CONCEPTS & SYNTHESIS

EMPHASIZING NEW IDEAS TO STIMULATE RESEARCH IN ECOLOGY

The distribution and role of functional abundance in cross-scale resilience

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Abstract. The cross-scale resilience model suggests that system-level ecological resilience emerges from the distribution of species' functions within and across the spatial and temporal scales of a system. It has provided a quantitative method for calculating the resilience of a given system and so has been a valuable contribution to a largely qualitative field. As it is currently laid out, the model accounts for the spatial and temporal scales at which environmental resources and species are present and the functional roles species play but does not inform us about how much resource is present or how much function is provided. In short, it does not account for abundance in the distribution of species and their functional roles within and across the scales of a system. We detail the ways in which we would expect species' abundance to be relevant to the cross-scale resilience model based on the extensive abundance literature in ecology. We also put forward a series of testable hypotheses that would improve our ability to anticipate and quantify how resilience is generated, and how ecosystems will (or will not) buffer recent rapid global changes. This stream of research may provide an improved foundation for the quantitative evaluation of ecological resilience.

Key words: abundance; community ecology; cross-scale resilience; functional diversity; macroecology; resilience; scales.

Introduction

Throughout history, humans have observed the natural world and noted what species are present and in what numbers (e.g., Aristotle's History of Animals circa fourth century BCE). Such basic knowledge remains integral to the most advanced current natural science theories. One such theory arises from complex systems science, which is focused on the dynamics, behaviors, and properties of systems. Resilience theory argues that the resilience of ecological and other complex systems emerges from a suite of attributes that allow the system to absorb and adapt to disturbances in a way that promotes the long-term persistence of the system in a recognizable configuration of structure and function (Holling 1973). This is analogous to remaining in a regime or on an attractor (Scheffer and Carpenter 2003, Folke et al. 2004).

One of the core attributes that drives resilience is the distribution of species' functional traits within and across the spatial and temporal scales of the system, as a resilient distribution balances the tension between diversity and redundancy that is common across evolved systems (Peterson et al. 1998, Hillebrand et al. 2008, Page 2010). This attribute is captured in the cross-scale resilience model, which argues that ecological resilience is generated by diverse but overlapping function within a scale, and redundancy in function distributed across the scales of the system (Peterson et al. 1998). Species perform many ecological functions that contribute to system maintenance and processes; these include nutrient cycling, soil formation, primary production, pollination, and more. Recent research has made it clear that system persistence and stability is strongly dependent on functional diversity, as represented by the differing roles species play (Hooper et al. 2005, Petchey and Gaston 2006, Hillebrand and Matthiessen 2009). Diversity, however, can occur at the expense of redundancy; high diversity means fewer species overlap in their functional traits thus the loss of any one species can mean a loss of that functionality

(Mouillot et al. 2013, 2014). Redundancy, in the form of multiple species with similar functional roles, provides critical functional reinforcement. Resilience emerges, in part, from the balance of functional diversity and functional redundancy within and across the scales of ecosystems (Peterson et al. 1998).

The cross-scale resilience model links the mechanisms governing how individual species self-organize and the emergence of the ecosystem-level property of resilience (Peterson et al. 1998). However, although the model accounts for which species are present, the scales at which they operate, and the functional roles species play, it does not address the numbers in which they are present. Metrics like abundance, biomass, and energetics inform us about how much resource is present, and therefore, how much specified function is provided, which is currently missing from the cross-scale resilience model. Incorporating abundance into the cross-scale model is not straightforward. It is not certain what configuration of cross-scale abundance would provide the most relative resilience to disturbances, because compensation processes, when broadly defined, can include negative covariation as a result of competitive release, positive facilitation, and intraspecies behavioral plasticity.

Our purpose was to detail the ways in which we would expect abundance to be relevant to the cross-scale resilience model based on research on species' abundance that has occurred elsewhere in ecology. To improve our ability to anticipate and quantify how resilience is generated and how ecosystems may (or may not) buffer recent rapid global changes (Milly et al. 2008), we offer a series of testable hypotheses. These hypotheses provide an explicit research agenda that bridges the gap between the mechanisms driving species' abundances with the emergence of system-level ecological resilience.

BACKGROUND AND RESEARCH MOTIVATION

Holling (1973) changed the trajectory of ecology when he proposed that ecological resilience "is a measure of the persistence of systems and of their ability to absorb change and disturbance and still maintain the same relationships between populations or state variables" and contrasted it to engineering resilience, which focuses on "stability near an equilibrium steady state, where resistance to disturbance and speed of return to equilibrium are measured" (Holling 1996). In effect, he proposed a new paradigm for ecosystem dynamics that described ecosystems as complex adaptive systems with thresholds, emergent phenomena at larger scales that cannot be predicted from aggregating knowledge at smaller scales, and non-equilibrium dynamics with multiple alternative stable states. This perspective was in contrast to prevailing views of ecosystems as having linear, predictable dynamics, and a single fixed equilibrium state. Resilience sensu Holling provides a way to conceptualize, measure, quantify, and manage the vulnerability of complex adaptive systems.

As part of his theory of ecological resilience, Holling and colleagues presented a framework to capture both the cycles of change that occur in ecosystems, and the different spatial and temporal scales at which these cycles operate (Gunderson and Holling 2002). The Textural Discontinuity Hypothesis

(Holling 1992), hereafter referred to as the discontinuity hypothesis, was developed to test a basic proposition about the scales of cycling dynamics (C. S. Holling, *personal communication*). It states that the key processes that structure ecosystems occur at distinct and limited ranges of spatial and temporal scales, thus scaling ecological structure into scale domains. The species interacting with this scaled structure are more likely to persist if they have body masses that allow them to take advantage of the available scale domains of resource opportunity, as body mass is allometric with many life history and behavioral traits (Peters 1983). The transition from one scale domain of process and structure to another is nonlinear, creating discontinuities in both ecological structure and animal body mass distributions. These discontinuities exist where there is either extreme variability in structuring processes or no persistent structuring processes. In short, the scale domains identified by analyzing distributions of animal body masses and ecological structure for discontinuities reveal the hierarchical structure of pattern and process that is the ecological theater upon which individual, population, and community interactions play out (Gunderson and Holling 2002). Discontinuities found in both organism body mass distributions and in ecological structure have since confirmed these ideas (Thibault et al. 2011, Nash et al. 2014a, b, Raffaelli et al. 2015, Spanbauer et al. 2016), as has work on scaling and body mass in other disciplines (Haskell et al. 2002, Fisher et al. 2011, Hatton et al. 2015).

The cross-scale resilience model (Peterson et al. 1998) bridged resilience theory and the discontinuity hypothesis and captured four elements that were the essence of Holling's original argument for ecological resilience. These are as follows: (1) ecosystems are spatially and temporally multi-scaled, discontinuous, and hierarchical; (2) ecosystems may have multiple alternative states in which they can exist under the same environmental conditions; (3) resilience is an emergent phenomenon and, as such, results from the interactions of individuals; and (4) the persistence of relationships, processes, and functions is more important for resilience than stability or stationarity in either species presence or abundance. The model specifically proposes that ecological resilience emerges from the diversity of overlapping functions within a scale domain, and the redundancy of functions across the scale domains, as this is most likely to buffer system-level properties against disturbances that occur at particular scales within the system (Fig. 1). Wohlleben (2016), for example, describes the reproductive strategy of Central European deciduous trees that produce large seeds coveted by mice, squirrels, and jays for their high oil and starch content (oaks, chestnuts, and beeches). Mice often bury their seed stores at the base of the trunk from which they gathered the seeds or within 10 m of the tree, while squirrels do so up to 100 m from the tree, and jays will transport the seeds up to 5 km away. Because the seeds are most successful when growing in the shade of their mature counterparts, this overlapping function by seed dispersers across spatial scales provides resilience to the tree community because disturbance at one spatial scale leading to the loss of a seed disperser can be compensated for by seed dispersers operating at other scales.

