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Adaptive capacity in ecosystems

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Summary

Understanding the adaptive capacity of ecosystems to cope with change is crucial to management. However, unclear and often confusing definitions of adaptive capacity make application of this concept difficult. In this paper, we revisit definitions of adaptive capacity and operationalize the concept. We define adaptive capacity as the latent potential of an ecosystem to alter resilience in response to change. We present testable hypotheses to evaluate complementary attributes of adaptive capacity that may help further clarify the components and relevance of the concept. Adaptive sampling, inference and modeling can reduce key uncertainties incrementally over time and increase learning about adaptive capacity. Such improvements are needed because uncertainty about global change and its effect on the capacity of ecosystems to adapt to social and ecological change is high.

Keywords

adaptive capacity; resilience; management; ecological memory; ecological traits; global change

Introduction

Future global environmental sustainability requires research that integrates human-nature interactions with sustainable practices to foster ecosystem regimes that are desirable (Kates et al. 2011). Ecosystems are subject to stresses (increasing intensification of agriculture, increasingly over-appropriated water supplies, and climate change), and these stresses are

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dangerously approaching the planetary boundaries of sustainable use of natural resources (Rockström et al. 2008). The ability of ecosystems to adapt to these changes is limited. Eventually, ecosystems may undergo *regime shifts* (for definition of terms in italics see Box1) to alternate species assemblages and ecosystem functioning at local, regional, and even global scales (Hughes et al. 2013). The outcomes of regime shifts are highly uncertain, potentially having substantial negative effects on human health, security and welfare (Horner-Dixon 1991; McMichael et al 2008). Therefore, it is important to determine the capacity of ecosystems to adapt to swiftly-changing social-ecological baselines towards a future without historical analogue, and how management and conservation can contribute to this adaptation.

The concept of *adaptive capacity* has been rapidly assimilated in the social sciences and transdisciplinary social-ecological research (Gunderson 2000; Folke et al. 2003), with multiple attempts made to formalize its meaning. Adaptive capacity is related to resilience (Holling 1973) and panarchy (Gunderson and Holing 2002), which has taken center stage in the effort to understand ecosystem dynamics during change. The concept of adaptive capacity has, in parallel with the transdisciplinary development of resilience theory, helped to diversify the meanings and definitions of systems undergoing change (Gallopín 2006). Adaptive capacity has been mainly used qualitatively in climate change, vulnerability and a risk/disaster management context in the social sciences and varies between different contexts and systems (Adger et al. 2007). Similarly, in the ecological sciences, *adaptation*, *adaptedness*, *adaptability* and *adaptive capacity*, terms with different meanings, have often been used interchangeably (Gallopín 2006, Smit and Wandel 2006). Consequently, operationalizing the concept of adaptive capacity, and by extension resilience theory for application and management, has been difficult, because of a loss of clarity and loose, incorrect and often normative use of these disparate concepts (Brand and Jax 2007; Angeler and Allen 2016). Misuse of terms can have significant negative impacts, because resilience and adaptive capacity are being used to help guide responses to natural disasters. Further, assessments of ecosystems that drive international research priorities depend on a comprehensive understanding of these concepts (Smit and Wandel 2006).

Because the concept of adaptive capacity is muddied with multiple meanings, its current use often makes it indistinguishable from resilience. In this paper, our goal is to clearly define the concept of adaptive capacity in ecosystems with the aim of differentiating it from similar concepts, particularly *ecological resilience*. Since approaches for operationalization and quantification of these concepts are needed, we describe components of adaptive capacity in ecosystems and discuss how they might mitigate and direct ecological response to ongoing environmental change. Further, we identify a research agenda to test hypotheses related to adaptive capacity and the ability of ecosystems to cope with environmental change.

Definitions and formalization

Much of the terminology and definitions used in the ecological adaptive capacity context has a Darwinian adaptation focus on species and populations. This is reflected in the currently most comprehensive definition of adaptive capacity (Beever et al. 2015; Nicotra et al. 2015). These authors define adaptive capacity for species and populations as a combination of evolutionary potential, dispersal ability, life-history traits and phenotypic plasticity, which are influenced by genetic, epigenetic, and behavioral and acclimation processes.

