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A Quantitative Framework for Assessing Ecological Resilience

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Synthesis

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 suggest a quantitative framework for assessing ecological resilience. 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 toward a broader measurement of its general resilience. We provide a framework that is based on reiterative testing and recalibration of hypotheses that assess 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.

Key Words: *ecological resilience; inference; management; quantification; unifying framework*

INTRODUCTION
The term resilience has become commonplace as a boundary concept in social, health, technological, and ecological sciences (Brand and Jax 2007, Baggio et al. 2015). In each science, multiple definitions of resilience have been proposed and debated (Myers-Smith et al. 2012, Angeler and Allen 2016). 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 predisturbance conditions. Pimm's definition has also been referred to as engineering resilience (Gunderson 2000), bounce back, or recovery (Standish et al. 2014). Engineering resilience was already proposed by Tredgold (1818) as a property in timber and refined by Mallett (1856) in relation to the capacity of specific materials to withstand specific disturbances. 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), acknowledging the existence of alternative (stable) regimes, e.g., a clear-water versus a turbid lake. This behavior of complex adaptive systems is reflected in the definition that is now commonly known as ecological resilience (Gunderson 2000).

Holling (1973) originally defined ecological resilience as a measure of the persistence of systems and their ability to absorb disturbances while maintaining the same relationships between populations and state variables. Walker et al. (2004) extended Holling's definition from the population to the system level as the ability of a social-ecological system to absorb disturbances and re-organize while undergoing change, so as to still retain essentially the same functions, structures, identity, and feedbacks. The ecological resilience definitions by Gunderson and Holling (2002; "the magnitude of disturbance that can be absorbed before the system changes its structure by changing the variables and processes that control behavior") and Angeler and Allen (2016; "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") make the existence of alternative regimes and thresholds explicit.

Engineering resilience can be quantified in relatively straightforward ways using time as the unit of measurement. However, the quantification of ecological resilience remains challenging. This is due to the complexity that is inherent to ecosystems, which ecological resilience 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 measureable 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 uncertainty, because these may depend on context and vary among ecosystems as a function of their disturbance and management regimes, or how tightly

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Table 1. Definition of attributes (measurable surrogates) of ecological resilience.

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 et al. 2003) or terrestrial systems that can exist in alternative forest and grassland regimes (Staver et al. 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 et al. 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 et al. 2014).
Implicit	
Threshold	Thresholds indicate that ecosystems can undergo nonlinear 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 et al. 2009) or the encroachment of woody plants into grasslands as a function of fire intensity (Twidwell et al. 2013).
Scale	Ecosystem structure is compartmentalized by spatial and temporal scales (Levin 1998), which can be assessed objectively using statistical tools (Angeler et al. 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 et al. 1998). Resilience assessments can be refined when accounting for multiple functional traits (e.g., body size, dispersal characteristics, recolonization ability, reproductive phenology, etc.), and response diversity (Elmqvist et al. 2003) that determines an organism's response to disturbances, and its effects on ecosystem functioning (Díaz and Cabido 2001).

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 (Spears et al. 2015). In this paper, we suggest a framework to overcome these problems, both with regard to definition and quantification of ecological resilience. Our framework is based on the decomposition of ecological resilience as an ecosystem phenomenon into complementary attributes. We review the attributes of resilience that are inherent to ecological resilience definitions and provide a hypotheses framework for testing these. The hypotheses can be tested reiteratively and recalibrated constantly using adaptive management, inference, and modeling approaches. This allows for incremental reduction of uncertainty about how ecosystems respond to environmental change over time. The resilience quantification framework presented in this paper presents an ideal way forward, toward an assessment of the broader general, rather than specific resilience of an ecosystem. The framework could therefore be useful for a more holistic and integral ecosystem management.

ATTRIBUTES OF ECOLOGICAL RESILIENCE
Ecological resilience is an emergent phenomenon in ecosystems and other complex systems that consists of distinct system attributes (Table 1). In our framework, we decompose resilience into four measurable attributes inherent to ecological resilience

definitions: (1) scale, (2) adaptive capacity, (3) thresholds, and (4) alternative regimes.

Scale
This attribute of ecological resilience reflects the hierarchical organization of ecosystems wherein structures, functions, and processes are compartmentalized by distinct scales of space and time (Allen et al. 2014). 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 or decomposition, and feedbacks that stabilize processes and maintain a specific 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, with the invasion of a nuisance alga in a landscape of boreal lakes (Angeler et al. 2012). 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). Recent research in response-effect trait frameworks and ecological network structure are contributing to a refined understanding of response diversity (Mori et al. 2013, Díaz et al. 2013, Oliver et al. 2015, Schleuning 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 impacts are less resilient because of 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

The definition of ecological resilience focuses on the capacity of ecosystems to absorb disturbances, a system feature that has been studied mainly qualitatively (Engle 2011), and that varies between different contexts and systems (Adger et al. 2007). In ecology adaptive capacity is often used in a population context (Nicotra et al. 2015, Beever et al. 2016), but can also emphasize the constant adjustment of ecosystem properties to changing environmental conditions (Carpenter et al. 2001, Smit and Wandel 2006).