The cross-scale model was seminal because it provided a metric of resilience that captured critical system features
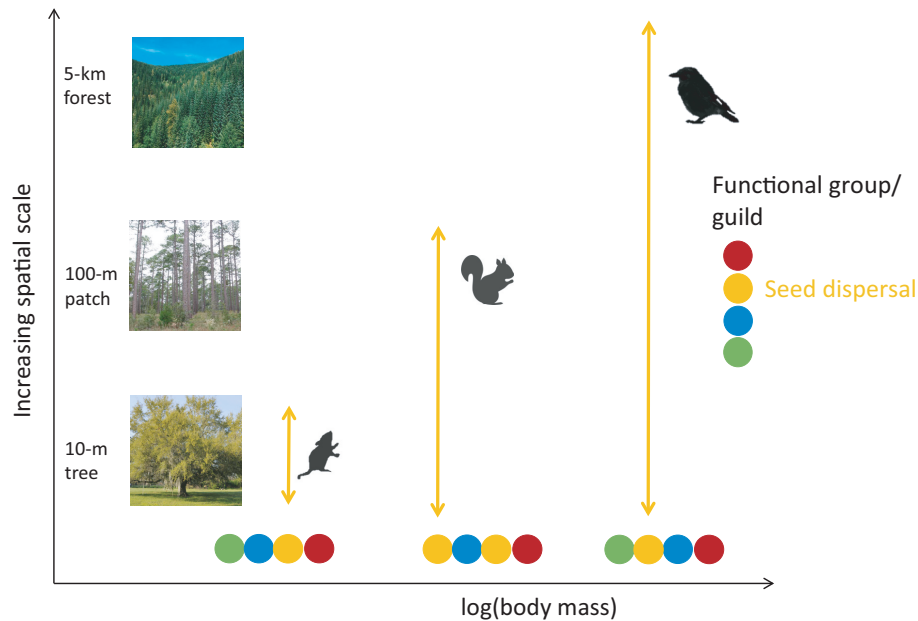
Fig. 1. Resilience emerges from an overlapping diversity of functions within a body mass aggregation and a redundancy of functions across body mass aggregations. Species within a body mass aggregation interact with their environment at similar spatial and temporal scales. In this stylized example, seed dispersal is performed by three species that operate at distinct spatial scales: a mouse, a squirrel, and a jay. Adapted from Holling (1992) and Wohlleben (2016).

that had been neglected by the traditional ecological literature and provided a much-needed mechanism to address the provisioning of resilience (Oliver et al. 2015). The model evaluated species presence not in terms of species richness but in terms of the functional composition represented by the community (number of different functions and number of species representing a given function). Functional composition has subsequently been shown to be more critical to system-level features like primary productivity and persistence within a regime than species diversity (Rudolf and Rasmussen 2013, Soliveres et al. 2016). Additionally, the model explicitly incorporated an objective evaluation of the scales at which process and pattern unfold, something long argued as paramount to any robust understanding of ecosystem dynamics and behavior (O'Neill et al. 1986, Wiens 1989, Levin 1992). However, what is currently missing from the model is an understanding of the importance of the *abundance* of organisms and their functional traits with regard to how they are distributed within and across the scales of an ecosystem. If the cross-scale hypothesis is accurate, the resilience of ecosystems is dependent (in part) on the distribution of these functional traits within and across scales. As the function is imparted by species that are themselves unevenly distributed within and across scales, what is the effect of fluctuating organism abundance on ecosystem function and thereby resilience?

The cross-scale resilience model has assumed that the primary mechanism by which the cross-scale distribution of species' functions copes with disturbance is via changes in the abundance of species within the same functional group as a result of either compensatory dynamics or differential responses to environmental drivers (response diversity). Despite the critical role response diversity is presumed to play in mediating cross-scale resilience, there have been few

tests of this assumption (though see Angeler et al. 2013, 2014, 2015). The case for response diversity was made in the original cross-scale resilience paper (Peterson et al. 1998), but validations of its importance have been generic in the sense that they have confirmed that response diversity facilitates the coexistence of species and maintenance of ecosystem properties (Elmqvist et al. 2003, Baskett et al. 2014, Scranton and Vasseur 2016, Wieczynski and Vasseur 2016), as opposed to determining whether the distribution of species with different responses to disturbances within and across system scales is non-random and contributes to or diminishes system resilience (though see Nash et al. 2015). Adding response diversity to a cross-scale resilience assessment is conceptually straightforward but in practice difficult due to the lack of necessary species-specific knowledge (Lefcheck et al. 2015). The primary aim of this paper was to clarify and expand our understanding of resilience by discussing the relevance of species' abundances to the cross-scale resilience model, and in the process generate a series of testable hypotheses. In doing so, it is necessary to touch on response diversity and the role it likely plays in mediating the effectiveness of various distributions of cross-scale function and abundance.

OVERVIEW OF ABUNDANCE AND THE CROSS-SCALE RESILIENCE MODEL

According to the cross-scale resilience model, species within a functional group will be distributed non-randomly across the scale domains of a system such that interspecific competition is reduced because species that forage and use ecological resources in a similar way will be separated by the scales at which they do so as they have distinctly different body sizes (Peterson et al. 1998, Greenfield et al. 2016). Niche

compartmentalization by size has been demonstrated by several ecological theories (Vergnon et al. 2012, Rudolf and Rasmussen 2013, Scheffer et al. 2015), but they do not explain how abundance among species will be distributed within a functional group or at specific scales. Both phylogeny and broader abiotic factors constrain the number of scale domains at which a functional group can occur. For example, in a North American dry mixed grassland, aerial insectivores tend to occur at smaller size classes (scale domains) than do aerial carnivores. The largest aerial insectivore is the Common Nighthawk (*Chordeiles minor*) at 76 g, whereas the largest aerial carnivore is the Golden Eagle (*Aquila chrysaetoes*) at ~4 kg (Sundstrom et al. 2012); in other words, not all functions occur within all body size classes.

The ecological literature is filled with research on the spatial distribution of abundance and the role of abundance in ecosystem processes and stability. Some basic tenets have emerged from this work, including the following: there are few common species and many rare (Gaston and Fuller 2007, Connolly et al. 2014); there are more small species than large species (Damuth 1981); species' abundances are typically unevenly distributed within their geographic range (Maurer 2009); and species with a high abundance/biomass have large effects on ecosystem processes (Suding et al. 2008, Petchey and Gaston 2009, Stuart-Smith et al. 2013) although rare species can also contribute to the maintenance of system-level processes (Mouillot et al. 2013). These tenets shape our expectations for the patterns of abundance and function within the context of the cross-scale resilience model.

In the following sections, we discuss four interrelated concepts at the heart of this inquiry. For each concept, we summarize the key findings from the ecological literature, discuss how each concept pertains to the cross-scale model, and generate a prediction for how that concept may operate mechanistically within the context of cross-scale resilience. The concepts are the relationship between abundance, body size, and functional traits; the role of compensation in mediating abundance and functional traits; the relationship between abundance, energetics, and biomass; and the relationship between abundance and system-level regime shifts, or movement to another basin of attraction defined by different processes, structures, and functions.

Abundance distributions, body size, and functional traits

Prior research on patterns between body size, abundance, and functional traits/guilds suggests that abundance distributions within and across scales will be skewed; specifically, the most abundant species will be in different functional groups and will also have distinctly different body sizes (Fig. 2; Damuth 1981, Petchey and Gaston 2006, Vergnon et al. 2009, Magurran and Henderson 2012). Species with similar body sizes use resources at similar spatial and temporal scales, but competition is reduced by utilizing different resources (Rudolf and Rasmussen 2013). Vergnon et al. (2009) found that the most abundant phytoplankton species were far apart in terms of body size (the scale domain at which they operated), suggesting that strong interspecific competition prevents similarly sized species from attaining high abundances. Functional diversity within a scale domain is both more diverse than expected by chance and robust to

community change (Forys and Allen 2002, Sundstrom et al. 2012), meaning that species that have a similar size are more diverse in their functions than is expected by chance; even with species turnover, that diversity of function among similarly sized species is retained (Forys and Allen 2002). However, rare species tend to be more vulnerable to extinction due to their small population sizes (Davies et al. 2000, Gaston and Fuller 2007, Rohr et al. 2016, though see Sundstrom and Allen 2014), which suggests that generally, a more even distribution of abundance across species would reduce extinction risk and increase resilience (Rohr et al. 2016) because the loss of function represented by a loss of a species would be lessened.

