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A quantitative framework for assessing ecological resilience

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Abstract

Quantitative approaches to measure and assess resilience are needed to bridge gaps between science, policy and management. In this paper, we revisit definitions of resilience and suggest a quantitative framework for assessing ecological resilience sensu Holling (1973). Ecological resilience as an emergent ecosystem phenomenon can be decomposed into complementary attributes (scales, adaptive capacity, thresholds and alternative regimes) that embrace the complexity inherent to ecosystems. Quantifying these attributes simultaneously provides opportunities to move from the assessment of specific resilience within an ecosystem towards a broader measurement of its general resilience. We provide a framework, based on testable hypotheses, which allows assessment of complementary attributes of ecological resilience. By implementing the framework in adaptive approaches to management, inference and modeling, key uncertainties can be reduced incrementally over time and learning about the general resilience of dynamic ecosystems maximized. Such improvements are needed because uncertainty about global environmental change impacts and their effects on resilience is high. Improved resilience assessments will ultimately facilitate an optimized use of limited resources for management.

Keywords

ecological resilience; engineering resilience; quantification; unifying framework; management; inference

Introduction

The term resilience has become commonplace in social, health, technological and ecological sciences. In each science, multiple definitions of resilience have been proposed and debated

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(Brand and Jax 2007, Myers-Smith et al., 2012). One of the important definitions for managers can be traced to Holling (1973): “The quantity of disturbance a system can tolerate before it changes into an alternative regime”. However, the lack of implementation of quantitative resilience measures for management is problematic for resilience practice (Spears et al. 2015). Despite recent advances in quantification of resilience (Angeler and Allen 2016), gaps between science, policy and management persist (Garmestani and Benson 2013).

In ecology, the term resilience has been used in at least two different contexts, each based on assumptions of system states. Pimm (1991) defined one as the time needed for an ecosystem to return to pre-disturbance conditions. Pimm's definition has also been referred to as engineering resilience (Gunderson 2000), bounce back or recovery (Standish et al. 2014). Engineering resilience presumes a single equilibrium regime, which is at odds with a growing body of literature on ecosystems as complex adaptive systems (Gunderson and Pritchard 2002). In practice, this means that once an ecosystem has shifted from one regime to another (e.g., a clear water to a turbid lake), an engineering view of resilience would incorrectly assume that the system would eventually rebound to the original regime without, and sometimes even with, substantial intervention. In reality, there is evidence that breaking the feedbacks that maintain the system in an alternative regime (e.g., the eutrophic regime of a lake) can be very difficult (Scheffer et al. 2001). Holling's resilience definition reflects this behavior of complex adaptive systems and is now commonly known as ecological resilience (Gunderson 2000). Contrary to engineering resilience, which can be quantified in relatively straightforward ways using time as the unit of measurement, the quantification of ecological resilience remains challenging. This is due to the complexity that is inherent in ecosystems, which the ecological resilience concept emphasizes, but that has hardly been disentangled. In turn, this leads to arbitrary definitions of system elements, and thus subjectivity, in attempts to operationalize the concept and its measurable elements (Cumming et al. 2005).

There have been many recent calls for quantifying and measuring ecological resilience to improve management and conservation (e.g., Curtin and Parker 2014, Nash et al. 2014; Standish et al. 2014). The many forms of environmental pressures (e.g., agriculture, land-use and climate change, species invasions, and infectious diseases) that rapidly change current ecological baselines highlight the pressing nature of this problem. Ecologists and managers are aware that the capacity of ecosystems to adapt to environmental change may be exhausted in the future. This may lead to a widespread erosion of ecosystem resilience and, ultimately, to regime shifts and reorganization in distinct, alternative, undesirable and potentially stable regimes on local, regional and planetary scales (Hughes et al. 2013). However, predicting regime shifts and how these affect ecosystem service provisioning is fraught with high uncertainty, because these may depend on context and vary among ecosystems as a function of their disturbance and management regimes, or how tightly social systems are linked with their underlying ecological system (Lindenmayer et al. 2008; Pope et al. 2014; Shantz and Burkepile 2014). Also, restoration efforts based on historical reference conditions may become untenable (Seastedt et al. 2008), requiring management approaches that consider novel conditions of ecological and combined social-ecological systems in the future (Kofinas and Chapin 2009; Perry et al. 2011). Ideally, these novel

regimes should show “desired resilience” to provide ecosystem service provisioning without costly management and restoration intervention (Hallett et al. 2013, Standish et al. 2014).

It is clear that current problems related to the operationalization of resilience theory and concepts must be overcome to make them useful for management. In this paper, we suggest a framework to overcome these problems, both with regard to definition and quantification of ecological resilience. We build this framework on the common notion that ecological resilience is an “emergent phenomenon” that derives from scale specific structure and interacting processes that, in turn, depend on structural and functional attributes of ecosystems (Levin 1998, Gunderson 2000). The consideration of ecological resilience as an emergent phenomenon is useful because it makes clear that resilience cannot be quantified or tested within a single hypothesis. Following from its definition are basic assumptions regarding ecosystem organization that should manifest if the propositions are true. This provides opportunities for testing specific hypotheses regarding individual attributes (or surrogates) of ecological resilience. These attributes include the hierarchical and dynamic organization of ecosystems (i.e. “scales”), non-linear phenomena (thresholds), self-organization, and adaptive capacity, i.e. the ability to adapt to and “learn” from change (Carpenter et al. 2001, Allen et al. 2014). Specifically, our framework is based on the decomposition of ecological resilience as an ecosystem phenomenon into its complementary attributes that are considered in Holling's original definition (the quantity of disturbance a system can tolerate before it changes into an alternative regime with different structures, functions and feedbacks). Ecological resilience, which derives from these attributes, describes the complexity of ecosystems better than related concepts (variability, recovery, resistance, persistence and robustness). These related concepts have been studied under the umbrella of ecological stability (Donohue et al. 2013), but they are reductionist in the sense that they are less integrative of the dynamic and complex system components from which resilience emanates (i.e. the recognition of alternative regimes in complex systems).