In our presentation of attributes, scale and adaptive capacity are treated distinctly for the purposes of distinguishing mechanistic aspects related to ecosystem responses to environmental change. We emphasize species 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). Time series and spatial modeling may therefore compose a more objective method to identify dominant and rare species compared to methods based on arbitrary definitions (Gaston 1994).

Baho et al. (2014) and Angeler et al. (2015a) provided a motivation for separating scale from adaptive capacity. For instance, 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 scale and adaptive capacity across lakes that were attributable to dominant and rare/stochastic species, respectively, they found no substantial difference in the scaling structure, but a significantly higher amount of stochastic species, and thus presumably higher adaptive capacity, in the limed lakes. Results

of this study suggested that limed lakes might provide a potentially broader response spectrum to future disturbances (increased adaptive capacity).

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 combinations of functional traits that can have a disproportionate influence on adaptive capacity (Mouillot et al. 2013). Mouillot and colleagues suggested that with ongoing environmental change, these rare species may eventually go extinct, which may have disproportionately negative effects on ecosystem processes through a loss of adaptive capacity, even within ecosystems with high biodiversity. 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 postfire 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-Ascensio 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. There is need to assess adaptive capacity as a function of temporal patterns of species replacements, changes in the species dominance structure, and the stability of functional traits (redundancy and response diversity) in the community and their effects on ecosystem processes and feedbacks.

Thresholds

We consider thresholds to be mechanistically different from the other attributes in the ecological resilience definitions. That is, a threshold emphasizes the point of dynamic reorganization, 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. Standish et al. (2014) reported 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 for ethical, practical (resources), and ecological (accounting for organisms with very long regeneration times) reasons. In contrast, observational studies provide opportunities to identify thresholds based on retrospective analysis of disturbances associated with observed changes between alternative ecosystem regimes. Retrospective analysis can be useful when data are scarce and when disturbances can be

removed and controlled. A lack of return to predisturbance regimes could indicate the presence of a threshold. Although the location of the threshold might not be identified, relevant information would be obtained about which types of intervention are insufficient, or which may be required to nudge the ecosystem back to the predisturbance regime. However, Rocha et al. (2015) showed that selected drivers causing regime shifts commonly co-occurred, and that these changes also affected common sets of ecosystem services across distinct marine ecosystems. This suggests that identification of management intervention for controlling drivers and conserving ecosystem services based on retrospective analysis can be complex.

When monitoring data are available, a series of early warning indicators can be used to identify when a system approaches a threshold and reorganization into an alternative regime occurs (Scheffer et al. 2012). If a transition, manifested as increasing variability of ecosystem responses to a combination of drivers, is detected early enough, management may be geared toward steering systems away from a regime shift (Biggs et al. 2009). The performance of selected univariate regime shift indicators in real ecosystems can be uncertain (Burthe et al. 2016, Spears et al. 2016), but this uncertainty can potentially be decreased by using multivariate approaches of regime shift indication in both space (Sundstrom et al. 2017) and time (Eason et al. 2016). If such multivariate metrics (e.g., Fisher Information) detect a potential transition, sampling regimes can be adjusted for obtaining multiple lines of evidence for a regime change. In our framework we will discuss how the measurement of structural and functional attributes of ecological communities can help in such a task.

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 from community and ecosystem perspectives (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). Both perspectives are not mutually exclusive and have management relevance. Overfishing of top predators in marine environments releases lower trophic levels from top-down pressure in the food webs, which, combined with climate warming and eutrophication, can lead to ecosystem regimes with more frequent jellyfish outbreaks and reduced ecosystem services (Purcell et al. 2007).

Alternative stable regimes are stabilized by self-reinforcing feedbacks, which are complex sets of mechanistically intertwined processes that can operate over different spatial and temporal extents. A well-described example are the clear-water, macrophyte-dominated, and the alternative turbid, phytoplankton-dominated regimes in shallow lakes (Scheffer et al. 2001), in which the interplay between phytoplankton, submerged vegetation and planktivorous and piscivorous fish affect and are affected by water quality, particularly nutrient concentrations (Scheffer 2004). Breaking the feedbacks of the turbid regime to restore the clear-water regime in shallow lakes has proven difficult in many cases, despite high financial and other resource investments (sediment stabilization, control of planktivorous and benthivorous fish, stocking of piscivorous fish, nutrient precipitation, and macrophyte replanting in restoration programs; Moss 1990, Gulati and van Donk 2002, Jeppesen et al. 2007). Lake restoration efforts often fail because self-organized patterns are characterized by hysteresis that complicates restoration after regime shifts (Suding et al. 2004, Hobbs 2007).