This definition is well aligned with the broad use of the term adaptation in ecology, which is defined as an organism's ability to cope with environmental changes in order to survive and reproduce (Smit and Wandel 2006). The term adaptation itself is often used interchangeably with the term *adaptability*, which, as defined in biology, means the ability to become adjusted and to live and reproduce under a certain range of environmental conditions (Conrad 1983). Another term, *adaptedness*, has a more specific meaning than adaptation or adaptability. Dobzhansky (1968) defined adaptedness as the adaptive traits (structure, function and behavior of an organism) that are crucial for an organism to thrive in an environment. Adaptedness embraces species- or population-specific adaptation to a certain range of environmental conditions. Adaptedness is therefore context dependent and not a generic property as adaptability or adaptation would suggest. That is, high adaptedness does not necessarily mean high adaptability because a species may be highly adapted to a special and constant environment but have little capacity to adapt to other environments or to changes in its environment (Gallopín 2006). For example, a cold-stenothermic mayfly may thrive in an arctic stream, but it does not have the necessary adaptation to live in tropical lakes or to keep pace with warming of the arctic stream environment. Adaptedness can be tested through reciprocal transplant experiments to assess phenotypic fitness to local ecological niches.

Despite the dominant focus of adaptive capacity on lower levels of biological hierarchical organization in the literature, the term is increasingly used as an ecosystem property, recognizing that the ability of ecosystems to cope with disturbances is limited and that regime shifts can occur. Gunderson (2000) defined adaptive capacity as a system property, where adaptive capacity modifies ecological resilience (or "*basin of attraction*"). This definition is very similar to the earlier definition of ecological resilience: "Resilience is a measure of the persistence of systems and of their ability to absorb change and disturbance and still maintain the same relationships between populations or state variables" (Holling 1973).

Underlying ecological resilience is the capacity of ecosystems to undergo regime shifts, meaning that ecosystems can exist in more than one regime (Holling 1973). Gunderson and Holling (2002) defined ecological resilience as "the magnitude of disturbance that can be absorbed before the system changes its structure by changing the variables and processes that control behavior". Similarly, in a recent overview of resilience definitions, Angeler and Allen (2016) refer to ecological resilience as "a measure of the amount of change needed to change an ecosystem from one set of processes and structures to a different set of processes and structures".

Ecological resilience encompasses broader systems dynamics by considering both adaptation within, and shifts between, alternative basins of attraction (i.e., *alternative regimes*). The distinction between single *vs* multiple regimes helps distinguish adaptive capacity from ecological resilience. Adaptive capacity focuses on dynamics within a specific regime, and therefore adaptive capacity is a subset of ecological resilience, which is explicitly concerned with dynamics both within and between regimes. Thus, similar to the view of Gunderson (2000), ecosystem adaptive capacity can be formalized and defined as follows (Figure 1, Box 1): *Adaptive capacity is the latent potential of an ecosystem to alter resilience in response to change.* In particular, adaptive capacity is the capability of an ecological system or other complex system to alter its basin of attraction in response to change such that the current regime is maintained.

Considering adaptive capacity as a subset of ecological resilience has applied relevance. Research is increasingly focused on the assessment of early warning signals of impending regime shifts (e.g., Dakos et al. 2015; Spanbauer et al. 2014, 2016), with the goal of employing management intervention if appreciable signals are detected (Batt et al. 2016). Although such studies implicitly consider an exhaustion of adaptive capacity, underlying mechanisms are not fully accounted for. However, scrutinizing adaptive capacity may provide such a mechanistic understanding. We discuss components of adaptive capacity and forward hypotheses to test these.

Components of adaptive capacity

Adaptive capacity as a latent potential of ecosystems is comprised of components that are dynamically interlinked (Table 1):

Ecological memory

The composition and distribution of organisms, their interactions in space and time and their life-history experience with environmental fluctuations contribute to *ecological memory* (Nyström and Folke 2004). Ecological memory has been defined as “the capability of the past states or experiences of a community to influence the present or future ecological responses of the community” (Zhong-Yu and Hai 2011). Specifically, ecological memory comprises all structural and functional features of ecological communities, which have been shaped by the interaction of past disturbances (natural and anthropogenic), spatial aspects (dispersal, habitat connectivity), biological interactions (competition, predation), evolutionary (speciation, extinctions, anagenesis, random mutations) and phylogenetic processes. This memory of ecological communities allows for a “learning process” (Carpenter et al. 2001). From this learning at the community level patterns and processes emanate, which enable ecosystems to prepare for and respond to future disturbances. This highlights that aspects of ecological memory compartmentalize by scales of space and time. Adaptive capacity explicitly accounts for pattern-process relationships of ecological memory that operate within and across the hierarchy of biological organization (i.e., they contribute to *cross-scale resilience*) (Table 1).