The resilience quantification framework presented in this paper ideally presents a way forward towards an assessment of the broader, general, rather than specific resilience of an ecosystem, which is necessary for more holistic and integral ecosystem management. We review facets of resilience that are inherent in Holling's resilience definition and provide a framework for hypotheses testing. These hypotheses are then discussed in the context of adaptive management, inference and modeling to incrementally reduce uncertainty about the consequences of global environmental change over time.

Attributes of ecological resilience

Ecological resilience is an emergent phenomenon in ecosystems and other complex systems that consists of distinct system attributes. Some of these attributes are explicitly accounted for while others are implicit in Holling's (1973) definition (Table 1). In our framework, we decompose resilience into four measurable attributes inherent in this definition: 1) scale, 2) adaptive capacity, 3) thresholds and 4) alternative regimes. We discuss each in the following sections.

Scale

An implicit attribute in the ecological resilience definition reflects the very nature of ecosystems; that is, their hierarchical organization wherein structures, functions, and processes are compartmentalized by distinct scales of space and time. The consideration of scale is important in resilience assessments in at least three ways. First, resilience is derived from the redundancy of species with similar functional traits within and across the scales present in a system (Peterson et al. 1998, Allen et al. 2005, Allen and Holling 2008). Specifically, functional traits are important for understanding processes (e.g., primary production, decomposition) and feedbacks that stabilize processes and maintain a specific system regime (Cadotte et al. 2011). Assessing the distribution and redundancy of functional traits can therefore be used as a measurable surrogate of resilience. Second, the impact of disturbance in ecosystems is scale-specific (Pickett and White 1985, Nash et al. 2014), which has been demonstrated, for instance, in boreal lakes. Angeler et al. (2012) found that slow changes in water clarity and acidification patterns resulting from environmental change coincided with the speed of regional spread and increasing complexity of biomass scaling patterns of an invasive nuisance flagellate (*Gonyostomum semen* (Ehrenberg) Diesing) across the boreal lake landscape. At the scale of individual lakes however, invasion outcomes were evident in faster dynamics, with blooming events of the flagellate recurring seasonally. Third, species can differ in their colonization and dispersal abilities, body weights, and reproductive phenology, which provides a range of response patterns to disturbances in a community even within a single scale (i.e., response diversity) (Elmqvist et al. 2003, Tomimatsu et al. 2013). There have been also recent conceptual developments in response-effect trait frameworks, and also ecological network structure and how these may affect resilience (Mori et al. 2013, Díaz et al. 2013, Schleuning et al. 2014, Oliver et al. 2015).

The integration of scales, functional redundancy and response diversity offers a means to assess resilience. So far, many resilience assessments have used the discontinuity approach to objectively identify the scaling structure present in ecosystems (Angeler et al. 2016). This approach is based on the evaluation of discontinuities in the distribution of animal body-mass, an integrative variable allometric with many physiological and ecological attributes (Peters 1983). The underlying assumption is that the discontinuous organization of ecological systems, in terms of nonlinear distributions and availability of shelter, food and other resources in the environment and the interactions between species, is ultimately mirrored in the size or mass structure of animal communities (Scheffer and van Nes 2006, Nash et al. 2014). The body-mass discontinuity approach has been used, for example, with forest and woodland birds in fragmented agricultural landscapes (Fischer et al. 2007) and coral reef fish subjected to fishing pressure (Nash et al. 2013). Both studies found that communities subjected to human impact are less resilient due to the selective extinction of particular body mass and functional groups. Both studies make clear that our mechanistic understanding of ecological phenomena relevant for management, such as extinctions, can be improved when accounting for scales that are defined objectively in the analyses (Allen et al. 2015). Discontinuity analysis has also shown promising application in other areas of management and conservation, including environmental monitoring, regime shift prediction, and biological invasions (Angeler et al. 2016).

Adaptive capacity

Holling's definition describes a facet of resilience as “the capacity of ecosystems to absorb disturbances”. As with the resilience concept itself, adaptive capacity or adaptability has been used qualitatively in the social and ecological sciences, mainly in the climate change context, while few efforts have been made to quantify the concept objectively (Engle 2011). Adaptive capacity varies between different contexts and systems (Adger et al. 2007). In ecology adaptation is perhaps best understood in a Darwinian sense, whereby individual species evolve to adjust to changing environmental conditions. However, adaptive capacity, of which adaptation is a component (Nicotra et al. 2015, Beever et al. 2016), can be extended to emphasize the “constant adjustment” of ecosystem properties, including community composition and function to changing environmental conditions (Carpenter et al. 2001, Smit and Wandel 2008).

In our presentation of attributes, scale and adaptive capacity are treated distinctly for the purpose of distinguishing mechanistic aspects related to ecosystem responses to environmental change. However, these attributes are not mutually exclusive, and will there for be combined in our quantification framework (see below). Angeler et al. (2015a) assessed the spatial structure in a boreal lake landscape. They found that this found that this structure homogenized over time. Functional diversity traits associated with benthic invertebrates decreased over time as a result of this homogenization process. Concomitantly, stochastic species, which were not associated with the spatial scaling patterns identified and which have been suggested to confer adaptive capacity in response to disturbances (Baho et al. 2014), increased. In this example it is clear that resilience associated with scaling structure, and that associated with facets conferring adaptive capacity may not respond in the same way to a disturbance, highlighting the need to consider the two separately. However, cases might exist where both attributes either increase or decrease simultaneously. In these cases, clear management implications are derived. Simultaneous decrease of adaptive capacity and scaling patterns could indicate that systems approaching critical thresholds require management to stave off an impending regime shift (Biggs et al. 2009), while fluctuations around a long-term mean or even increase of both components might highlight a system's ability to absorb perturbation, conferring it ability to maintain a specific ecosystem regime without management.