However, it is possible that response diversity may be more relevant than evenness of abundance. Consider a situation where response diversity is high, but abundance is strongly skewed. As long as less abundant species have a differential capacity to cope with a disturbance and can maintain or increase their abundance in response to a disturbance, then they can compensate and provide critical function until the dominant (with regard to abundance) species rebound. If all species that share a similar functional role or operate at similar spatial and temporal scales have the same response to a disturbance, then that functional role or functionality at that particular scale domain will be effectively eliminated unless populations rebound. Therefore, within the context of the cross-scale model, either relative evenness coupled with low response diversity or relatively high skewness coupled with high response diversity could result in resilient distributions of abundance. Unfortunately, there is a lack of data on the differing response thresholds of species to disturbances that limits researchers from incorporating response diversity into general modelling efforts (Lefcheck et al. 2015).

Researchers investigating abundance skewness have made a strong case that common or dominant species provide the bulk of ecological function, while other researchers have shown that rare species provide unique functions that are also critical, especially as insurance against particular disturbances (Ellingsen et al. 2007, Gaston 2010, Mouillot et al. 2013, Inger et al. 2015). Claims that high species evenness is a feature of undisturbed natural communities go back to Odum (1969) but were poorly substantiated at the time. More recent theoretical and empirical work argues that dominance vs. evenness is a function of how niche space is partitioned; dominance is associated with homogenous and low dimensional resource structure found in disturbed biotas, whereas evenness is associated with more diverse and complex resource structure found in undisturbed biotas (Sugihara and Bersier 2003, Hurlbert 2004, Rohr et al. 2016). As most real communities are dominated by a few common species (Dangles and Malmqvist 2004, McGill et al. 2007, Connolly et al. 2014, Winfree et al. 2015), this suggests that the debate is perhaps moot. However, changes in the degree of dominance/evenness may be an important indicator of changing system resilience (O'Gorman et al. 2012).

Given the general patterns in body size, abundance, and functional groups just discussed, our expectation regarding general abundance patterns within and across functional groups and system scale domains is that the most abundant species will belong to different functional groups and will

operate at different spatial and temporal scales (Fig. 2; Hypothesis 1) (Walker et al. 1999, Sugihara and Bersier 2003, Vergnon et al. 2009, 2012, Magurran and Henderson 2012). We also expect that the degree of skewness in both abundance within a functional group and abundance within a particular scale domain will differ among systems based on the innate degree of species and functional richness of the system and the degree of anthropogenic degradation it has experienced (Hypothesis 2). Systems with more habitat complexity that experience less anthropogenic disturbance will have less dominance and more evenness than their simpler or more highly disturbed counterparts. Testing these patterns across multiple data sets as well as comparing systems with different patterns of heterogeneity and human disturbance would be informative. We argue that if degree of dominance (skewness in abundance) primarily reflects the diversity and complexity of niche space as per Sugihara and Bersier (2003), then changes in dominance/evenness will signal changes to the underlying resource template.

Finally, there are two other aspects of abundance to consider: expectations regarding the shape of the distribution of abundance within a scale domain, and the role of variability in abundance as it relates to resilience. Recall that the species within a particular scale domain are similarly but not identically sized. Thus, if we plot their abundance and retain their size ranking, we would expect their distribution to be unimodal with the mode near the middle of the distribution (Fig. 3). This is different than plotting abundance against body size because it conserves their location in the scale

domain relative to each other's body mass, as well as their distance from a discontinuity. We expect species within a scale domain to have peak abundance near the middle of the distribution (Hypothesis 3) because evidence suggests resources in the center of a scale domain are more stable over space and time, whereas the edges or discontinuities are areas of high spatial and temporal variability (Allen et al. 1999, Allen and Saunders 2002, Sundstrom and Allen 2014). Stable resources should sustain greater abundances relative to resources that are highly variable in space and time (Wardwell and Allen 2009). Although it is also possible that there will be higher abundance at the edges of the scale domains or that abundance will be uniform, there is less biological basis for either of these possibilities (Fig. 3).

As for the role of variability as it relates to resilience, variability in the spatial and temporal dimensions of resource structure is also associated with variability in abundance. Evidence from the Everglades has shown that species whose body masses place them close to a discontinuity experience higher variability in their abundance (in both space and time) than species located near the center of a scale domain, and this is believed to be related to the increased variability in resources at discontinuities (Wardwell and Allen 2009). Furthermore, Vergnon et al. (2012) found that within a scale domain, species closer to the discontinuities had lower abundance than species in the center. Variance in abundance is a typical early warning indicator of a regime shift (Carpenter and Brock 2006). We predict that variance in total abundance of a functional group may be an early warning signal
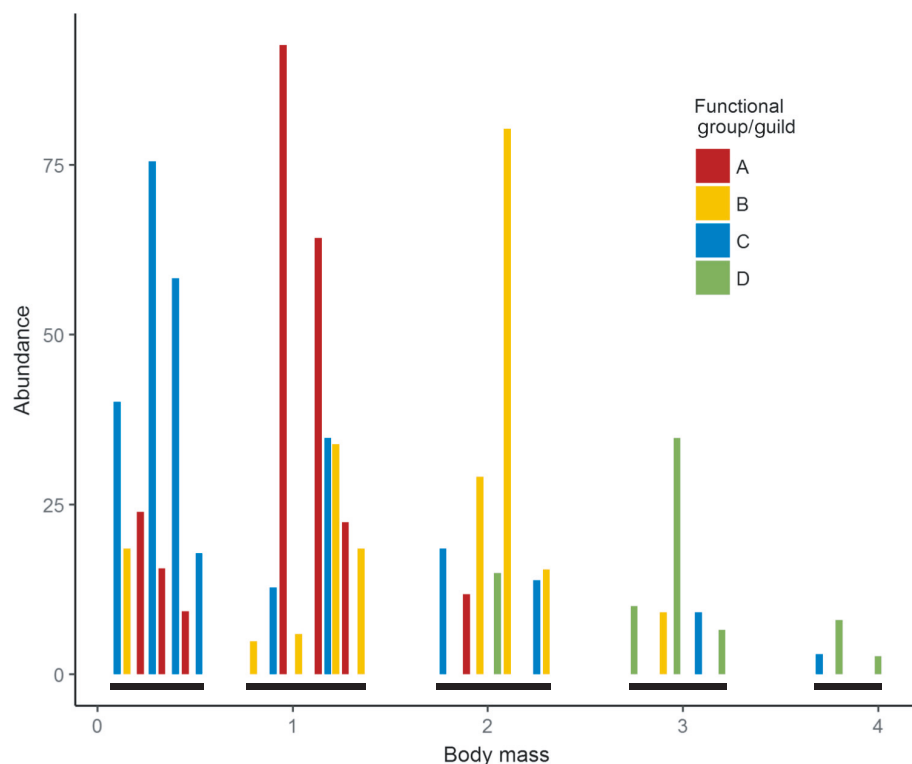