Restoration interventions may become further confounded because of 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. That is, for management purposes approaches are needed to identify the stability of alternative regime and the factors that create the feedbacks that confer this stability (Nyström et al. 2012). Thus indicators as a diagnostic of alternative ecosystem regimes are needed. Such indicators can build on the assessment of the aforementioned resilience attributes that are related to adaptive capacity and scale of a specific regime and will make up part of our assessment framework.

A HYPOTHESIS FRAMEWORK GUIDING ECOLOGICAL RESILIENCE MEASUREMENTS
By highlighting the four cornerstones of the ecological resilience definitions, current quantification approaches can be put into a 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 a community ecology focus of ecological resilience assessments, and these often scrutinize structural aspects of community composition and functional traits of specific taxonomic groups and how they are influenced by environmental factors (Truchy et al. 2015). Targeting the quantification of some of these attributes using the structure of specific taxon groups 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). However, resilience assessments based on specific taxon groups might not reflect the broader systemic or general resilience of an ecosystem, which would emanate from the broader interaction of all biological and environmental components, i.e., how an entire lake responds to interacting multiple stressors. A focus on specified resilience can become problematic in a management context 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 the ecological resilience definition, will ideally bring resilience assessment one step forward toward 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 the ecological resilience 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. 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; Fig. 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 (Fig. 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 ecological resilience in a logical sequence and reiteratively, that is, measurement of an ecological regime when it moves toward a threshold, when it passes a threshold, and when it reorganizes and stabilizes in a new regime (Fig. 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 food webs (Burthe et al. 2016). Some of the hypotheses are framed 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.

Fig. 1. Schematic of system behavior when increasing pressure from stressor(s) contributes to the erosion of resilience, 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 structure/redundancies) increase/decrease over time and how they can be evaluated sequentially based on a range of time series modeling approaches (dynamic system order, early warnings) when time series data are available. In the absence of time series data the relative resilience based on cross-scale and within-scale redundancy can be assessed during snapshots over time (indicated by the vertical arrows originating from the redundancy surrogate measures). The sequence of ball-in-cup visuals shows how the stability landscape changes along with the changes in stressor(s), and how the snapshot sampling can reveal changes in the relative resilience of the system over time.
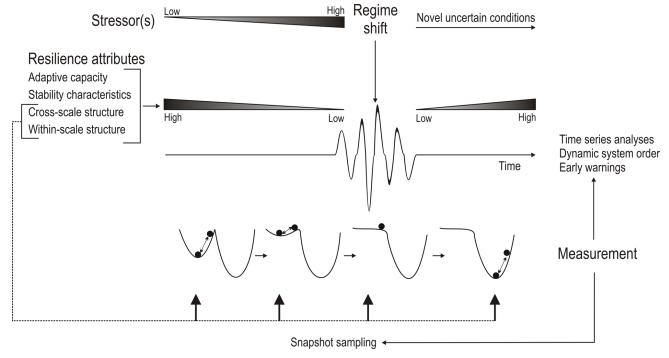
Adaptive capacity and scale

We treated adaptive capacity and scale distinctly when defining the four pillars of ecological resilience for showing different mechanistic aspects. However, they 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 or decomposition, show the following patterns in relation to disturbances: presumably high resistance, persistence, and engineering resilience, and low variability around a long-

Table 2. Premises of resilience components and simple, management-relevant hypotheses that can serve as a starting point for testing these and that 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	Ecological metrics show "high" resistance, persistence, and engineering resilience, and low variability;	Time series analyses of metrics	Boucher et al. (1994), Bellingham et al. (1995)
	Response diversity is high;	Functional trait analyses based on snapshot data and/or time series	Kühsel and Blüthgen (2015), Nash et al. (2016)
	Stochastic species increase response diversity;	Objective evaluation of deterministic vs. stochastic species in ecosystem and functional diversity and redundancy of these species	Walker et al. (1999), Mouillot et al. (2013), Baho et al. (2014), Angeler et al. (2015a)
	Within-scale redundancy is high; Cross-scale redundancy is high;	Discontinuity analyses based on snapshot data or time series analyses	Allen et al. (2005), Angeler et al. (2016)
(2) Adaptive capacity erodes; ecosystem regime loses resilience	Resistance and persistence of metrics decrease, variability increases, and engineering resilience slows down or does not attain equilibrium conditions;	As in Premise 1	Carpenter and Brock (2006), Dakos et al. (2008), Mumby et al. (2014)
	Species sensitive to changing disturbance regimes lost from the system;		Hooper et al. (2012)
	Response diversity decreases;		Nyström (2006), Nash et al. (2016)
	Within-scale redundancy changes; Cross-scale patterns change;		Spanbauer et al. (2016); Angeler, Allen, Garmestani, et al. (*unpublished manuscript*)
Threshold			
(3) Adaptive capacity is exhausted; ecosystem undergoes a regime shift	Community composition and abundances unstable; Species dynamics are stochastic; Population dynamics are unsynchronized; 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 and gained adaptive capacity to stay in the new basin of attraction	As in premise 1; additionally: Within-scale structure has changed relative to the previous regime; Cross-scale structure has changed relative to the previous regime;	As in premise 1	As in premise 1

term mean. [Note: "high" is normative and needs to be understood in the absence of data as an arbitrarily defined 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 if their traits are not present in dominant species.