These considerations make it clear that adaptive capacity cannot be understood without including a temporal dimension to analyses. The concept of adaptive capacity helps to elucidate how communities change over time, both in their structural and functional composition, in response to, and anticipation of, disturbances in order to maintain ecosystem processes and feedbacks of desired regimes. It follows that for quantifying adaptive capacity in ecosystems, we need to account for temporal patterns of species replacements, changes in the species dominance structure and the stability of functional traits (redundancy and response diversity) in the community. In contrast, scaling structure can be determined based on snapshot samples in time. Herewe emphasizespecies dominance and rarity patterns in ecosystems as a means to assess adaptive capacity and separate these patterns from scale attributes. The rationale is that in multivariate time series and spatial modeling, dominant species can generally be associated with the scaling patterns that are identified by the

models, while rare species show stochastic dynamics that do not correlate with the scaling patterns (Angeler et al. 2014). Thus, modeling provides an *a priori*, numerical approach for defining and separating scale and adaptive capacity in resilience assessments.

In most ecosystems, many species are represented by only a small number of individuals and/or are restricted to selected habitats. However, these rare species can have a disproportionate influence on adaptive capacity. Mouillot et al. (2013) found that distinct combinations of functional traits are supported predominantly by rare species across ecosystems, including coral reefs, alpine meadows and tropical forests. With ongoing environmental change, these rare species may ultimately go extinct and lead to disproportionately negative effects on ecosystem processes with a consequent loss of adaptive capacity, even within ecosystems with high biodiversity.

There is also evidence that rare species may actually replace dominant species following disturbances, contributing to the maintenance of an ecosystem in its desired stable regime (Walker et al. 1999, Lyons et al. 2005). A well-known example is post-fire dynamics in shrublands, whereby rapid recruitment of otherwise uncommon plant species from seed banks may stabilize soils and maintain vegetative cover in recently burned openings until more common species recolonize (Quintana-Ascencio and Menges 2000). Similarly, a study in row crops demonstrated the importance of temporal variability in species composition and abundance of native bees for maintaining pollination services (Kremen et al. 2002). These examples highlight that rare species may contribute an important but, to some extent, unpredictable degree of adaptive capacity to ecosystem change. More recently, Baho et al. (2014) used time series modeling to determine the dominant temporal frequencies of phytoplankton dynamics in managed (liming to mitigate acidification effects) and unmanaged (acidified and circumneutral) lakes. They found that the temporal scaling patterns identified were due to dominant phytoplankton species, while rare species showed stochastic dynamics that were unrelated to the identified temporal scaling patterns. Comparing patterns of scales and adaptive capacity associated with stochastic species across lakes, they found no substantial difference in the scaling structure but a significantly higher amount of stochastic species, and thus adaptive capacity, in the limed lakes. Results of this study suggest that management may not necessarily restore pre-disturbance conditions, in terms of approaching community structure present in circumneutral lakes that comprise management targets. However, the increase of stochastic species in limed lakes may provide a broader response spectrum to respond to future disturbances (increasing adaptive capacity). More generally, this example highlights the need to separate the attributes of scale and adaptive capacity for understanding specific management outcomes and to improve resilience assessments.

Thresholds

We consider thresholds an implicit attribute in Holling's definition of resilience because it differs mechanistically from the other attributes. That is, a threshold emphasizes the point of dynamic reorganization ("a zone of turmoil"), i.e. when novel pattern-process relationships in complex systems and thus the foundations for innovation are created (Allen and Holling 2010). In contrast, alternative stable regimes emphasize the aftermath of threshold dynamics;

that is, when system dynamics have stabilized and locked in the new basin of attraction (see below).

Standish et al. (2014) reviewed the threshold literature in an attempt to provide a measurable approach and thus make the concept of thresholds operational for management. They showed a generally clear understanding of the threshold concept and a consensus as to its importance for measuring resilience in the literature, whichever resilience definition is adopted. The main finding of Standish et al. (2014) is that the identification of thresholds has so far been based on experimental and observational data, which both have benefits and drawbacks. Experimental approaches are useful to determine the location of thresholds as a function of the manipulation of disturbances. However, a common problem in experimental ecology is that manipulation of disturbance regimes at the ecosystem and landscape scale to identify thresholds is often impossible because of ethical, practical (resources) and ecological (accounting for organisms with very long regeneration times) reasons. Studies of thresholds in ecosystems are therefore rare, especially in terrestrial systems. Most research is therefore biased towards small-scale experiments using communities with fast turnover (e.g., protists and fungi) and are therefore less broadly applicable.

Observational studies can partly overcome the limitations regarding ecological realism with experimental approaches for determining thresholds. Observational studies provide opportunities to identify thresholds based on retrospective analysis of disturbances associated with observed changes between alternative ecosystem regimes. Retrospective analysis can help identify an impending regime shift, and thus an approaching threshold, using a series of indicators (Scheffer et al., 2012). If a transition is detected early enough, management may be geared towards steering systems away from a regime shift (Biggs et al. 2009). However, there is uncertainty regarding the performance of regime shift indicators in real ecosystems (Spears et al. 2016). For instance, Burthe et al. (2016) evaluated the potential of increased auto correlation and increased variance to indicate regime shifts across multiple trophic levels in marine and fresh water habitats. Their study concluded that these early warning indicators failed to predict regime changes across all levels of the food web in freshwater and marine populations. A further uncertainty is to what extent retrospective analysis can be used to predict thresholds to unmeasured or novel disturbances that may arise from ongoing environmental change (Standish et al. 2014).

Standish et al. (2014) highlight the need for managers to make decisions in the absence of data, a common problem in management and conservation. They suggest that the threshold concept can still be useful if ecosystem dynamics are assessed after the removal of a disturbance. If there is a lack of return to the pre-disturbance regime, that may be an indication of the presence of a threshold, although the location of the threshold cannot be identified. Despite the inability to locate thresholds, relevant information can be provided about which types of intervention are insufficient, or which may be required, to nudge the ecosystem back to the pre-disturbance regime.