Fig. 2. Prediction for the distribution of abundance within functional groups and across scale domains. Clusters of similarly sized species (black polygons on bottom of x-axis; x-axis is a continuous scale of log[body mass]) interact with their environment at similar spatial and temporal scales, so experience the strongest direct competition. The most abundant species belong to different functional groups or guilds (A–D) and occur at different spatial and temporal scales.
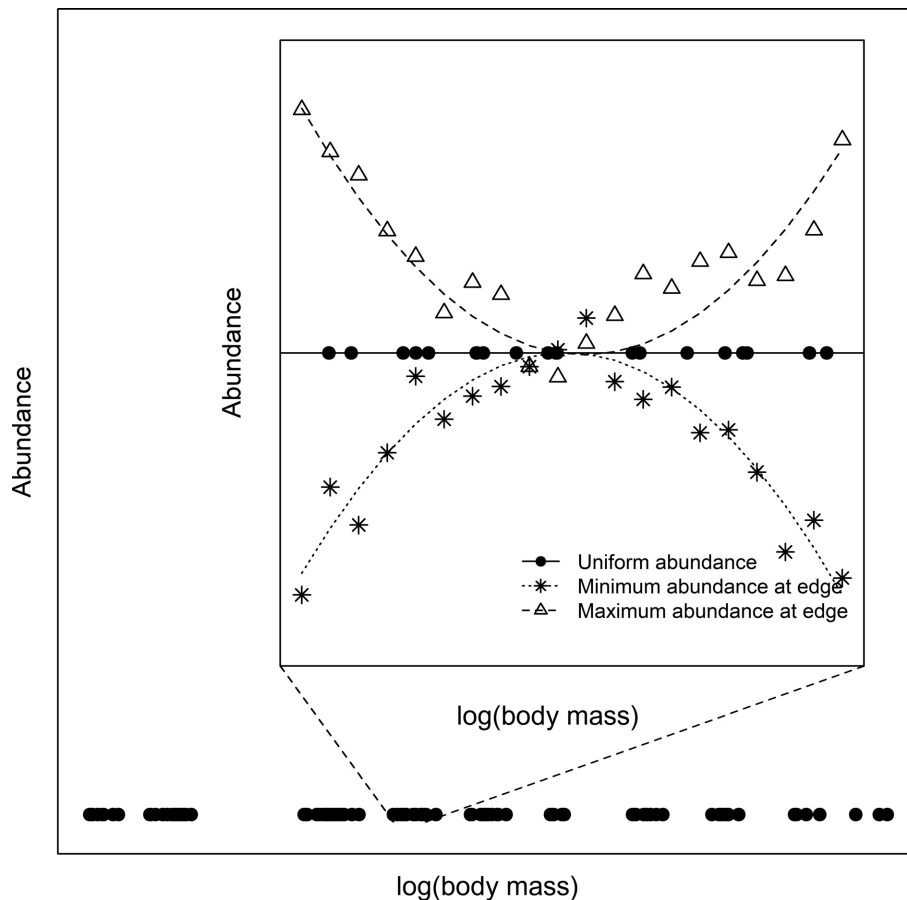
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FIG. 3. Testable hypotheses regarding how species abundances are distributed within one body mass aggregation. Clusters of similarly sized species along the *x*-axis are represented by filled circles. Clusters are separated by discontinuities where no species fall. Inset graph depicts three hypotheses for how abundance within a cluster might be distributed: species with maximum abundance occur at the edges of the body mass cluster (open triangles); maximum abundance occurs in the center of the body mass cluster (asterisks); and abundance is uniformly distributed across species in the body mass cluster (closed circles).

of a regime shift because it accounts for changes in abundance from compensatory processes and provides a signal of changes to the underlying resource template and resilience (Hypothesis 4). Temporal data would be necessary to understand the natural range of variation present in both species abundances and system-level provision of functionality.

The role of compensation in mediating cross-scale resilience and abundance

Compensation or functional redundancy can occur via several pathways, ranging from classic compensatory dynamics such as density dependence and negative covariation via competitive release, as well as positive facilitation, differential response diversity, and synchrony, or positive covariance (good times for one is good times for all; Houlahan et al. 2007, Thrush et al. 2008, Gonzalez and Loreau 2009). There is no consensus in the literature as to the relative prevalence or importance of these different mechanisms, or the degree to which compensation is even likely. Most biodiversity–function models, including the cross-scale resilience model, assume that species in the same functional group will provide functional redundancy in the event that a disturbance reduces abundance of individuals within the

functional group. This is strongly supported by the work of Soliveres et al. (2016), which shows that there is little overlap (~30%) among different functional groups; in other words, different functional groups provide different services. Work in experimental grassland communities also suggests that compensation is more likely to occur by species in the same functional group (Roscher et al. 2011). Therefore, we expect that functional compensation would first occur via species in the same functional group operating at the same scale domain, if there are any, and then by species operating at nearby scale domains, and this compensation would be reflected in either increases in abundance, behavioral plasticity, or both (Hypothesis 5).

This expectation is driven by the simple fact that resource utilization is scaled to body size. While a moose and a mouse may forage on similar resources, a mouse may perceive something as a resource that is not discernible to a moose. Species in the same functional group that operate at similar spatial and temporal scales are most likely to provide compensatory functionality. In long-term rodent community data, Ernest et al. (2008) found that when the largest granivore, kangaroo rats (*Dipodomys* spp.), were experimentally removed from plots, smaller species in the same functional group increased in abundance but only utilized 14% of the

energy made available. It was not until a new species of similar size to the kangaroo rat colonized 18 yr later that those resources were once again used at a rate comparable to when the kangaroo rat was present. There are, however, two important limitations with regard to the capacity of a community to show compensation (Kremen 2005, Davies et al. 2012). The first is that the substitutability of species is imperfect and may be especially limited when quantifying the *amount* of function. It is not clear how to account for the spatial and temporal extent at which a large, but far less abundant species performs its functional roles, as opposed to the much smaller spatial and temporal extent of more abundant species. For example, scraping function (i.e., the removal of algae and opening up bare substratum for coral larval settlement) has a non-linear relationship with body mass in herbivorous coral reef fishes (Lokrantz et al. 2008), so the loss of a larger herbivorous scraper likely has a disproportionate effect on the provision of that function (Nash and Graham 2016).

These are particularly difficult questions to answer when different species are providing the functional compensation and therefore are not only potentially operating at a different scale domain but also have imperfect redundancy in functionality as no species can be an exact replacement for another. Second, species in the same functional group may not be able to provide compensatory function if they are prevented from colonizing due to dispersal limitation or habitat fragmentation (as in the dispersal limitations in the rodent example) or if they have the same response to the disturbance. Given that resilience is often assessed at the ecosystem level, it is reasonable to expect that the reduction in functions resulting from localized extinctions or disturbances within that system may remain uncompensated if other species within that functional group cannot overcome barriers to dispersal. Although testing data from different systems to assess patterns is necessary, comparing abundance distributions within a functional group between degraded and undegraded habitats would also be valuable.

Despite the limitations on compensation discussed, we also expect that even the small amount (~30%) of overlap in function between functional groups documented by Soliveres et al. (2016) in their assessment of 150 grasslands, would, if typical of other ecosystems, provide a resilient balance between direct competition amongst species operating at the same spatial and temporal scales, and redundancy, or insurance against disturbances, as predicted in the original cross-scale model (Peterson et al. 1998). Both trait overlap and behavioral plasticity could provide secondary compensatory function (Chong-Seng et al. 2014, Nash et al. 2016). Measuring changes in abundance over time would allow us to test whether functional compensation occurred first via species in the same functional group operating at the same scale domain. Compensation occurring from changes in behavior as a result of trait overlap or behavioral plasticity would be more difficult to track and would require energetics analyses such as Ernest et al. (2008), or foraging behavior studies such as Nash et al. (2012). Plasticity in foraging behavior may also eventually manifest in morphological change to traits like body size; despite widespread beliefs that body size is conservative there are examples of rapid evolutionary change in body size and other morphological traits (White et al. 2004, Ozgul et al. 2010, Brown and Bomberger Brown 2013).

The importance of response diversity (Elmqvist et al. 2003), positive covariance, and positive facilitation should not be neglected, as they operate independently of competitive release, and may be more important than previously understood (Bruno et al. 2003, Houlahan et al. 2007, Thrush et al. 2008, Werner et al. 2014). The contradictory evidence in the literature with regard to the relative importance and frequency of competitive release vs. positive facilitation, degree of response diversity, or positive covariance suggests that the strength of their roles is likely to differ from one context to another, making generalized predictions difficult. Nonetheless, we predict that a reduction in abundance of one member of a functional group is most likely to be compensated for by a similarly sized species within the same functional group, regardless of whether it is due to competitive release or response diversity (Hypothesis 5).