Cross-scale interactions

Ecosystems are hierarchically organized and have distinct patterns of structure, function, and processes that are compartmentalized by spatiotemporal scales. Considering cross-scale interactions is important because the impact of disturbance in ecosystems can be scale-specific (Pickett & White, 1985; Nash et al., 2014). That is, if disturbances affect components of ecological memory at one scale, other components at other scales might buffer the disturbances in the entire ecosystem to maintain functioning and resilience (Peterson *et al.*, 1998; Allen et al., 2005; Allen & Holling 2008). This buffering ability is critical to the understanding of the latent potential of adaptive capacity because it can be expected that adaptive capacity to absorb disturbances and maintain ecosystem regimes increases with the buffering ability conferred through cross-scale interactions. This buffering ability can be further explored through assessments of functional ecosystem characteristics.

Ecological functioning

Ecosystem reactions to disturbances, including buffering, rely on functional responses to perturbations, which in turn depends on the diversity of traits (e.g., reproductive phenology, seed bank potential, colonization and dispersal abilities [*functional diversity*]) that provide a range of response patterns to disturbances (i.e., *response diversity*) (Elmqvist et al., 2003). A recent study on coral-reefs (Nash et al. 2016) and a meta-analysis of forest resilience (Cole et al. 2014) support the importance of response diversity and cross-scale resilience after disturbances. Additionally, response-effect trait patterns and ecological network structure influence response diversity and ecosystem service provisioning (Mori et al. 2013, Oliver et al. 2015, Schleuning et al. 2015). In addition to diversity, redundancies of functional traits (*functional redundancy*) are important to stabilize processes (e.g., primary production, decomposition) and feedbacks, and therefore contribute to the resilience of an ecosystem (Folke et al. 2004). Assessing the distribution, diversity and redundancy of functional traits within and across spatiotemporal scales can therefore be used as a measurable surrogate for adaptive capacity, and may provide an indicator of the erosion of adaptive capacity as a result of environmental change (Laliberté et al. 2010). Important in such assessments is the consideration of rare species.

Rare species

Mouillot et al. (2013) found that rare species in alpine meadows, coral reefs, and tropical forests supported functional trait combinations that were not represented by abundant species. This suggests that if rare species go extinct with ongoing environmental change, negative effects on ecosystem processes may ensue with a subsequent loss of adaptive capacity. Such effects may occur even if biodiversity associated with abundant species is high (Mouillot et al. 2013).

The importance of rare species is also evident in their ability to replace dominant species after perturbation and maintain ecological functions in the system, which in turn contributes to ecological resilience (Walker et al.1999). For instance, rare shrub species with larger root crowns than dominant species were able to compensate for the loss of dominant shrub species to mechanical disturbance by re-sprouting prolifically, thus maintaining a shrub-dominated system despite disturbance (Wonkka et al. 2016). This example shows that rare species may contribute an important but, to some extent, unpredictable degree of adaptive capacity to ecosystem change.

Assessing adaptive capacity

The integration of scales, and functional and structural features between abundant and rare species offers a means to assess adaptive capacity. Resilience assessments have used discontinuity approaches to objectively identify the scaling structure present in ecosystems (Angeler *et al.*, 2016). The discontinuity analyses have so far shown promising results in assessing resilience of aquatic and terrestrial ecosystems (Angeler et al. 2016) and also other complex systems (economic, anthropological, social-ecological; Garmestani et al. 2005; Garmestani et al. 2009; Sundstrom et al. 2014). Discontinuity analysis may therefore also be useful in assessing the adaptive capacity of ecosystem regimes. The implementation of this approach will be examined from an adaptive capacity assessment point of view.