Alternative regimes

First proposed by Lewontin (1969), the idea that ecological systems can exist in alternative stable regimes has gained much empirical support. Ecologists have used the concept in two

contexts, one focused on communities and the other one on ecosystems (Beisner et al. 2003). The community approach originated from theoretical population ecology where stability is measured by the ability of populations to withstand direct perturbations, for example, changes in the structure of predators in food webs. This continues to be the focus in community ecology where different configurations of the communities represent different regimes resulting from community assembly and succession (e.g., Jiang et al. 2011). The ecosystem approach is derived from the parameter perturbation framework in population ecology and focuses on how environmental shifts affect parameters that determine the resilience of particular ecosystem regimes (Scheffer et al. 2001, Dent et al. 2002). These perspectives are not mutually exclusive and both have management relevance. Overfishing of top predators in marine environments releases lower trophic levels from top-down pressure in the foodwebs, which combined with climate warming and eutrophication, can lead to ecosystem regimes with more frequent jellyfish outbreaks. A more “gelatinous future” may have negative impacts on tourism, coastal fisheries and aquaculture, and cooling-water intake screens of power plants (Purcell et al. 2007).

Alternative stable regimes are stabilized by self-reinforcing feedbacks. A well-described example of these regimes is the alternative occurrence of different vegetation types in terrestrial environments (DeAngelis 2012). Feedbacks arise because vegetation communities can modify biomass accrual rates, soil nutrient capital and the light environment in a direction that enhances their own growth and survival, and simultaneously hinders or constrains other vegetation types under given environmental conditions. An example from the aquatic realm is the clear-water, macrophyte-dominated, and the alternative turbid, phytoplankton-dominated regimes in shallow lakes (Scheffer et al. 2001). The clear-water regime is based on a feedback between submerged vegetation and water quality, whereby vegetation density influences water clarity through a series of mechanisms. These mechanisms include reduced resuspension of sediment, increased sedimentation, providing phytoplankton-grazing zooplankters refuge from fish predation, competition with phytoplankton for nutrients, and suppressing algae through allelochemicals (Hilt et al. 2011). Excessive nutrient loading can eventually break these mechanisms, leading to the turbid-water regime, which perpetuates itself through a new set of feedback mechanisms. Sediment resuspension can fuel eutrophication, and thus algal growth. Phytoplankton growth is further spurred because of limited biological interaction with macrophytes and altered trophic cascades. That is, piscivorous fish, which use macrophytes for hunting (Jacobsen and Perrow 1998) and refuge areas (for younger individuals to escape from intraspecific predation, Grimm and Backx 1990) areas, are disfavored in the turbid regimes (Jeppesen et al. 2000), thereby relieving planktivorous fish from predation. Planktivores, in turn, excessively control zooplankters that normally graze down phytoplankton.

This example makes two issues very clear. First, feedbacks are complex sets of mechanistically intertwined processes that can operate over different spatial and temporal extents that limit their quantification. The second relates directly to management. For instance, stability of the turbid regime in shallow lakes, reinforced by the feedbacks outlined above, dictates that removing the stressors that caused the regime shift (nutrient loading) will not switch the lake back to a clear-water regime. Breaking feedbacks to restore previous regimes is fundamental (Suding et al. 2004). There exists an abundant literature on lakes

documenting a combination of management interventions, including sediment stabilization, control of planktivorous and benthivorous fish, stocking of piscivorous fish, nutrient precipitation, and macrophyte replanting, to restore shallow lakes (Moss 1990, Gulati and van Donk 2002, Jeppesen et al. 2007). Shallow lakes are therefore an example representative of broader problems that restoration ecologists and managers face in general: an often high financial and resource demand for breaking feedbacks. Additionally, the lakes exemplify that restoration efforts often fail because self-organized patterns are characterized by hysteresis (i.e., “the way out is not the same as the way in”) that complicates restoration after regime shifts (Hobbs 2007). Also, restoration interventions may become further confounded due to the effects of climate change in the future (Harris et al. 2006). This highlights the enormous challenges for future management and mitigation strategies, and the need for managers to assess alternative regimes based on more simple indicators as a diagnostic of alternative ecosystem regimes. We will elaborate on this further in the next section.

A hypothesis framework guiding ecological resilience measurements

By highlighting the four cornerstones of Holling's resilience definition, current quantification approaches and their application to management can be put into the broader context. Although the four attributes of the ecological resilience definition cannot be decoupled, most studies have focused on these attributes rather independently. Most of the examples above highlight the community-level focus of resilience assessments, and these often scrutinize structural aspects of community composition and functional traits of specific taxonomic groups (Truchy et al. 2015). Although targeting the quantification of some of these attributes using the structure of specific taxa was crucial to operationalizing the concept in terms of “resilience of what – to what” (Carpenter et al. 2001), e.g., the resilience of phytoplankton communities to liming (Baho et al. 2014), or assessing the relative resilience of ecosystems by comparing resilience attributes of communities across sites (Allen et al. 2005), this specified assessment of resilience might not reflect the broader systemic or general resilience of an ecosystem (i.e., how an entire lake responds to interacting multiple stressors). In a management context, a focus on specified resilience can become problematic because increasing resilience of particular parts of a system, especially in terms of managing for predictable outcomes of disturbances, may cause the system to lose resilience in other ways (Carpenter et al. 2015). Walker et al. (2004) exemplified this with the example of international travel in Europe that increasingly focused on developing air travel, while deemphasizing international ground and water transportation. The volcano eruption on Iceland in 2010 revealed the low resilience of this transportation system to the extensive cloud of ash in the air that interfered with the operation of aircrafts.

Assessing and quantifying the multiple aspects of resilience, as those represented in Holling's definition, will ideally bring resilience assessment one step forward towards understanding the general resilience of ecosystems and other complex systems. The general resilience of a system is defined as its broad ability to cope with disturbances without changing regime. It does not define the part of the system that might cross a threshold and the kinds of shocks the system needs to deal with, and it copes with uncertainty of all types (Folke et al. 2010). It follows that managing for general resilience will require the simultaneous assessment of not only specified resilience patterns across multiple taxon

groups, but also processes and feedbacks operating within and across spatiotemporal scales to cover generic system properties and create possibilities for integral, resilience-based ecosystem management.

