

FORUM

Sustaining ecosystem functions in a changing world: a call for an integrated approach

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Summary

1. With ever-increasing human pressure on ecosystems, it is critically important to predict how ecosystem functions will respond to such human-induced perturbations. We define perturbations as either changes to abiotic environment (e.g. eutrophication, climate change) that indirectly affects biota, or direct changes to biota (e.g. species introductions). While two lines of research in ecology, biodiversity–ecosystem function (BDEF) and ecological resilience (ER) research, have addressed this issue, both fields of research have nontrivial shortcomings in their abilities to address a wide range of realistic scenarios.

2. We outline how an integrated research framework may foster a deeper understanding of the functional consequences of perturbations via simultaneous application of (i) process-based mechanistic predictions using trait-based approaches and (ii) detection of empirical patterns of functional changes along real perturbation gradients. In this context, the complexities of ecological interactions and evolutionary perspectives should be integrated into future research.

3. *Synthesis and applications.* Management of human-impacted ecosystems can be guided most directly by understanding the response of ecosystem functions to controllable perturbations. In particular, we need to characterize the form of a wide range of perturbation–function relationships and to draw connections between those patterns and the underlying

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ecological processes. We anticipate that the integrated perspectives will also be helpful for managers to derive practical implications for management from academic literature.

Key-words: biodiversity, ecological thresholds, environment, evolution, interaction network, perturbation, species traits, stability

Introduction

Human activities dramatically alter natural habitats, influence biogeochemical cycles, modify biotic communities by extirpating or introducing species and increase climatic variability from local to global scales (MA 2005). Because humans depend on benefits provided by ecosystems (i.e. ecosystem services), it is essential to manage ecosystems so that they are able to continue functioning and delivering services in the face of such perturbations. Thus, two key issues are to predict how perturbations influence ecosystem functions and how mitigation can aid in recovering functions.

Ecologists have been addressing these issues largely using two approaches (Table 1). Concerned with global biodiversity loss, biodiversity–ecosystem function (BDEF) research aims to understand how the loss of diversity influences ecosystem processes. While BDEF studies take a variety of approaches, most have involved small-scale experiments (e.g. Tilman *et al.* 2001) in which diversity (typically, species richness) is manipulated to examine its effects on ecosystem properties measured in a common environment. Recent reviews have confirmed that experimental diversity loss within an assemblage tends to reduce ecosystem process rates or stocks, such as primary productivity and biomass (Cardinale *et al.* 2011, 2012). In contrast, ecological resilience (ER) research is explicitly concerned with the response of ecosystems to external changes in environment or biota. Many ER studies describe dramatic transitions of ecosystems between alternative states with different functionality (Holling 1973). Examples include the shifts of

shallow lakes from clear to turbid water (Scheffer *et al.* 1993) and the shifts of coral reefs towards dominance by macroalgae (Mumby, Hastings & Edwards 2007). ER research provides a theoretical framework for understanding the mechanisms mediating such transitions, emphasizing thresholds and feedbacks (Gunderson 2000; Scheffer & Carpenter 2003; Folke *et al.* 2004).

Despite remarkable progress, both fields of research have nontrivial shortcomings in their ability to address the full sweep of realistic perturbations and functional changes in nature. BDEF research essentially focuses on the relationship between biological diversity and ecosystem function (Fig. 1b) without either specifying the perturbations (Fig. 1a) that cause diversity change in the first place or recognizing that perturbations (e.g. species additions) often cause local-scale diversity to increase rather than decrease (Srivastava & Vellend 2005). As such, the results of such experiments can only be used to predict the functional consequences of extinctions occurring in random order, although the consequences of realistic species loss have increasingly been examined (e.g. Dangles, Carpio & Woodward 2012; Eklöf *et al.* 2012). In addition, most BDEF studies do not consider the direct influence of environmental changes on ecosystem functions (Fig. 1c). In contrast, while ER research explicitly considers how perturbations can cause ‘catastrophic shifts’ in the identities and abundances of species, it tends to focus on the stability of ‘ecosystem states’ as surrogates for overall ecosystem functioning (Fig. 1a). However, this ignores the fact that different ecosystem functions may be uncorrelated, if they depend on different species and func-

Table 1. A summary of the questions, typical approaches and potential shortcomings in biodiversity–ecosystem function (BDEF) and ecological resilience (ER) research