Because information about ecosystems is frequently limited adaptive capacity can be assessed following a recently proposed hypothesis-testing framework for quantifying ecological resilience (Baho et al. 2017). This evaluation comprises initial assessments of specific facets of adaptive capacity and then tests and recalibrates hypotheses iteratively to increase knowledge and provide learning opportunities about its general adaptive capacity.

Surrogates of adaptive capacity can be evaluated using simple measures of ecological *stability* (*resistance, persistence, variability,* and *engineering resilience*) (Donohue et al. 2013), biodiversity (Magurran 2004), and resilience (Angeler et al. 2016). The stability aspects can be evaluated for structural and functional variables (e.g., diversity, abundance, evenness, community composition, functional redundancies and diversity and process rates) within and across scales.

The initial step for quantifying adaptive capacity builds on Carpenter et al. (2001) to test for the "adaptive capacity of what to what". However, testing for specific aspects of adaptive capacity may not be representative of the general adaptive capacity of an ecosystem. This is because there is limited surrogacy of metrics when assessing ecological responses to stressors (Johnson and Hering 2009). In addition, focusing on specified adaptive capacity can be problematic because managing adaptive capacity of particular parts of an ecosystem, especially in terms of managing for predictable outcomes of disturbances or provision of ecosystem services, may cause the system to lose adaptive capacity or resilience in other ways (Carpenter et al., 2015). Specified assessments of adaptive capacity shall therefore be regarded as an initial step towards assessing the broader systemic or general adaptive capacity of an ecosystem.

It follows that assessing and managing for general adaptive capacity will require the simultaneous assessment of a range of variables to cover generic system properties and create possibilities for integral, resilience-based ecosystem management, which is difficult for most ecosystems.

Hypothesis testing to clarify adaptive capacity concepts

We suggest that this problem can be overcome by implementing adaptive monitoring and management. For this purpose, posing hypotheses that test premises of adaptive capacity are helpful (Table 2). We propose hypotheses that are not mutually exclusive and are well aligned with our adaptive capacity definition, allowing for the evaluation of its attributes in a logical, iterative sequence. These hypotheses can be tested using quantifiable stability and resilience measures (Angeler *et al.*, 2016) based on multiple lines of evidence (e.g., taxa across distinct trophic levels; Burthe et al., 2016). Most hypotheses can be framed specifically from a management perspective to facilitate the quantification of adaptive capacity without sacrificing the complexity inherent in management-related assessments. Also, most of our proposed hypotheses are supported by empirical observations (examples in Table 2), suggesting implementation of our quantification framework with ecological realism.

Hypothesis testing is carried out sequentially, which first objectively identifies key species in ecosystems that might serve as sentinels of system change (Angeler et al. 2016a). Next, sampling can be adapted to select appropriate spatial and/or temporal scales for monitoring to account for the cross-scale structure present in the system (Thompson and Seber 1996). This can contribute to pattern identification following population responses of sentinel species to disturbances. Incorporation of genetic, evolutionary, molecular and physiological variables and the measurement of process rates in monitoring can increase inference about ecosystem change, providing information for recalibration of management hypotheses. Monitoring can be refined by subsequently recalibrating hypotheses in an adaptive process that first focuses on reducing Type II errors (identifying false negatives) prior to reduce uncertainty sufficiently such that subsequent analyses can focus on Type I error (identifying false positives) reduction (adaptive inference, Holling and Allen 2002). Type II errors can be reduced by assessing adaptive capacity attributes (e.g., cross-scale and within scale structure and associated functional diversity redundancy) when ecological information of the ecosystem is limited. This can be done with the analysis of temporal snapshots, which are often the only resource available to managers. Subsequently, monitoring can be designed, implemented and sequentially modified to successively reduce Type I errors; that is, by improving knowledge of a broader range of adaptive capacity characteristics that need to be sampled over time (e.g., how fast is recovery after a disturbance). Such recalibrations can target functional assessments of sentinel species to change and, in further iterations, be extended to other taxa. This type of hypothesis testing builds on adaptive management (Allen et al., 2011), sampling (Thompson and Seber 1996), modeling (Uden et al., 2015) and inference (Holling & Allen, 2002). It allows revealing, refining, understanding and ultimately managing general ecosystem adaptive capacity, while increasing learning and reducing uncertainty. In this process, experiments can be designed that sequentially recalibrate strategies based on the outcomes of previous experiments and from which decisions about further data generation and monitoring can be made (Figure 2).