Abundance vs. biomass and energetics

Discontinuities in body size distributions and ecological structure tell us about the scales at which resources and species are present, and functional classifications inform us about the roles species play, but abundance, biomass, and energetics inform us about how much resource is present, or how much function is provided (i.e., area of reef scraped by herbivorous fishes, or amount of carbon stored by soil microorganisms). White et al. (2007) describe abundance, biomass, and energetics as alternative currencies that do not always show the same pattern, so metric selection for use in a cross-scale assessment will depend on the research question. Each metric captures only a piece of the puzzle of resource partitioning. Classifying species by functional roles often resorts to trophic levels and thus indirectly assumes that who eats what is the most critical functional contribution. Similarly, energetics quantifies how much energy an individual or species consumes, but tells us little about the provision of other functions. Abundance and biomass both speak to amount of function in the sense that either more individuals or more biomass of individuals will theoretically translate into more function provided. However, abundance does not incorporate differences in how the rate or amount of function provided by an individual scales to body size, a relationship that is unlikely to be linear or static. If the goal is to understand how changes in the distribution of species and the functions they provide within and across scales drives system-level resilience, it may be that quantifying total functional biomass at scales (i.e., area of reef scraped/ mass of herbivorous fish) is more informative than total functional abundance. However, tracking variance in amount of function provided within a functional group will in some circumstances likely require energetics, as functions such as carnivory require understanding the various consumption rates of carnivores of differing sizes.

Biomass in a size class or age class, rather than abundance, is commonly used in aquatic research (White et al. 2007). Magurran and Henderson (2012) argue that biomass within functional groups explained processes structuring an estuarine community more clearly than numerical abundance. Biomass may also be meaningful for terrestrial systems when trying to

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quantify, compare, and weigh functional contribution by differently sized species operating at different scale domains. However, it is possible that abundance and biomass in terrestrial systems express the same general pattern over time, as robust evidence suggests that these patterns are highly conserved at the ecosystem scale, even while component populations can vary widely (Ernest and Brown 2001, Hatton et al. 2015). Regardless of which metric is used, we expect that, in a resilient system, total amount of function provided by a functional group should exhibit no net direction over time as a result of response diversity to environmental drivers (Houlahan et al. 2007, Thrush et al. 2008) and/or compensatory responses (Hypothesis 6; Gonzalez and Loreau 2009). This expectation assumes that the system remains within a regime (basin of attraction) and that all species in a functional group do not have the same response to environmental disturbance (Fischer et al. 2001, Elmqvist et al. 2003). We propose testing this hypothesis with both abundance and biomass. Declining trends in total biomass within a functional group (total functional abundance) would be a predictor of declining resilience as it would indicate a reduced ability to compensate (Gonzalez and Loreau 2009). Directional trends in the total biomass within a scale domain would indicate changes to the underlying resource template and thus a possible regime shift (Dossena et al. 2012, O'Gorman et al. 2012).

The relationship between abundance and a system-level regime shift

Species' abundances can vary with time in response to local, regional, and climate-driven processes. For example, in response to climate-driven drought, chorus frog (*Pseudacris triseriata*) abundance waxed and waned, transforming from rare and narrowly distributed to abundant and widely distributed, and then back again, due to their species-specific response to the climate disturbance (Werner et al. 2014). Only sufficient temporal data can detangle whether such transitions are indicative of a directional change in chorus frog abundance indicative of fundamental changes to key system processes and the underlying spatial and temporal scales of ecological structure, or if the changes fluctuated within a normal range of variation. Without monitoring data that include other species within the community, it can also be difficult to assess whether directional changes within one species are compensated by other species, or indicate a directional change to the underlying resource template indicative of a regime shift. As an example, the long-term rodent community work by White et al. (2004) showed abundance shifting down the body mass axis, moving from larger rodents to smaller rodents. To further complicate things, they found that four of the nine species actually increased in average body size over time. The landscape was transitioning from a grass-dominated regime to a shrub-dominated regime, driving the aforementioned shifts within the rodent community. The scales at which resources were available were shifting, and this was reflected in both intraspecies plasticity (adjusting body size) and a shift in the location of abundance for granivorous rodents along the body size axis.

In a classic freshwater example, Carpenter et al. (1985) demonstrated how trophic cascades can shift biomass both across trophic levels and along a body mass axis; an increase in piscivore biomass drove reduced planktivore biomass, increased herbivore biomass, and decreased phytoplankton biomass. The dynamic biomass shift across trophic levels demarcates the changing scales at which resources are available. Furthermore, community composition in a presence/absence sense may not change at all, even while changes in the key processes structuring the system have changed the amount of biomass at particular trophic levels and spatial and temporal scales. Two highly conservative features of trophic communities, which can be understood as functional groups, are particularly relevant here. Hatton et al. (2015) found that both aquatic and terrestrial trophic communities maintain a near constant size structure, in that the mean body mass for a trophic community (total biomass in community divided by total numerical density, giving mean body mass) is constant for both predator and prey communities. In other words, the carnivore to herbivore body mass ratio is constant, though the biomass ratio fits a power law, so that as the biomass of prey increases, the biomass of predators increases more slowly. This makes sense in the context of the discontinuity hypothesis and cross-scale resilience model, which propose that body mass is most directly related to the scales at which resources are available, while biomass reflects the amount of resources available. Furthermore, the constancy of the carnivore to herbivore body mass ratio suggests strong compensatory dynamics, as the amount of prey fit the expectations of the body mass ratio despite variable abundances of species within the functional group (Hatton et al. 2015). Given the robustness of this body mass ratio, a directional change in the total amount of biomass may indicate a regime shift, and the scales at which biomass is lost or gained will provide clues about the drivers of that shift. Others have also shown that patterns of abundance over time at the system level are stable relative to individual population abundances (Ernest and Brown 2001, Ernest et al. 2008). We predict that this general relationship wherein variability within population abundances is higher than variability in system-level provisioning such as total amount of biomass or aggregate energy use should hold unless a regime shift is close, in which case variability in system-level properties should increase (Hypothesis 7). An impending regime shift should be preceded by either a change in the scales at which abundance and/or biomass are allocated, or a directional change in the overall biomass within a functional group. Discriminating between abundance changes resulting from stochastic disturbance that may be buffered or compensated by other species, and bottom-up changes to the resource template will be critical.

PUTTING THEORY INTO PRACTICE

A cross-scale resilience assessment begins with a discontinuity analysis as a means of objectively identifying the scale domains within a given system and serves as the foundation for understanding how species, and therefore their functional roles and abundance, are distributed within and across system scales. The details of performing a discontinuity analysis are documented elsewhere (Peterson et al. 1998, Allen and Holling 2008, Nash et al. 2014*a*) so will not be described here. Typically, discontinuities are identified in rank-ordered data sorted by taxon, so birds, for example,

have been evaluated separately from mammals. However, Holling (1992) showed that bird and mammal discontinuity patterns are correlated as they utilize resources as a function of their size irrespective of taxonomy, so community analyses are theoretically possible. The next step is to classify species into functional groups that are biologically reasonable given the taxon and system under question, and then to analyze how function is distributed within and across scales. Our objective was to articulate general expectations regarding how abundance, as another layer of information about the structure of the system, would be distributed within and across system scales, and how we would expect this to relate to compensatory processes and therefore resilience. In the following subsections, we summarize the major hypotheses/expectations we presented (see Table 1 for complete list).