	BDEF research	ER research
Questions	Does biological diversity (e.g. genetic, species and functional diversity) <i>per se</i> enhance ecosystem functions? What mechanisms underlie the effects of diversity on ecosystem functions and its stability?	Can nonlinear changes of ecosystems be identified along a perturbation gradient? Can nonlinear changes of ecosystems be reversed? What mechanisms constrain the recovery of degraded ecosystems after a critical threshold has been crossed?
Typical approaches	Genetic, species and functional diversity at a single-trophic level are manipulated	Searching for the existence of critical threshold across space or time
Potential shortcomings	Perturbations or environmental changes that cause diversity loss are often not specified Multitrophic species interactions are often not considered Many environmental changes are likely to influence ecosystem functions directly	Critical transitions of ecosystem states are premised on simultaneous changes in ecosystem functioning Environmental/ecological contexts where critical transitions are likely to occur are largely unknown Early-warning signals for critical transitions in real data are rarely developed

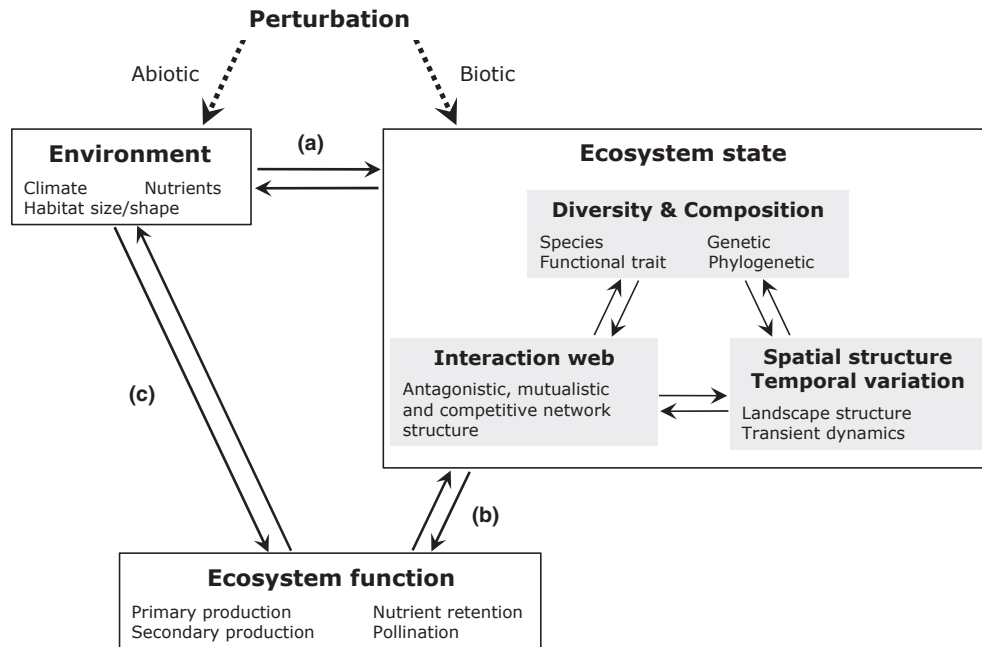


Fig. 1. Schematic diagram describing pathways between human-induced perturbations and ecosystem function. Three primary components, environment (i.e. abiotic environment), ecosystem state (i.e. any biotic variables potentially affecting ecosystem function) and ecosystem function can influence one another and provide positive or negative feedbacks. Potential perturbations are either changes to environmental conditions that indirectly affect ecosystem state variables ('abiotic') or direct changes to ecosystem state variables ('biotic'). BDEF research has focused on the effect of biodiversity (i.e. ecosystem state) on ecosystem function (b) without specifying perturbations behind diversity changes in most cases, while environmental change can also affect ecosystem function directly (c). ER research has primarily focused on ecosystem behaviour in response to changes in environment (a) without explicitly quantifying ecosystem function.

tional groups (Hector & Bagchi 2007). In order for theory to be more widely applicable to realistic situations, we need to specify the type of perturbation and ecosystem function of interest and how the effects of perturbations ramify through different abiotic and biotic pathways (but see e.g. Escobar *et al.* 2012). Here, we outline how our understanding of the functional consequences of perturbations may be fostered by an integrated research framework, highlight gaps in our knowledge, and suggest some future directions to allow more direct links between fundamental research and management in the real world.