Managing adaptive capacity

Our suggested hypotheses are very general at this stage, but they can provide an initial step to inform management. First, managing for adaptive capacity may help maintain ecosystems in a regime desirable for humans (Allen et al. 2011). In this case maintaining adaptive capacity is fundamental for managing ecosystems away from critical thresholds (Batt et al. 2016). Crucial to managing for adaptive capacity is the consideration of cross-scale interactions across hierarchical levels and temporal scales. Upholding our premises while testing hypotheses iteratively can be useful for designing management interventions to foster the adaptive capacity of a specific desired regime. A combination of ecological and technological approaches might be necessary to this end (Rist et al. 2014). Some of these approaches, e.g. assisted translocations or introductions of species invasions to compensate for lost crucial functions in an ecosystem (Chaffin et al. 2016b), are debated and thus potentially limited in their application to management. Second, when an ecosystem is in an undesired regime, management can reduce adaptive capacity, induce a shift towards a more desired regime and foster the adaptive capacity of this new regime (Chaffin et al. 2016a) (Figure 2). There is, for instance, a rich body of literature on lake biomanipulation, which exemplifies transformation of degraded lakes into more desirable systems (Hansson et al. 1998).

The biomanipulation example is useful because while it offers possible management options, it also highlights potential limitations when managing for adaptive capacity. Lake biomanipulation has adopted a series of management interventions, based on ecological (food web manipulations) and technological interventions (water column aeration, sediment dredging or lining, nutrient precipitation). However, lessons from biomanipulation have shown that these solutions can incur short- to long-term costs that may not be tenable for most systems.

It is clear that a series of ecological, resource and ethical issues may currently complicate the translation of a solid body of theory on adaptive capacity to its management on the ground. Current environmental policy further limits the implementation of resilience to management (Green et al. 2015).

Conclusion

This paper suggests a way forward to enhance our ability to explicitly define and reduce uncertainties and promote more holistic and effective modeling, management and monitoring of adaptive capacity. In addition to testing premises and hypotheses of adaptive capacity, defining highly-related concepts will aid in continuing toward operationalizing adaptive capacity. For instance, although we have defined how adaptive capacity relates to the width of the basin of attraction in the iconic ball-and-cup heuristic, methods for defining the actual basin of attraction are few and lack rigorous testing (Gunderson et al. 2000). Estimating the basin of attraction would allow estimates of adaptive capacity to move beyond point estimates comparable only between subsequent measures and toward a direct estimate of adaptive capacity relative to the system’s potential adaptive capacity (Carpenter et al. 2001). Defining the basin of attraction would also allow the buffer that the current level of adaptive capacity provides against system transformations to be estimated, and it would allow transformative elements (e.g. invasive species) to be distinguished from elements that contribute to adaptive capacity (e.g. rare species; Elmqvist et al. 2003, Folke et al. 2010). However, new methods for detecting spatial regimes and discontinuous resource aggregations show promise for delineating basins of attraction in space and over time (Angeler et al. 2016, Allen et al. 2016, Sundstrom et al. 2017).

Uncertainty will not be eliminated completely or immediately, but it can be reduced incrementally while an ecosystem is monitored, modeled and managed over time. Explicit learning during this process can overcome common management problems, such as delayed action under uncertainty (Conroy et al., 2011), prioritization of limited financial resources (Stewart-Koster, Olden & Johnson, 2015), and the limited coordination in governance of natural resources (Cumming et al., 2013). Such improvements are needed because of uncertainty about global change impacts on an ecosystem's ability to absorb disturbances. An improved understanding of adaptive capacity can ultimately help to facilitate ecosystem management within current ecological, economic and ethical constraints. Our approach to assess adaptive capacity provides insight into the challenges to account for ecological complexity in ecosystem management. It particularly highlights enormous resource needs to the practical implementation and pinpoints persistent problems for closing gaps between science, policy, and management (Garmestani and Benson 2013).

