapshot of ecosystems at one point in time. Comparisons among aquatic systems with differing degrees of degradation using a suite of ascendency-related measures in a network analysis are relatively common (Patrício et al., 2004; Heymans et al., 2014; Meddeb et al., 2018), while temporal analyses are less so (Scharler, 2012); some, but not all, support the contention that ascendency is higher in less disturbed or stressed systems. Modeling and the use of simulated networks are also used in the search for patterns of behavior for ascendency and its related measures (Grami et al., 2011; Saint-Béat et al., 2013; Brinck and Jensen, 2017; Ludovisi and Scharler, 2017), but robust patterns have not emerged. For example, over evolutionary time scales, ascendency and average mutual information increase over time and drop during periods of 'hectic transitions' or high disturbance periods (Brinck and Jensen, 2017), whereas Ludovisi and Scharler (2017) found that average mutual information and diversity of interactions between ecosystem components both systematically increased along food web succession, whereas ascendency did not have a consistent trend. While tracking system development or dynamics of change via ascendency, overhead, and related indicators at scales within a system to elucidate expected patterns of change in the context of the adaptive cycle could provide rich insight, the data demands remain highly challenging for non-aquatic systems, and the necessary temporal data is missing for highly resolved aquatic food webs.

4.6. Fisher information

Fisher Information is a measure of the amount of disorder contained in any given parameter or system characteristic, and is based on the probability of observing a particular system state (Fath and Cabezas, 2004; Mayer et al., 2006). It has been used to detect spatial and temporal regime shifts in ecosystems (Karunanithi et al., 2008; Spanbauer et al., 2014; Eason et al., 2014; Sundstrom et al. 2017) but has the potential to track system change as ecosystems move among the phases of the adaptive cycle because the degree of order can be reflected in patterns of species richness, abundance, functional richness, growth rate, connectance, and complexity, all of which are anticipated to change in systematic ways among the phases of the adaptive cycle. Whereas a drop in Fisher Information indicates a loss of order or pattern in the data from unstable dynamics and a loss of resilience, as we would expect during the collapse phase of the adaptive cycle, a rise in order indicates less change and possible movement to more consistent patterns, as we would expect in the growth phases, and a stable value for Fisher Information ought to occur during the conservation phase where the system spends the most time in a stable regime (Fath and Cabezas, 2004). Because Fisher Information can handle any kind and amount of multivariate data, there is the opportunity to exploit a variety of data types that characterize system dynamics in order to explore changes in Fisher Information over time and within scale domains. For example, Müller (2005) presents a list of simplified thermodynamic variables (number of species, index of abiotic heterogeneity, primary production, respiration per biomass, transpiration per evapotranspiration, and loss of nutrients) which could be adapted for use in a Fisher Information analysis to generate a holistic view of ecosystem change over time and at scales.

4.7. Connectance

Network theory is commonly used to examine ecosystems as ecological networks, where each species is typically a node in the network, and the relationships between nodes is captured either via topographical features such as connectance (the number of other species to which a species is connected), or flows of energy or matter (Woodward et al., 2005; Ludovisi and Scharler, 2017), which has significant data requirements (Fath et al., 2007). Scale is often only an indirect feature

of network analyses, either when species are classified by trophic levels, which can be a crude classification of scale (such as O'Gorman et al. 2012), or when organism body size is embedded in the network (Woodward et al., 2005). Although Gunderson and Holling (2002) did not reference network studies in his explication of adaptive cycles and panarchy, connectedness is an axis in the graphical depiction of an adaptive cycle. His depiction of connectedness is more akin to topological studies than flow network studies such as ascendency theory (Ulanowicz, 1997), as it focuses on connectivity between system elements, and its relationship to the degree to which system elements are influenced by external variables. Low connectivity between elements means their behavior is primarily controlled by external variability in processes, whereas high connectivity between system elements can act to strongly mediate and buffer external variability. However, high connectivity between system elements also renders the system more vulnerable to collapse (Ulanowicz, 1997), because the degree to which elements such as nutrients are bound up in existing pathways and relationships between elements reduces the system's ability to "sample alternative and potentially better configurations" (Kurakin, 2007). It is expected that connectance will increase during the renewal and exploitation phase, peak during the conservation phase, and decrease during the release phase. Unlike some of the thermodynamic indicators that are expected to be maximized, a less-than maximum degree of connectance appears to be optimal for system stability and resilience (Wagensberg et al., 1990; Zorach and Ulanowicz, 2003; Fath et al., 2004; Burkhard et al., 2011; Ulanowicz et al., 2014).