Despite the solid theoretical foundations of resilience theory, assessing the four attributes of resilience in Holling's definition simultaneously can be difficult, costly, unfeasible or discouraged (Quinlan et al. 2016). It is clear that difficulties with measuring the collective attributes of resilience simultaneously make management for general resilience of ecosystems highly uncertain. However, awareness of knowledge gaps related to the application of theory in practice might help identify research priorities for closing these, and allow a move from qualitative, subjective, and normative resilience assessments to a refined framework for quantification. Such knowledge gaps exist, for example, in the determination of the many abiotic and biotic factors that interact dynamically and at different scales to build the feedback loops necessary for maintaining resilience. Understanding feedbacks mechanistically would be a first step towards understanding the management dimensions of resilience. Shallow lakes are well-studied ecosystems that show how feedbacks change under the pressure of nutrient enrichment. However, measuring feedbacks is often unfeasible because of high resource demands for measuring essential system components (Meadows 2008, Holland 2014).

In light of these limitations, we present a quantification framework for ecosystem resilience that distills complexity into relatively simple, well-known and measurable entities that are well-grounded in ecological (stability) theory (Donohue et al. 2013) (Figure 1). These measures focus on resistance (how much metrics change after a disturbance), persistence (time of species to coexist with other species before going extinct), variability (variability is high when stability is low and vice versa) and engineering resilience (recovery). That is, the quantification of these metrics using structural and functional aspects in ecosystems after disturbances is relatively straightforward and covers relevant patterns and processes of system dynamics. These metrics are combined with more recently applied diagnostics (dynamic order [Eason et al. 2016], scaling structure [Angeler et al. 2016]) and resilience theory (Peterson et al. 1998) to increase inference. Similar to the study by Seidl et al. (2016) on forest ecosystems, our framework extends the single equilibrium perspective of ecological stability measurements into a multiple equilibrium context (Figure 1). The framework builds on premises that are based on the fundamental aspects of resilience and poses hypotheses to test these premises (Table 2). These hypotheses are well aligned with and allow evaluation of the four attributes of the ecological resilience definition in a logical sequence and reiteratively; that is, measurement of an ecological regime when it moves towards a threshold, when it passes a threshold and when it reorganizes and stabilizes in a new regime (Figure 1). These hypotheses can be tested using available quantitative methods for measuring resilience (Angeler et al. 2016) and the components of resilience analyzed based on multiple lines of evidence (e.g., using taxonomic groups across entire foodwebs; Burthe et al. 2016). Some of the hypotheses are framed specifically from a management perspective to facilitate the quantification of resilience without sacrificing the consideration of complexity inherent in management-related assessments. Also, most hypotheses are based on empirical observation made across distinct studies (examples in Table 2), thus conferring ecological realism to our resilience assessment framework.

Adaptive capacity and scale

We treated adaptive capacity and scale distinctly when defining the four pillars of the ecological resilience definition for showing different mechanistic aspects. However, both are not mutually exclusive and will therefore be combined in this quantification framework.

Premise 1—The system is able to absorb disturbances to stay within a defined basin of attraction. If the premise is supported, patterns of persistence, resistance, variability and/or engineering resilience should fluctuate around a long-term mean. Because surrogacy in ecology is limited when extrapolating stress-response patterns across taxa (Rodrigues and Brooks 2007), the use of multiple taxon groups for hypothesis testing will increase the strength of the inference. Persistence, resistance, variability within specific bounds, and/or recovery are evident independent of disturbance types, their combinations, magnitudes and frequencies. Collectively, system attributes, whether biological or physical that collectively form the basin of attraction, fluctuate around a long-term mean, which is reflected in dynamic system order and which indicates stability of the basin of attraction (Eason et al. 2016).

Hypotheses

1. Specific structural aspects of community composition, functional traits and process performance (e.g. productivity, decomposition) show the following patterns in relation to disturbances: presumably high resistance, persistence, and engineering resilience and low variability around a long-term mean. [note: “high” is normative and needs to be understood as the starting point against which patterns in the reiterative testing process can be benchmarked].
2. High response diversity increases adaptive capacity and facilitates engineering resilience.
3. Stochastic or rare species add to response diversity.
4. High within-scale redundancy increases adaptive capacity.
5. High cross-scale redundancy confers adaptive capacity.

Premise 1 is supported if these hypotheses are verified reiteratively while monitoring the system. If these hypotheses are increasingly falsified in the iterative testing process, evaluation of premise 2 can begin.

Premise 2—Adaptive capacity erodes, manifested in changing baselines associated with the ecosystems equilibrium dynamics, and the ecosystem transitions towards a regime shift. Support for this premise requires dynamics of collective structural and functional system attributes to be reflected in a decrease of dynamic system order over time, potentially indicating an erosion of the basin of attraction of a specific regime (Spanbauer et al. 2014). These dynamics may also be indicated by early warnings of system transition (i.e. critical slowing down in time series), although such indicators may not universally pick up signals of change in some systems (Dakos et al. 2015; Burthe et al. 2016). The patterns of decreasing adaptive capacity can be scrutinized as follows.

Hypotheses

1. The structural and functional community metrics used to test the first hypothesis in premise 1 show the following patterns in relation to disturbances: slowed down engineering resilience if detectable in time series (Dakos et al. 2015), decreasing resistance and persistence, and higher variability.
2. Species sensitive to disturbances are lost from the system.
3. Response diversity is reduced.
4. Within scale redundancy is changed (Spanbauer et al. 2016).
5. Cross-scale structure is altered (Spanbauer et al. 2016).

This premise is supported if in the course of reiterative hypotheses testing the response variables show incremental change while monitoring the system (for instance, when engineering resilience slows and species are lost incrementally). Upholding the premise while testing hypotheses reiteratively can warn managers that a system is approaching a threshold (Biggs et al. 2009) and may help to design management intervention to foster system resilience. If, with management, the hypotheses testing outcomes conform to those of premise 1, insight might be gained about successful management.

Thresholds

Premise 3—Adaptive capacity is exhausted and the system undergoes reorganization into an alternative regime. This premise, to be supported, requires that in the reiterative hypothesis testing process of premise 2, managers may detect a potentially abrupt change in ecological patterns and processes with highly incongruent or chaotic temporal dynamics of structural and functional metrics. To the authors' knowledge, these assumptions have not been explicitly tested empirically during threshold dynamics in real ecosystems thus far. The following hypotheses might provide opportunities for doing so.