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Box 1.

Definitions

Adaptive capacity

Latent property of an ecological system (or other complex system) to respond to disturbances in a manner that maintains it within its current basin of attraction by altering the depth and/or breadth of that basin (Figure 1).

Contrasted with

Adaptation

Alterations in the structure or function of an organism due to natural selection by which the organism becomes better fitted to survive and reproduce in its environment

Adaptability

ability to become adapted to live and reproduce under a particular range of environmental conditions

Adaptedness

adaptive traits (structural, functional, and behavioural), that are necessary for an organism to thrive in a particular environment

Ecological Resilience

ecological resilience is the capacity of a system to absorb disturbance to avoid a regime shift (multiple equilibrium focus), and a measure of the amount of disturbance a system can withstand before collapsing.

Engineering Resilience

return time to equilibrium after disturbance

Alternative State/Regime

a potential alternate configuration in terms of the structural and functional composition, processes, and feedbacks of a system

Basin of Attraction (stability domain)

configuration in terms of the abundance, composition, and processes of a system in which the system tends to remain

Cross-scale Resilience

resilience in ecological systems is enhanced when functional traits are diverse within scales and reinforced across scales

Ecological Memory

The collective representation of functional and structural attributes in an ecosystem that has been shaped by the systems disturbance history

Stability

Stability is a system characteristic whereby system variables remain unchanged following disturbance. Adaptive capacity can increase stability, but system components can fluctuate (therefore being unstable) while still remaining within the range of values that signify a particular state, and therefore, a system can be somewhat unstable while still possessing high adaptive capacity

Persistence

duration of species existence before it becomes extinct (either locally or globally)

Resistance

the external force or pressure needed to displace a system by a certain amount.

Variability

inverse of ecological stability; fluctuation in ecosystem parameters over time.

Functional Diversity

Diversity of reproductive phenology, seed bank potential, colonization and dispersal abilities, and other traits. This can enhance adaptive capacity by increasing functional redundancy and response diversity (see below).

Functional Redundancy

Existence of more than one species or process delivering the same ecological function. This contributes to adaptive capacity in ecosystems by providing buffering for loss of function due to extinction.

Response Diversity

Response diversity is variability in combinations of traits that provides a range of response patterns to disturbances and therefore increases the overall adaptive capacity in the system.