More recent studies suggest that highly complex food webs (networks) can be simplified to just a handful of functional groups that describe the types of direct and indirect interactions species have, and that these functional groups are well predicted by body mass (Kefi et al., 2015; Kéfi et al., 2016). Since the size of a species is directly related to the spatial and temporal scales at which it interacts with its environment, this is a promising outcome. It may be possible, therefore, to understand changes in relatively simple network metrics like connectance or the number of trophic and non-trophic interaction types within scale domains in order to track system change over time. Since many interactions would naturally cross scale domains (in general, predators are larger than prey), it is not immediately clear how to calculate these metrics when partitioned by scale domains. Furthermore, as with calculating flows in metrics such as ascendency, the data needs are fairly prohibitive because of the extent of monitoring and expert knowledge needed to populate these food webs (for example, see Kefi et al., 2015; Kéfi et al., 2016). Such efforts are likely to have a high reward, however, as the need to integrate network theory, which is focused on relationships between network elements and therefore accounts for scale only indirectly, and resilience theory via the discontinuity hypothesis, which is focused on the scales at which species and processes operate, is an open topic for research. Jorgensen et al. (2016) has argued for the need to integrate vertical and horizontal topology in network studies by bringing together hierarchy theory with thermodynamic theory via networks, but his conceptualization of hierarchy focuses on levels of organization, rather than the more objectively defined scale domains driven by pattern and process that underpin discontinuity theory (Holling, 1992) . Tracking connectedness at each scale domain and across time may be a robust signal of changing dynamics, but it may also fail to sufficiently capture critical dynamics without also incorporating thermodynamic relationships in network flows sensu Ludovisi and Scharler (2017).

4.8. Biomass

Perhaps the simplest possible signal of dynamics of change is biomass. Biomass is expected to accumulate rapidly during the re-organization and exploitation phases, and then plateau or slowly increase during the conservation phase when connectivity and recycling of nutrients and material increases (Odum, 1969; Fath et al., 2004; Holdaway et al., 2010; Lu et al., 2015). In a resilient system, system-level biomass should remain relatively stable while collapse and re-organization phases play out at smaller spatial and temporal scales, resulting in increased variability in biomass at the particular spatial and temporal scales of the disturbance as compensation processes occur; empirical data supports this contention (Ernest and Brown, 2001; Hatton et al., 2015). Changes in biomass in both flora and fauna ought to reflect movement among the phases of the adaptive cycle within scale domains, and biomass could be converted to a measure of carbon similar to exergy analyses in order to have common currency for the modeling of stocks of carbon in vegetation and animal species among scale domains and across time (Scharler, 2012). Understanding how biomass changes across scale domains, such as rate of increase in biomass, or a change in the distribution of biomass across functional groups, captures the basic thermodynamic changes that drive system growth, development, collapse and renewal (Kurakin, 2010), and can be an indicator of a regime shift at the system level (White et al., 2004; Sundstrom et al. 2018). Other features of resilience, such as functional diversity and functional redundancy, which mirror Ulanowicz's 'overhead' and provide the buffering capacity that prevents system-level regime shifts, can be easily incorporated into models of changing biomass at scale domains, merely by partitioning biomass within scale domains into functional groups (Peterson et al., 1998; Forys and Allen, 2002).

5. Discussion

Challenges in advancing ecological research in this area relate to both the difficulties of implementing some of the indicators, and methodological impediments. We have discussed a variety of indicators, some of which may be unfeasible due to data limitations, and some of which may operate in the sweet spot of complexity science—simple enough to be feasible, but complex enough to capture system patterns. We also make the case that evaluating these indicators at scale domains within the system may increase the complexity of system dynamics that are captured while reducing the need for multiple indicators. Although the discontinuity hypothesis, used to identify scale domains of adaptive cycle dynamics, is well developed and tested in multiple ecosystems and other types of complex adaptive systems (Holling, 1992; Garmestani et al., 2008; Nash et al. 2014; Sundstrom et al., 2014), there remain challenges in our ability to detect scale domains in ecological systems. Typically, researchers identify discontinuities in animal body mass distributions for a specific taxa, such as mammals, or birds. Discontinuity theory argues that ecological processes, and therefore ecological structure, occur at discrete and limited ranges of scale (Holling, 1992). Since animals forage and interact with their environment in ways that are highly allometric with body mass, animal body masses fall into size classes, separated by discontinuities, that reflect those spatial and temporal scale domains of process and structure (Holling, 1992; Nash et al., 2013; Raffaelli et al., 2015). In short, animal body mass distributions are lumpy, consisting of groups of similarly-sized organisms that are separated by gaps, or scale breaks, where there are no species. Discontinuity researchers have used a variety of methods to identify scale breaks in animal data (Allen, 2006; Nash et al. 2014; Raffaelli et al., 2015), but the vast majority of analyses use rank-ordered body size data of a single faunal taxon, and to our knowledge, few researchers have looked for scale breaks in multiple taxa concurrently (Holling, 1992; Havlicek and Carpenter, 2001; Raffaelli et al., 2015). Yet any effort to understand ecological change at adaptive cycles across multiple scale domains requires the identification of scale breaks and scale domains in multiple taxon within a system concurrently.