Dominance or degree of skewness

It is well established that abundance is generally skewed, in that there are a few dominant species with high abundance and many species with low abundance. We expect that abundance will also be skewed both within a functional group (Fig. 2) and within an individual scale domain (Fig. 3), and furthermore, that the most abundant species will belong to different functional groups and will occur at different scale domains (Fig. 2). Others have argued that degree of skewness speaks to the degree to which an ecosystem has been disturbed, disrupted, or homogenized (Odum 1969, Sugihara and Bersier 2003). Regardless of the current degree of skewness in a given system and what it reflects about system heterogeneity/homogeneity, we expect that any persistent directional change to the degree of skewness may be an early warning signal of a regime shift, because such a change will reflect a change to the underlying resource template.

Compensation/response diversity

Resilience as per the cross-scale model is predicated on the assumption that if there is the loss or reduction in abundance of a dominant species, their functional role will be compensated for by other species in that functional group who either experience competitive release, or have a different response diversity than the afflicted dominant species. We expect that in that event, compensation will first occur via species in the same functional group and from the same scale domain (body size class), and then from species operating at nearby scale domains. Furthermore, we know that system-level stability in the provision of a function can be maintained despite (or because of) substantial variance in the abundance of the individual species comprising a functional group (Ernest and Brown 2001, Ernest et al. 2008), so we also expect that an increase in the variance in abundance of an entire functional group is likely to be more relevant than the total amount of abundance within a functional group. Increased variance suggests a reduction in compensatory or response diversity processes and may be an early warning signal of a regime shift.

Outlook

We have proposed general predictive hypotheses for the role abundance may play in cross-scale resilience. However, as the adage goes, the devil is in the details, and the role of abundance may be as complicated as our understanding of abundance in other ecological relationships. Although we expect that there are broad and general patterns regarding the distribution of abundance and the mechanisms by which abundance mediates ecological resilience, there is also the possibility that other factors outweigh the contribution of

TABLE 1. Primary testable hypotheses regarding patterns of abundance or biomass and how they relate to ecosystem resilience.

Hypothesis	Concept	General prediction	Indicator of resilience
1	distribution of abundance	The most abundant species will belong to different functional groups and will operate at different spatial and temporal scales.	More evenness and less dominance indicate lower levels of disturbance and higher habitat complexity.
2	distribution of abundance	The degree of skewness in abundance within a functional group and within a scale domain will differ among systems based on the system's innate degree of species and functional richness and the degree of anthropogenic disturbance it has experienced.	Changes in the degree of skewness will indicate changes to resilience.
3	distribution of abundance	Species' abundances within a scale domain will be unimodal and highest near the center of the scale domain because resources are more stable over space and time.	Increasing variance in abundance of species near the center of a scale domain will provide an early warning indicator of a regime shift.
4	regime shift	Variance in abundance of a functional group may be an early warning indicator of a regime shift.	Increasing variance suggests changes to the underlying resource template and resilience.
5	compensation	Functional compensation will first occur via species in the same functional group operating at the same scale domain if present, and then by species operating at nearby scale domains.	Degree of compensatory processes available within the system will be strongly mediated by response diversity and will be an indicator of resilience.
6	regime shift	The total amount of function provided by a functional group should exhibit no net directional change over time due to response diversity and other compensatory processes.	Net directional change will indicate changes to underlying resource template and system-level resilience and thus a possible regime shift.
7	regime shift	Variability of abundance within a population should be higher than variability in system-level properties.	Increased variance in system-level properties will be an early warning indicator of a regime shift.

abundance to resilience. First, abundance per se may be less important than species functional richness. We know that rare and seemingly redundant species play a critical role in the persistence of resilience and stability because they are a functional "reserve" that comes into play when disturbances impact key species. Species can also be rare and perform a key function, despite having a low abundance. Their abundance is less relevant than their presence. The importance of abundance, then, may be restricted to species that play a role in key feedback loops or keystone processes, or the few highly common species that provide the majority of function (Gaston 2008, 2010). For example, in the classic spruce-budworm example (Ludwig et al. 1978), budworms were controlled by insectivorous birds in the young, growing forest. Qualitative analysis indicated that if other factors controlling budworm outbreak were held constant, bird populations would have to be reduced by two-thirds before there would be a qualitative change in budworm–forest dynamics (Holling 1988).

Second, sampling methods and statistical issues may impede our ability to quantify the impact of abundance. Methods that assume spatial or temporal stationarity are not appropriate, as directional changes in abundance resulting from climate change and other anthropogenic impacts that simplify or homogenize ecosystems are likely. Sampling protocols for abundance must be able to track changes in functional abundance over time, but also account for scales within the system. For example, sampling across the entire system for the abundance of a particular function averages out the body mass aggregations, and only tells us about system-level abundance rather than the cross-scale resilience. Monitoring programs that incorporate species and/or processes that occur at distinct spatial and temporal scales would facilitate tracking change within and across scales. In particular, temporal data, which is always challenging to procure due to changes in funding policies and priorities over time, is essential for understanding system change over time and in time spans that are ecologically relevant.

The creation of the cross-scale resilience model was novel, bold, and elegant. It articulated a simple model with clear testable hypotheses. It is possible to summarize in one sentence the primary conclusion of the model: system-level resilience emerges from the overlapping diversity of functions occurring within a scale domain, and the redundancy of functions spread across the scale domains. For the cross-scale resilience model to more realistically capture the role of species in contributing to system-level resilience, it is necessary to understand not just how function is distributed within and across system scales, but how the distribution of the abundance or volume of function within and across scales impacts resilience. We believe broad-scale and general patterns are likely to emerge from sufficient hypothesis testing and be largely robust to secondary processes complicating the picture, similar to previous research on the cross-scale resilience model (Wardwell et al. 2008, Sundstrom et al. 2012).

The stable provision of functionality at the system level arises from the degree of compensatory function, response diversity, and behavioral plasticity contained within the system, all mechanisms that buffer disturbances but are rooted in variability in species abundances over time. Thus, it is likely that it is directional change in system-level function or

persistent changes in the scale domains at which functional biomass is present that is likely to denote changing resilience or a regime shift. We have articulated some of the primary ways in which abundance may affect the emergence of resilience as represented by the functional roles species provide, as well as a set of testable hypotheses with which to test these ideas. We feel that this stream of research will provide a rigorous foundation for the quantitative evaluation of ecological resilience.

LITERATURE CITED

Allen, C. R., and C. S. Holling, editors. 2008. Discontinuities in ecosystems and other complex systems. Island Press, New York, New York, USA.

Allen, C. R., and D. A. Saunders. 2002. Variability between scales: predictors of nomadism in birds of an Australian Mediterranean-climate ecosystem. Ecosystems 5:348–359.

Allen, C. R., E. A. Forys, and C. S. Holling. 1999. Body mass patterns predict invasions and extinctions in transforming landscapes. Ecosystems 2:114–121.

Angeler, D. G., C. R. Allen, and R. K. Johnson. 2013. Measuring the relative resilience of subarctic lakes to global change: redundancies of functions within and across temporal scales. Journal of Applied Ecology 50:572–584.

Angeler, D. G., C. R. Allen, H. E. Birgé, S. Drakare, B. G. McKie, and R. K. Johnson. 2014. Assessing and managing freshwater ecosystems vulnerable to environmental change. Ambio 43:113–125.

Angeler, D. G., C. R. Allen, D. R. Uden, and R. K. Johnson. 2015. Spatial patterns and functional redundancies in a changing boreal lake landscape. Ecosystems 18:889–902.

Baskett, M. L., N. S. Fabina, and K. Gross. 2014. Response diversity can increase ecological resilience to disturbance in coral reefs. American Naturalist 184:E16–E31.

Brown, C. R., and M. Bomberger Brown. 2013. Where has all the road kill gone? Current Biology 23:R233–R234.

Bruno, J. F., J. J. Stachowicz, and M. D. Bertness. 2003. Inclusion of facilitation into ecological theory. Trends in Ecology & Evolution 18:119–125.

Carpenter, S. R., and W. A. Brock. 2006. Rising variance: a leading indicator of ecological transition. Ecology Letters 9:311–318.

Carpenter, S. R., J. F. Kitchell, and J. R. Hodgson. 1985. Cascading trophic interactions and lake productivity: fish predation and herbivory can regulate lake ecosystems. BioScience 35:634–639.