Regime Shift

persistent change in structure, function, and feedbacks of an ecosystem

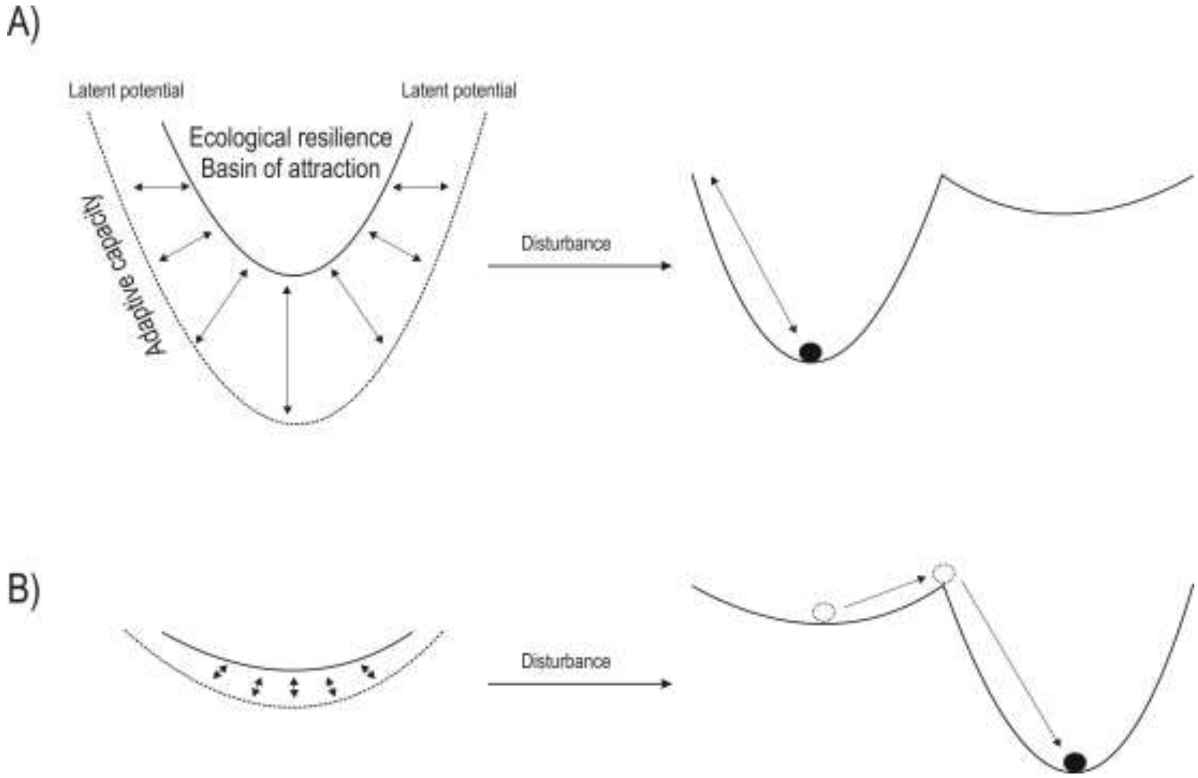

Figure 1:

Schematics illustrating high (A) and low (B) adaptive capacity. Adaptive capacity as a latent potential is shown by the dotted lines and the lengths of arrows that surround the basins of attraction that represent ecological resilience (left drawings). Drawings on the right show how high and low adaptive capacity can translate in rebound or a regime shift after a disturbance.