Second, finding discontinuities in ecological structure such as vegetation or coral reefs remains a significant challenge. Efforts to find objective size classes in ecological structure remains limited to several

authors who find breaks in the fractal dimension (Morse et al., 1985; Li, 2000; Nash et al., 2013). Most researchers fall back on subjective, user-defined spatial scales, as in Lu et al. (2015) who survey vegetation plots at 1 m^2 for herbs, 25 m^2 for shrubs, and 100 m^2 for trees in a forest exergy analysis. The recent application of light detection and ranging (LiDAR) technology in ecology (Lim et al., 2003) has the potential to transform our ability to find scale breaks in vegetation, as the airborne scanning laser provides 3D scanning of vegetation, improving our ability to estimate standing biomass and capture multiple components of vegetation structure (Lefsky et al., 1999; Asner and Mascaro, 2014; Coops et al., 2016), including the potential to calculate the fractal dimensions of forest vegetation (Yang et al., 2015). Given the timescales of some ecological systems, temporal data that captures the largest and slowest spatial scales will be difficult. Trees can live for many centuries, and deep-water lakes can have water turnover rates in the centuries, making space-for-time substitutions important to capture dynamics of change at system-level spatial and temporal scales.

6. Conclusion

Although the adaptive cycle and panarchy theory are conceptual and qualitative, important aspects of the theory have been empirically validated. A main premise of Gunderson's argument (2002) was that nested adaptive cycles occur at specific ranges of spatial and temporal scales structured by a few key processes, and evidence has accumulated to support this (Allen and Holling, 2008; Wardwell et al., 2008; Sundstrom, 2009; Nash et al. 2014; Spanbauer et al., 2016). Researchers across fields have found panarchy a useful way to frame questions regarding dynamics within their systems. Concepts like self-organized criticality, edge of chaos, power-law behavior, ascendency theory, thermodynamics, information theory and more tell a narrative of system dynamics and behavior that capture critical aspects of, and are consistent with, panarchy theory (Kauffman, 1993, 1995; Lindgren and Nordahl, 1994; Aronson and Plotnick, 2001; Jørgensen and Fath, 2004; Lockwood and Lockwood, 2008).

We propose that the adaptive cycle reflects the inevitable dynamics of complex adaptive systems as a result of the internal processes of self-organization and evolution over time. The qualitatively similar system dynamics described in a variety of systems are the result of system development in a thermodynamically non-isolated system, and as such, ought to manifest in signals of development and change that can be tracked across the spatial and temporal dimensions of a system in accordance with the theory of nested adaptive cycles. While others have developed thermodynamically-based indicators of system change over time (Ulanowicz, 1997; Fath et al., 2001; Müller, 2005; Burkhard et al., 2011), they are often formidable in their data requirements and the need to use multiple complementary indicators to capture essential elements of system dynamics. Tracking dynamics of change within the full set of nested adaptive cycles which comprise an ecosystem, region, or larger ecological entity would potentially reduce the need for multiple indicators, and perhaps allow the usage of indicators based on data that is more readily available than that required, for example, for measuring ascendency.

None of the metrics or indicators proposed here are based on a fixed species identity or a particular community structure beyond how species identity is related to rates of energy consumption, functional role, or type of interactions with other species. As Kurakin (2009) explains, "what is preserved are the spatio-temporal relationships between individual components, i.e. a certain organizational structure–a form–but not individual components. Members come and go, but the organization persists". Our interest is in system-level properties that remain stable *because of*, not *in spite of*, dynamics of change at smaller and faster spatial and temporal scales. While ecosystems do transform over geological time scales in response to global change, it is reasonable to expect many ecosystems to remain in an exploitation and conservation phase for human time-scales of decades to centuries, if not longer.

Maintaining system resilience for ecosystems that are currently in desirable states requires system signals which track dynamics of change at explicit and objective scales and use data that is realistic to acquire.

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