Hypotheses

1. Community composition and abundances are highly unstable in the system.
2. Species dynamics are stochastic (that is, limited intrinsic or extrinsic environmental determinism affecting community dynamics).
3. Population dynamics are highly unsynchronized.
4. Food web configurations and biological interactions are unstable (i.e., restructuring of feedback loops).
5. Lack of robustness and engineering resilience while the system passes the threshold.

Although transition periods between regimes can be long (Spanbauer et al. 2014), reiterative verification of these hypotheses suggests that a point of no return has been reached. In this case, managers may need to prepare for transformative change and engage in scenario planning to envision potentially different novel ecosystems with changed conditions for supporting human welfare (Chaffin et al. 2016).

New alternative regime

Premise 4—The ecosystem has locked into a new dynamic regime. This premise to be supported requires confirmation that the system operates in a new basin of attraction, which can be reflected in dynamic system order fluctuating around a new temporal mean (Spanbauer et al. 2016). The new system structure becomes evident in new scaling patterns, including new cross-scale structure (Spanbauer et al., 2016) and species distributions within scaling patterns (Angeler et al. 2013). Functional trait distributions within and across scales may or may not necessarily change in the new regime, because functional traits present in previous regimes can be maintained due to compensational processes related to species replacements (Angeler et al. 2015b). The new system structure reflects the new stability landscape of the basin of attraction (for instance when a lake locks in a nutrient-enriched, turbid water regime with frequent algal bloom outbreaks, relative to a low-nutrient clear water state of the previous regime). This new biophysical system structure builds feedback loops that maintain the system in the new regime.

Hypotheses: Testing of premise 4 is essentially based on the hypotheses outlined for premise 1 because the focus is on the assessment of adaptive capacity and resilience of a specific regime. In addition, the following hypotheses can be tested:

1. Within-scale structure has changed relative to the previous regime.
2. Cross-scale structure has changed relative to the previous regime.

Two implications follow from different test outcomes. If repeated hypotheses verification confirms the new system regime, management decisions may be taken based on normative values for society. That is, if the new regime provides desirable ecosystem service bundles to humans, management can aim at fostering this novel regime. In contrast, if the new regime is undesirable, management interventions can focus on weakening the resilience of this regime, transforming the system and stabilizing it in a new alternative regime (Figure 2).

Implementation

We acknowledge that our hypothesis-testing framework only provides one aspect of importance and relevance to management, namely the informational component. Much more than good ecological information is needed to realize adaptive management and build general ecosystem resilience. We emphasize that the framework can help provide quality and timely information to feed into management processes, and thereby contribute to building resilience without in advertently implying that improved understanding and monitoring is some sort of panacea.

Our hypotheses need to be regarded as a starting point for assessing premises of resilience attributes, which can be modified in the course of reiterative testing, refined and adapted to the biophysical characteristics of individual ecosystems. This approach provides opportunities to deal with and potentially reduce key uncertainties related to the effects of global environmental change. These tests offer the insight necessary for promoting adaptive and proactive management and monitoring approaches. Our hypothesis framework can be implemented within the context of adaptive management (Allen et al. 2011), inference

(Holling and Allen 2002) and modeling (Uden et al. 2015) for revealing, refining, understanding and ultimately managing general ecosystem resilience. Testing all hypotheses simultaneously is not feasible in most management situations because of the lack of monitoring data that is needed for assessing temporal dimensions to resilience aspects such as engineering resilience, persistence, variability, resistance or threshold dynamics. In this case, and similar to adaptive management, some of our hypotheses (e.g., those for assessing scaling patterns and functional trait combinations within and across scales, and relative resilience of alternative regimes) can be tested based on available, often snapshot data of ecosystems (Allen et al. 2005) (Figure 1). Controlled sequences of management interventions can then be implemented for concomitantly identifying and achieving management objectives (e.g., transformative management which targets intervention to shift systems from an undesired to a desired regime and foster this regime, or adaptive management which aims to maintain ecosystems in a desired regime) (see Chaffin et al. 2016). In this process, experiments can be designed that sequentially recalibrate management strategies based on the outcomes of previous experiments and from which decisions about further data generation and monitoring can be made (Figure 2).

The information obtained during monitoring can be used for adaptive approaches to sampling to select appropriate spatial and/or temporal dimensions for sampling (Thompson and Seber 1996). In the course of adaptive hypothesis testing, inferences about the general resilience of ecosystems can focus on balancing type I (false positive) and type II (false negative) errors by initially focusing on minimizing type II error and then successively reducing type I errors (Holling and Allen 2002). That is, to make decisions about the feasibility and implementation of adaptive or transformative management approaches, inference is achieved by first recognizing patterns. Type II errors can be reduced by assessing resilience attributes (e.g., cross-scale and within scale structure and associated functional diversity redundancy) in the face of limited availability of ecological information of the system. This can be done based on snapshots (i.e., information about an ecosystem obtained from a single time point), which are often the only resource available to managers. Subsequently, to reduce Type I errors, monitoring can be designed, implemented and sequentially modified to successively improve knowledge about a broader range of resilience characteristics that need a temporal dimension to measurement (e.g., how fast do system attributes recover from disturbances; what is an ecosystem's dynamic organization). By reiteratively testing hypotheses about system behavior, management can guide action towards the adaptive or transformative management goals (Figure 2).

Using our hypotheses within a broader single framework that incorporates adaptive management, sampling, inference, and modeling, will enhance our ability to explicitly define and reduce uncertainties. In turn, this will promote more holistic and effective modeling, management and monitoring of general resilience. This can overcome common management shortcomings, including delayed action in the face of uncertainty (Conroy et al. 2011), failed optimization of financial resources (Stewart-Koster et al. 2015), and the lack of coordinated effort and scale mismatches across space, time, and institutional boundaries (Crowl et al. 2008, Cumming et al. 2013). Using this approach, uncertainty cannot be eliminated immediately or entirely. However, it can be reduced incrementally over time, with monitoring, modeling and management that explicitly incorporates learning. Such

improvements are needed because uncertainty about global environmental change impacts and their effects on resilience is high.