Chong-Seng, K. M., K. L. Nash, D. R. Bellwood, and N. A. J. Graham. 2014. Macroalgal herbivory on recovering versus degrading coral reefs. Coral Reefs 33:409–419.

Connolly, S. R., et al. 2014. Commonness and rarity in the marine biosphere. Proceedings of the National Academy of Sciences USA 111:8524–8529.

Damuth, J. 1981. Population density and body size in mammals. Nature 290:699–700.

Dangles, O., and B. Malmqvist. 2004. Species richness-decomposition relationships depend on species dominance. Ecology Letters 7:395–402.

Davies, K. F., C. Margules, and J. F. Lawrence. 2000. Which traits of species predict population declines in experimental forest fragments? Ecology 81:1450–1461.

Davies, T. W., S. R. Jenkins, R. Kingham, S. J. Hawkins, and J. G. Hiddink. 2012. Extirpation-resistant species do not always compensate for the decline in ecosystem processes associated with biodiversity loss. Journal of Ecology 100:1475–1481.

Dossena, M., G. Yvon-Durocher, J. Grey, J. M. Montoya, D. M. Perkins, M. Trimmer, and G. Woodward. 2012. Warming alters community size structure and ecosystem functioning. Proceedings of the Royal Society B 279:3011–3019.

Ellingsen, K. E., J. E. Hewitt, and S. F. Thrush. 2007. Rare species, habitat diversity and functional redundancy in marine benthos. Journal of Sea Research 58:291–301.

Elmqvist, T., C. S. Folke, M. Nystrom, G. D. Peterson, J. Bengtsson, B. H. Walker, and J. Norberg. 2003. Response diversity, ecosystem change, and resilience. Frontiers in Ecology and the Environment 1:488–494.

Ernest, S. M., and J. H. Brown. 2001. Homeostasis and compensation: the role of species and resources in ecosystem stability. Ecology 82:2118–2132.

Ernest, S. K. M., J. H. Brown, K. M. Thibault, E. P. White, and J. R. Goheen. 2008. Zero sum, the niche, and metacommunities: long-term dynamics of community assembly. American Naturalist 172:E257–E269.

Fischer, J. M., T. M. Frost, and A. R. Ives. 2001. Compensatory dynamics in zooplankton community responses to acidification: measurement and mechanisms. Ecological Applications 11:1060–1072.

Fisher, J. T., B. Anholt, and J. P. Volpe. 2011. Body mass explains characteristic scales of habitat selection in terrestrial mammals. Ecology and Evolution 1:517–528.

Folke, C. S., S. R. Carpenter, B. H. Walker, M. Scheffer, T. Elmqvist, L. H. Gunderson, and C. S. Holling. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. Annual Review of Ecology, Evolution, and Systematics 35:557–581.

Forys, E. A., and C. R. Allen. 2002. Functional group change within and across scales following invasions and extinctions in the Everglades ecosystem. Ecosystems 5:0339–0347.

Gaston, K. J. 2008. Biodiversity and extinction: the importance of being common. Progress in Physical Geography 32:73–79.

Gaston, K. J. 2010. Valuing common species. Science 327:154–155.

Gaston, K. J., and R. A. Fuller. 2007. Commonness, population depletion and conservation biology. Trends in Ecology & Evolution 23:14–19.

Gonzalez, A., and M. Loreau. 2009. The causes and consequences of compensatory dynamics in ecological communities. Annual Review of Ecology, Evolution, and Systematics 40:393–414.

Greenfield, B. L., C. Kraan, C. A. Pilditch, and S. F. Thrush. 2016. Mapping functional groups can provide insight into ecosystem functioning and potential resilience of intertidal sandflats. Marine Ecology Progress Series 548:1–10.

Gunderson, L. H., and C. S. Holling, editors. 2002. Panarchy: understanding transformations in human and natural systems. Island Press, Washington, D.C., USA.

Haskell, J. P., M. E. Ritchie, and H. Olff. 2002. Fractal geometry predicts varying body size scaling relationships for mammal and bird home ranges. Nature 418:527–530.

Hatton, I. A., K. S. McCann, J. M. Fryxell, T. J. Davies, M. Smerlak, A. R. E. Sinclair, and M. Loreau. 2015. The predator-prey power law: biomass scaling across terrestrial and aquatic biomes. Science 349:aac6284.

Hillebrand, H., and B. Matthiessen. 2009. Biodiversity in a complex world: consolidation and progress in functional biodiversity research. Ecology Letters 12:1405–1419.

Hillebrand, H., D. Bennett, and M. W. Cadotte. 2008. Consequences of dominance: a review of evenness effects on local and regional ecosystem processes. Ecology 89:1510–1520.

Holling, C. S. 1973. Resilience and stability of ecological systems. Annual Review of Ecological Systems 4:1–23.

Holling, C. S. 1988. Temperate forest insect outbreaks, tropical deforestation and migratory birds. Memoirs of the Entomological Society of Canada 120:21–32.

Holling, C. S. 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. Ecological Monographs 62:447–502.

Holling, C. S. 1996. Engineering resilience versus ecological resilience. Pages 31–44 in P. Schulze, editor. Engineering within ecological restraints. National Academy, Washington D.C., USA.

Hooper, D. U., et al. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecological Monographs 75:3–35.

Houlahan, J. E., et al. 2007. Compensatory dynamics are rare in natural ecological communities. Proceedings of the National Academy of Sciences USA 104:3273–3277.

Hurlbert, A. H. 2004. Species-energy relationships and habitat complexity in bird communities. Ecology Letters 7:714–720.

Inger, R., R. Gregory, J. P. Duffy, I. Stott, P. Voříšek, and K. J. Gaston. 2015. Common European birds are declining rapidly while less abundant species' numbers are rising. Ecology Letters 18:28–36.

Kremen, C. 2005. Managing ecosystem services: what do we need to know about their ecology? Ecology Letters 8:468–479.

Lefcheck, J. S., V. A. G. Bastazini, and J. N. Griffin. 2015. Choosing and using multiple traits in functional diversity research. Environmental Conservation 42:104–107.

Levin, S. A. 1992. The problem of pattern and scale in ecology. Ecology 73:1943–1967.

Lokrantz, J., M. Nyström, M. Thyresson, and C. Johansson. 2008. The non-linear relationship between body size and function in parrotfishes. Coral Reefs 27:967–974.

Ludwig, D., D. D. Jones, and C. S. Holling. 1978. Qualitative analysis of insect outbreak systems: the spruce budworm and forest. Journal of Animal Ecology 47:315–332.

Magurran, A. E., and P. A. Henderson. 2012. How selection structures species abundance distributions. Proceedings of the Royal Society B 279:3722–3726.

Maurer, B. A. 2009. Spatial patterns of species diversity in terrestrial environments. Pages 464–473 in S. A. Levin, editor. The Princeton guide to ecology. Princeton University Press, Princeton, New Jersey, USA.

McGill, B. J., et al. 2007. Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. Ecology Letters 10:995–1015.

Milly, P. C. D., J. Betancourt, M. Falkenmark, R. M. Hirsch, Z. W. Kundzewicz, D. P. Lettenmaier, and R. J. Stouffer. 2008. Stationarity is dead: whither water management? Science 319:573–574.

Mouillot, D., et al. 2013. Rare species support vulnerable functions in high-diversity ecosystems. PLOS Biology 11:e1001569.

Mouillot, D., et al. 2014. Functional over-redundancy and high functional vulnerability in global fish faunas on tropical reefs. Proceedings of the National Academy of Sciences USA 111:13757–13762.

Nash, K. L., and N. A. J. Graham. 2016. Ecological indicators for coral reef fisheries management. Fish and Fisheries 17:1029–1054.

Nash, K. L., N. Graham, F. Januchowski-Hartley, and D. Bellwood. 2012. Influence of habitat condition and competition on foraging behaviour of parrotfishes. Marine Ecology Progress Series 457:113–124.