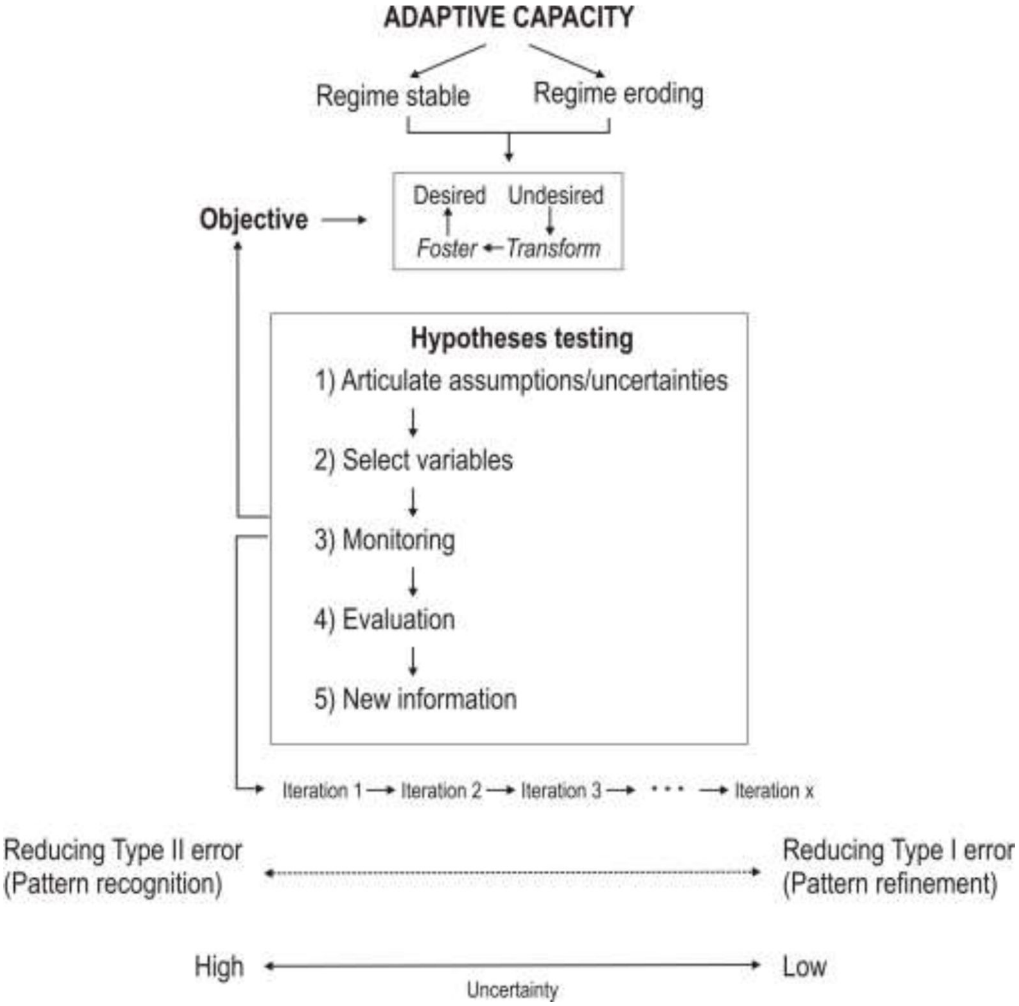

Figure 2:

Reiterative testing, recalibrating, and refining of explicit hypotheses of adaptive capacity within an adaptive management, inference and modeling framework. The approach first recognizes patterns (reducing risk of type II error) and then refines knowledge about patterns reiteratively (reducing risk of type I error) to meet adaptive or transformative management objectives and reduce uncertainty.

Table 1:

Factors that contribute to ecological memory and that mediate adaptive capacity across different scales of biological organization. Note: the table is not exhaustive and meant only to highlight the complexity of factors influencing adaptive capacity.

Hierarchy of organization and selected traits
• Sub-individual
○ Matching physiological conditions to fluctuating inputs or internal demands (allostasis) (Carpenter and Brock, 2008).
○ Genetic, epigenetic and molecular processes (e.g., mutation).
• Individual
○ Phenotypic plasticity.
○ Learning and dispersal ability.
○ Behavior
○ Adaptive evolution related to genetic diversity and evolutionary rates.
○ Links between life-history traits, phenotypic plasticity, and evolutionary potential.
• Population
○ Heritable life history characteristics: generation time, reproductive capacity, migration, habitat selection, genome size, survival characteristics (resting stages; hibernation, estivation), generalist vs. specialist species.
○ Population structure.
○ Metapopulation dynamics.
• Community
○ Taxonomic diversity.
○ Functional diversity (redundancy, response diversity).
○ Strength of species interactions.
○ Metacommunity dynamics (colonization and dispersal abilities).
○ Founder effects.
○ Priority effects.
○ Dormancy (resting eggs and propagule banks) and bet-hedging strategies.
• Ecosystem
○ Interaction of and connection between abiotic and biotic elements in feedback loops (balancing and reinforcing or negative and positive).
○ Changing shapes of basin of attraction/stability landscape (topography, soils, landforms)
• Biome
○ Biogeographical distributions of native an invasive species.
○ Phylogenetic dynamics.
○ Evolutionary, disturbance and climate histories.

Table 2:

Premises of resilience components and simple, management-relevant, mutually non-exclusive hypotheses. These serve as a starting point for reiterative hypothesis testing and can be refined, modified and adapted to specific ecosystems during monitoring.

	Adaptive capacity	
Ecological regime	**Premise 1 (stable)**	**Premise 2 (erodes)**
Hypotheses		
1. Adaptive capacity surrogates	High persistence, resistance and recovery; low variability.	Slowed down recovery, decreasing resistance and persistence, and higher variability.
2. Ecological memory	High structural and functional redundancy and diversity	Decreasing redundancy and diversity.
3. Key/deterministic/stochastic species	Contribute to ecological memory.	Increasing extinctions
4. Response diversity	High	Reduced
5. Functional compensation	High	Decreasing
6. Functional trait distributions	High diversity and redundancy within and across scales	Decreasing diversity and redundancy within and across scales.
Support	Allen et al. (2005); Angeler *et al.* (2016); Bellingham et al. (1995); Baho et al. (2014); Boucher et al. (1994); Kühsel & Blüthgen (2015); Mouillot et al. (2013); Nash et al. (2016); Walker et al. (1999)	Carpenter & Brock (2006); Dakos et al. (2008); Hooper et al. (2012); Mumby et al. 2014); Nyström (2006); Nash et al. (2016); Spanbauer et al. (2016)
Management implication	Maintain regime	1) Adaptive management and governance to stave off regime shifts. 2) Scenario planning and transformative governance if adaptive capacity gets exhausted.