Conclusions and implications for management

1. Ecological and social-ecological baselines are swiftly changing, with uncertain outcomes regarding the provisioning of crucial ecosystem services in the future. The continued provisioning of ecosystem services under this uncertainty is one of humankind's biggest challenges, highlighting the need to maintain ecosystems that are resilient to environmental change.
2. There is growing awareness among ecologists and managers of the need to assess resilience, but the qualitative rather than quantitative treatment of facets of resilience has limited its applicability. In this paper we address the first step towards overcoming current barriers to quantification needed to make the concept useful for management and conservation. We forward a quantitative framework that builds on the attributes of Holling's original definition and that are measurable.
3. Our framework provides relatively simple guidelines for making complex problems in ecology and management tractable. The quantification of attributes according to our framework is broadly applicable and can be tested within and across ecosystem types, using a range of specifically designed methods to evaluate resilience (e.g. discontinuity analysis and modeling, Angeler et al. 2014). Quantitative resilience research can also borrow from other widely used methods, like tools from metacommunity ecology or network theory that account for habitat structure and connectivity (Cumming et al. 2010, Göthe et al. 2013). That is, resilience assessments are not limited to ecosystems with discrete habitat boundaries or a clear insular metacommunity structure (lakes, ponds, islands, fragmented forests). Resilience can also be modeled for ecosystems that are hierarchically structured, comprise habitats with unclear boundaries and are highly variable in space and time (e.g. streams, floodplains, grasslands, forests, coral reefs). This offers opportunities to quantify resilience beyond local habitats to assess resilience in a regional context; that is, spatial resilience (Allen et al. 2016).
4. The application of these tools that allow managers to evaluate resilience across a broad range of ecosystems will ultimately depend on data availability. Data from long-term monitoring programs that cover multiple sites, or palaeoecological approaches, would likely be bestsuited to assess components of resilience locally and regionally.
5. Although our framework has a strong focus on ecosystems, it might also find transdisciplinary application and inform resilience assessments in other domains (social, social-ecological, economic) (Sundstrom et al. 2014), including risk and disaster assessment and governance (Linkov et al. 2014). Quantitative resilience research is needed to assess and understand the intricacies of environmental change and its repercussions on human welfare. We believe that our framework,

which is currently theoretically focused, might find practical application across disciplines in the future.

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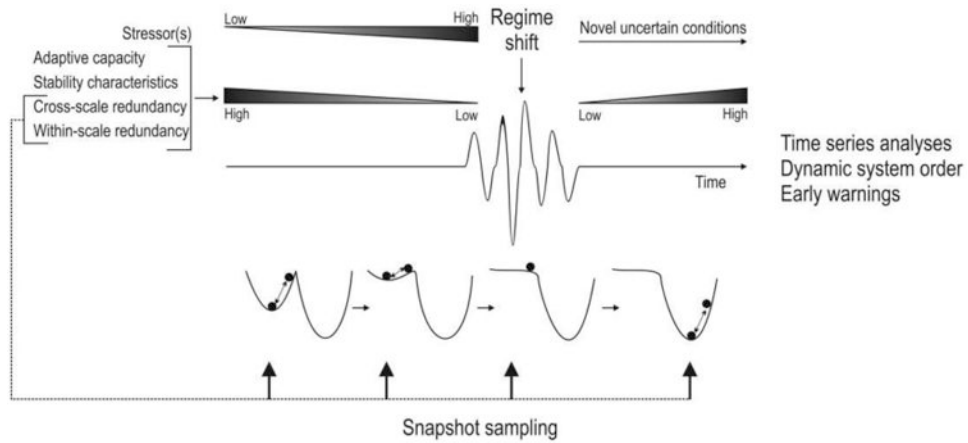


Figure 1. Schematic of system behavior when increasing pressure from stressor(s) contributes to the erosion of resilience (change of landscape of ball-in-cup visuals), leading to a regime shift and reorganization in a new stable regime characterized by novel conditions and uncertainty. Shown is how resilience attributes (adaptive capacity, stability [robustness, engineering resilience], within- and cross-scale redundancies) increase/decrease over time and how they can be evaluated sequentially based on a range of time series modeling approaches or snapshots.