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 toward 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. For this premise to be supported requires that, in the reiterative hypothesis testing process of premise 2, managers 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 explicitly been tested empirically during threshold dynamics in real ecosystems thus far. The following hypotheses might provide opportunities for doing so and help to address the uncertainty associated with retrospective analysis of thresholds and early warning signals (see above).

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 may suggest 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. In order for this premise to be supported, confirmation is required that the system operates in a new basin of attraction, which can be reflected in the 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 because of 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 into a nutrient-enriched, turbid water regime with frequent algal bloom outbreaks, rather than the low-nutrient clear water state of the previous regime). This new biophysical system structure has 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 (Fig. 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 high quality and timely information to feed into management processes, and thereby contribute to building resilience without inadvertently 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; Fig. 1). Controlled sequences of management interventions can then be implemented for concomitantly identifying and achieving management objectives, e.g., transformative management that targets interventions to shift systems from an undesired to a desired regime and foster this regime, or adaptive management that 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 (Fig. 2).

Fig. 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. The approach starts with an assessment of the relative system resilience. With reiterative hypothesis testing, it can be assessed whether resilience is high or low, and provide information for management objectives, i.e., whether systems in desired or undesired states should be fostered or transformed.
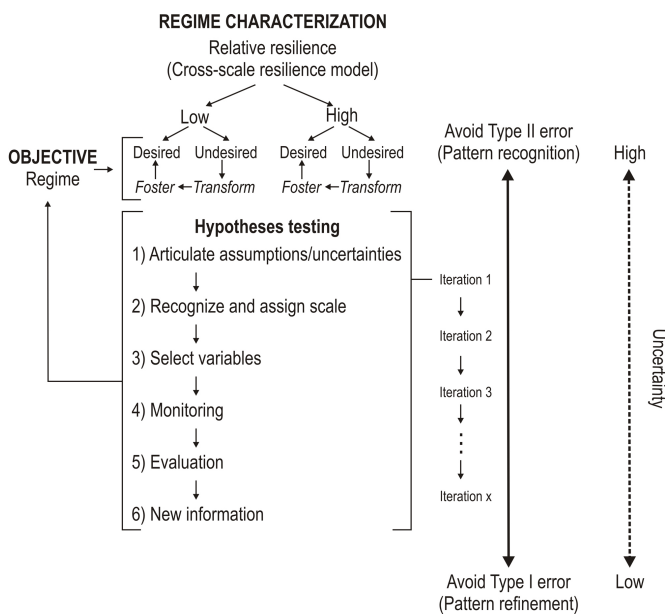
The information obtained during monitoring can be used for adaptive approaches to sampling to select appropriate spatial and/or temporal dimensions for sampling (Thompson and Seber 1996). In the course of adaptive hypothesis testing, inferences about the general resilience of ecosystems can focus on 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. In the face of limited availability of ecological information about the system, type II errors can be reduced by assessing resilience attributes, e.g., cross-scale and within scale structure and associated functional diversity redundancy. 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 toward the adaptive or transformative management goals (Fig. 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.

SUMMARY 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. This highlights the need to maintain resilience of desired ecosystems and transform undesired regimes.

(2) There is growing awareness among ecologists and managers of the need to assess resilience (Spears et al. 2015), but the qualitative rather than quantitative treatment of facets of resilience has limited its applicability. In this paper we address the first step toward overcoming current barriers to quantification needed to make the concept useful for management and conservation. We put forward a quantitative framework that builds on the attributes that are inherent to definitions of ecological resilience 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, time series modeling, spatial modeling, network analysis, and early-warning indicators. 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 paleoecological approaches, would likely be best suited to assess components of resilience locally and regionally using our quantitative framework. However, such data do not exist for most ecosystems. Our framework points out directions for building and guiding adaptive management and monitoring based on initial snapshot sampling when data are limited. However, high resource demands are a major obstacle to the practical implementation of our approach, especially when data are scare. Our framework is therefore theoretically focused. It highlights the enormous challenge to manage for ecosystem resilience and the persistent problems for closing gaps between science, policy, and management (Garmestani and Benson 2013).

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