Nash, K. L., et al. 2014a. Discontinuities, cross-scale patterns, and the organization of ecosystems. Ecology 95:654–667.

Nash, K. L., C. R. Allen, C. Barichievy, M. Nystrom, S. Sundstrom, and N. A. J. Graham. 2014b. Habitat structure and body size distributions: cross-ecosystem comparison for taxa with determinate and indeterminate growth. Oikos 123:971–983.

Nash, K. L., N. A. J. Graham, S. Jennings, S. K. Wilson, and D. R. Bellwood. 2015. Herbivore cross-scale redundancy supports response diversity and promotes coral reef resilience. Journal of Applied Ecology 53:646–655.

Nash, K. L., R. A. Abesamis, N. A. J. Graham, E. C. McClure, and E. Moland. 2016. Drivers of herbivory on coral reefs: species, habitat and management effects. Marine Ecology Progress Series 554:129–140.

Odum, E. P. 1969. The strategy of ecosystem development. Science 164:262–270.

O'Gorman, E. J., et al. 2012. Impacts of warming on the structure and functioning of aquatic communities: individual- to ecosystem-level responses. Advances in Ecological Research 47:81–176.

Oliver, T. H., et al. 2015. Biodiversity and resilience of ecosystem functions. Trends in Ecology & Evolution 30:673–684.

O'Neill, R. V., D. L. DeAngelis, J. B. Waide, and T. F. H. Allen. 1986. A hierarchical concept of ecosystems. Princeton University Press, Princeton, New Jersey, USA.

Ozgul, A., D. Z. Childs, M. K. Oli, K. B. Armitage, D. T. Blumstein, L. E. Olson, S. Tuljapurkar, and T. Coulson. 2010. Coupled dynamics of body mass and population growth in response to environmental change. Nature 466:482–485.

Page, S. E. 2010. Diversity and complexity (primers in complex systems). Princeton University Press, Princeton, New Jersey, USA.

Petchey, O. L., and K. J. Gaston. 2006. Functional diversity: back to basics and looking forward. Ecology Letters 9:741–758.

Petchey, O. L., and K. J. Gaston. 2009. Effects on ecosystem resilience of biodiversity, extinctions, and the structure of regional species pools. Theoretical Ecology 2:177–187.

Peters, R. 1983. The ecological implications of body size. Cambridge University Press, Cambridge, UK.

Peterson, G. D., C. R. Allen, and C. S. Holling. 1998. Ecological resilience, biodiversity, and scale. Ecosystems 1:6–18.

Raffaelli, D., A. Hardiman, J. Smart, T. Yamanaka, and P. C. L. White. 2015. The textural discontinuity hypothesis: an exploration at a regional level. Oikos 125:797–803.

Rohr, R. P., S. Saavedra, G. Peralta, C. M. Frost, L.-F. Bersier, J. Bascompte, and J. M. Tylianakis. 2016. Persist or produce: a community trade-off tuned by species evenness. American Naturalist 188:411–422.

Roscher, C., A. Weigelt, R. Proulx, E. Marquard, J. Schumacher, W. W. Weisser, and B. Schmid. 2011. Identifying population- and community-level mechanisms of diversity-stability relationships in experimental grasslands. Journal of Ecology 99:1460–1469.

Rudolf, V. H. W., and N. N. L. N. N. L. Rasmussen. 2013. Population structure determines functional differences among species and ecosystem processes. Nature Communications 4:2318.

Scheffer, M., and S. R. Carpenter. 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. Trends in Ecology & Evolution 18:648–656.

Scheffer, M., R. Vergnon, E. H. Van Nes, J. G. M. Cuppen, E. T. H. M. Peeters, R. Leijs, and A. N. Nilsson. 2015. The evolution of functionally redundant species; Evidence from beetles. PLoS ONE 10:1–10.

Scranton, K., and D. A. Vasseur. 2016. Coexistence and emergent neutrality generate synchrony among competitors in fluctuating environments. Theoretical Ecology 9:353–363.

Soliveres, S., et al. 2016. Biodiversity at multiple trophic levels is needed for ecosystem multifunctionality. Nature 536:456–459.

Spanbauer, T. L., C. R. Allen, D. G. Angeler, T. Eason, S. C. Fritz, A. S. Garmestani, K. L. Nash, J. R. Stone, C. A. Stow, and S. M. Sundstrom. 2016. Body size distributions signal a regime shift in a lake ecosystem. Proceedings of the Royal Society B 283:20160249.

Stuart-Smith, R. D., et al. 2013. Integrating abundance and functional traits reveals new global hotspots of fish diversity. Nature 501:539–542.

Suding, K. N., S. Lavorel, F. S. Chapin, J. H. C. Cornelissen, S. Díaz, E. Garnier, D. Goldberg, D. U. Hooper, S. T. Jackson, and M.-L. Navas. 2008. Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. Global Change Biology 14:1125–1140.

Sugihara, G., and L. Bersier. 2003. Predicted correspondence between species abundances and dendrograms of niche similarities. Proceedings of the National Academy of Sciences USA 100:5246–5251.

Sundstrom, S. M., and C. R. Allen. 2014. Complexity versus certainty in understanding species' declines. Diversity and Distributions 20:344–355.

Sundstrom, S. M., C. R. Allen, and C. Barichievy. 2012. Species, functional groups, and thresholds in ecological resilience. Conservation Biology 26:305–314.

Thibault, K. M., E. P. White, A. H. Hurlbert, and S. K. M. Ernest. 2011. Multimodality in the individual size distributions of bird communities. Global Ecology and Biogeography 20:145–153.

Thrush, S. F., G. Coco, and J. E. Hewitt. 2008. Complex positive connections between functional groups are revealed by neural network analysis of ecological time series. American Naturalist 171:669–677.

Vergnon, R., N. K. Dulvy, and R. P. Freckleton. 2009. Niches versus neutrality: uncovering the drivers of diversity in a species-rich community. Ecology Letters 12:1079–1090.

Vergnon, R., E. H. van Nes, and M. Scheffer. 2012. Emergent neutrality leads to multimodal species abundance distributions. Nature Communications 3:1–6.

Walker, B. H., A. P. Kinzig, and J. Langridge. 1999. Plant attribute diversity, resilience, and ecosystem function: the nature and significance of dominant and minor species. Ecosystems 2:95–113.

Wardwell, D. A., and C. R. Allen. 2009. Variability in population abundance is associated with thresholds between scaling regimes. Ecology and Society 14:42.

Wardwell, D. A., C. R. Allen, G. D. Peterson, and A. J. Tyre. 2008. A test of the cross-scale resilience model: functional richness in Mediterranean-climate ecosystems. Ecological Complexity 5:165–182.

Werner, E. E., C. J. Davis, D. K. Skelly, R. A. Relyea, M. F. Benard, and S. J. McCauley. 2014. Cross-scale interactions and the distribution-abundance relationship. PLoS ONE 9:e97387.

White, E. P., S. K. M. Ernest, and K. M. Thibault. 2004. Trade-offs in community properties through time in a desert rodent community. American Naturalist 164:670–676.

White, E. P., S. K. M. Ernest, A. J. Kerkhoff, and B. J. Enquist. 2007. Relationships between body size and abundance in ecology. Trends in Ecology & Evolution 22:323–330.

Wieczynski, D. J., and D. A. Vasseur. 2016. Environmental fluctuations promote intraspecific diversity and population persistence via inflationary effects. Oikos 125:1173–1181.

Wiens, J. A. 1989. Spatial scaling in ecology. Functional Ecology 3:385–397.

Winfree, R., J. W. Fox, N. M. Williams, J. R. Reilly, and D. P. Cariveau. 2015. Abundance of common species, not species richness, drives delivery of a real-world ecosystem service. Ecology Letters 18:626–635.

Wohlleben, P. 2016. The hidden life of trees: what they feel, how they communicate. Greystone Books, Vancouver, British Columbia, Canada.

CONCEPTS & SYNTHESIS