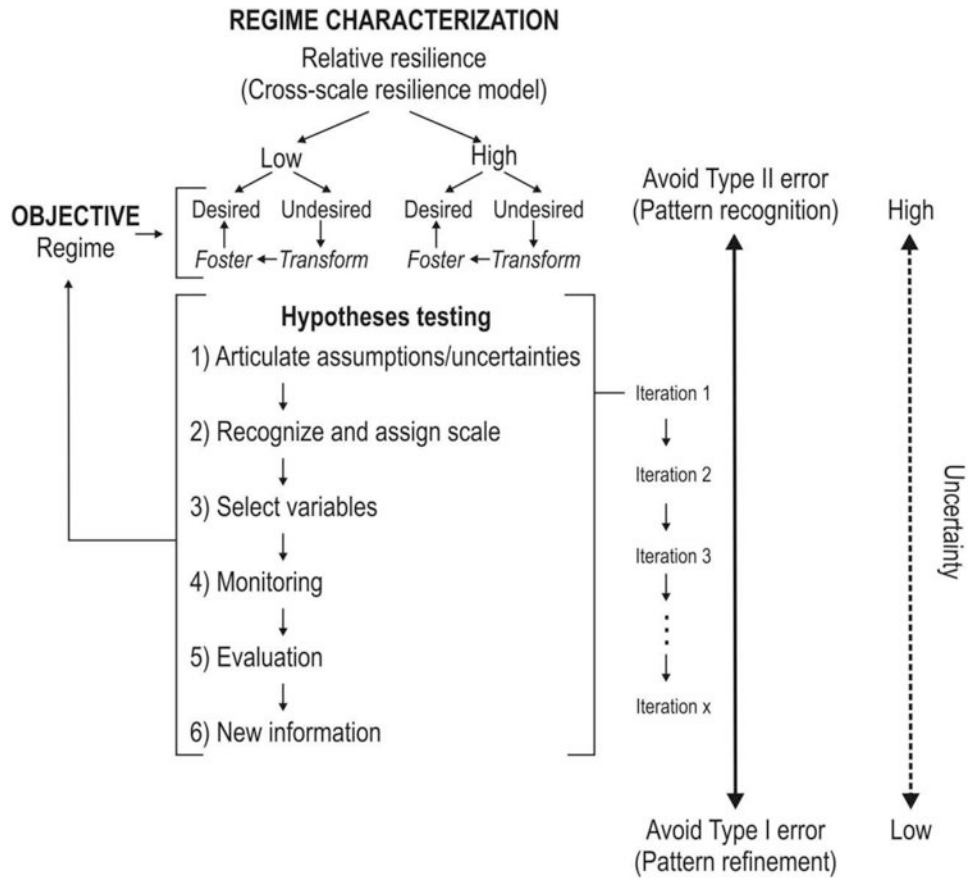


Figure 2. Implementation of resilience hypotheses within an adaptive management, inference and modeling framework that reiteratively tests, recalibrates, and refines explicit resilience-based hypotheses to meet management objectives (adaptive or transformative management approaches) by first recognizing patterns (reducing risk of type II error) and the refining knowledge about patterns (reducing risk of type I error), thereby reducing uncertainty.

Table 1

Definition of attributes (measurable surrogates) of ecological resilience that are explicit or implicit in Holling's (1973) definition.

Attribute	Definition
Explicit Alternative stable regime	Alternative stable regimes are defined by stable structures, functions, processes and feedbacks (Lewontin, 1969), such as shallow lakes that show clear-water and turbid alternative regimes (Beisner <i>et al.</i> , 2003) or terrestrial systems that can exist in alternative forest and grassland regimes (Staver, Archibald and Levin, 2011).
Adaptive capacity	The ability of a system to prepare for stresses and changes in advance or adjust and respond to the effects caused by the stresses (Smit <i>et al.</i> , 2001). In ecology, adaptive capacity can be related to genetic and biological diversity, which provide ecosystems with the ability to maintain critical functions and processes during changing and/or novel environmental conditions (Angeler <i>et al.</i> , 2014).
Implicit Threshold	Thresholds indicate that ecosystems can undergo non-linear change or shift between alternative regimes when critical disturbance levels are surpassed (Suding and Hobbs, 2009). When an ecosystem crosses a threshold or tipping point, its capacity to adapt to and cope with disturbances has been exhausted, and it abruptly reorganizes into a new regime with new structures, functions and processes. Thresholds have been assessed in, for instance, intertidal marine ecosystems switching from rock weed beds to mussel stands (Petraitis <i>et al.</i> , 2009) or the encroachment of woody plants into grasslands as a function of fire intensity (Twidwell <i>et al.</i> , 2013).
Scale	Ecosystem structure is compartmentalized by spatial and temporal scales (Levin, 1998), which can be assessed objectively using statistical tools (Angeler <i>et al.</i> , 2016). Scale detection is important because it allows quantification of the redundancy of functional traits (functional redundancy) of the organisms within and across scales present in an ecosystem. This in turn allows for an assessment of resilience in ecosystems (Peterson <i>et al.</i> , 1998). Resilience assessments can be refined when accounting for multiple functional traits (e.g. body size, dispersal characteristics, recolonisation ability, reproductive phenology, etc.), and response diversity (Elmqvist <i>et al.</i> , 2003) that determines an organism's response to disturbances, and its effects on ecosystem functioning (Díaz and Cabido, 2001).

Table 2

Premises of resilience components and simple, management-relevant hypotheses that can serve as a starting point for testing these and which can be refined, modified and adapted to specific ecosystems in the reiterative testing process.

Resilience component	Premise	Hypotheses	Test	Support
Adaptive capacity and scale	1) Ecosystem has adaptive capacity; stays within a basin of attraction after disturbances	<ul style="list-style-type: none"> Ecological metrics show “high” resistance, persistence and engineering resilience, and low variability 	Time series analyses of metrics	Boucher <i>et al.</i> (1994); Bellingham, Tanner and Healey (1995)
		<ul style="list-style-type: none"> Response diversity is high 	Functional trait analyses based on snapshot data and/or time series	Kühnel and Blüthgen (2015); Nash <i>et al.</i> 2016
		<ul style="list-style-type: none"> Stochastic species increase response diversity 	Objective evaluation of deterministic vs. stochastic species in ecosystem and functional diversity and redundancy of these species	Angeler <i>et al.</i> (2015a); Baho <i>et al.</i> (2014); Mouillot <i>et al.</i> (2013); Walker <i>et al.</i> (1999)
		<ul style="list-style-type: none"> Within-scale redundancy is high-Cross-scale redundancy is high 	Discontinuity analyses based on snapshot data or time series analyses	Allen <i>et al.</i> (2005); Angeler <i>et al.</i> (2016)
	2) Adaptive capacity erodes; ecosystem regime loses resilience	<ul style="list-style-type: none"> Resistance and persistence of metrics decrease, variability increases and engineering resilience slows down or does not attain equilibrium conditions. 	As in Premise 1	Dakos <i>et al.</i> (2008); Carpenter and Brock (2006); Mumby <i>et al.</i> 2014)
		<ul style="list-style-type: none"> Species sensitive to changing disturbance regimes lost from the system 		Hooper <i>et al.</i> (2012)
		<ul style="list-style-type: none"> Response diversity decreases 		Nyström (2006); Nash <i>et al.</i> (2016)
		<ul style="list-style-type: none"> Within-scale redundancy changes-Cross-scale patterns change 		Spanbauer <i>et al.</i> (2016); Spanbauer <i>et al.</i> (unpublished)
Threshold	3) Adaptive capacity is exhausted; ecosystem undergoes a regime shift	<ul style="list-style-type: none"> Community composition and abundances unstable Species dynamics are stochastic Population dynamics are unsynchronised Food web configuration and biological interactions are unstable 	Time series analyses; food web and network analysis	Hypothetical assumptions
New alternative regime	4) Ecosystem has stabilized	As in premise 1; additionally:	As in premise 1	As in premise 1

	and gained adaptive capacity to stay in the new basin of attraction	<ul style="list-style-type: none">• Within-scale structure has changed relative to the previous regime• Cross-scale structure has changed relative to the previous regime		
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