Integrated research framework

Many human-induced perturbations can, in principle, be controlled and therefore provide key targets for ecosystem management. Thus, we believe that research can guide management most directly by creating an understanding of the response of ecosystem functions to controllable perturbations with respect to both process and pattern (Fig. 2). If ecosystem function exhibits a threshold response to perturbations, we can avoid severely degraded functioning by preventing such thresholds from being reached. In contrast, if the response is gradual, management of perturbations (e.g. resource extraction) can be guided by analysis of the benefits (e.g. economic) and costs (e.g. to ecosystem services) according to a continuous function. In our discussion of process- vs. pattern-based approaches below, we

loosely equate the BDEF approach with a focus on process and the ER approach with a focus on pattern. However, while we believe this accurately characterizes the relative emphases in these lines of research, we recognize that both process and pattern feature in both BDEF and ER research.

For the process-based prediction of functional change, a first step would be to use a response-effect trait framework – a relatively recent development of BDEF research. Responses of ecosystem function to perturbations involve two processes: (i) the response of a community to perturbation and (ii) the effect of community change on function (Fig. 2a). Although traditional BDEF research has focused only on the latter process, recent trait-based approaches have been suggested as a means of integrating both processes (Naeem & Wright 2003; Hillebrand & Matthiessen 2009; Reiss *et al.* 2009). Species traits associated with contributions to function (effect traits) may differ from those associated with susceptibility to environmental changes (response traits). Responses of ecosystem function to perturbations can partly be understood by examining correlations between functional effect traits and response traits (Suding *et al.* 2008). However, two issues complicate the application of this approach. First, following initial extinctions, declines or species invasions caused by a particular perturbation, communities are often reorganized via secondary extinctions, succession, compensatory growth and spatial dynamics through dispersal (Loreau, Mouquet &

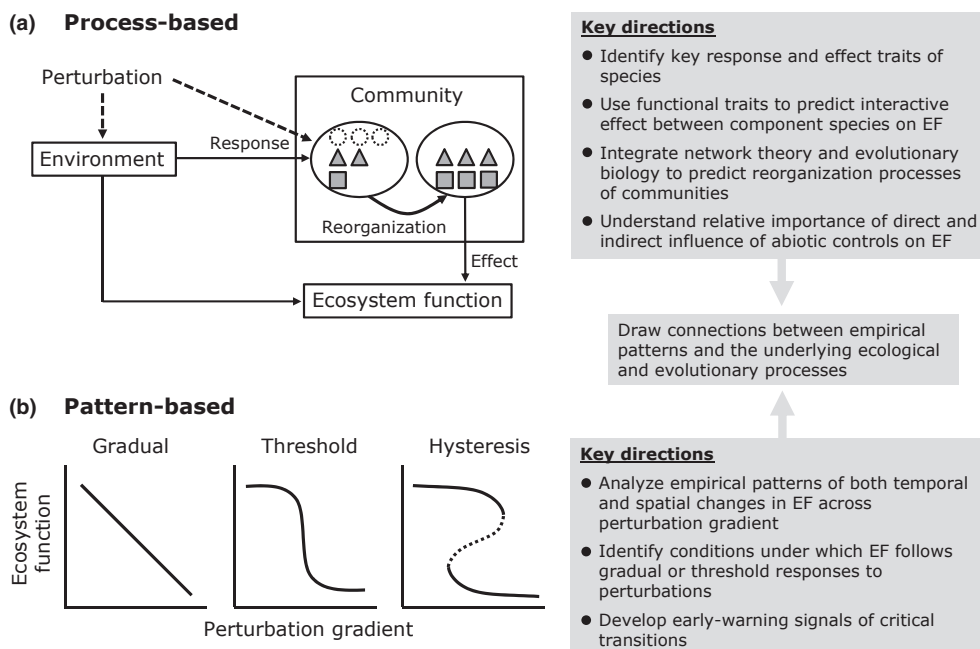


Fig. 2. The integrated framework for understanding the functional consequences of perturbations comprises (a) the process- and (b) pattern-based approach. (a) Response of ecosystem function to perturbations involves many processes, including response and reorganization of community, and the effects of this change in ecosystem state and abiotic controls on function. Each symbol represents a different species ('circle') became extinct during the response process. (b) Possible patterns of perturbation–function relationships: gradual, threshold and hysteresis. The distinction between gradual and threshold responses may be predicted by complementary application of the pattern-based and process-based approaches.

Gonzalez 2003; Duffy *et al.* 2009). Thus, predicting changes to ecosystem function requires knowledge of such processes of community reorganization. Second, many environmental changes are likely to influence ecosystem function directly through abiotic controls, in addition to indirect influence via changes in biota (Hooper *et al.* 2012). For example, litter decomposition rates depend not only on plant functional traits as leaf quality but also on climate due to the direct effects on the metabolism of bacteria and fungi.

Ecological resilience research provides an alternative 'pattern-based' approach to examining the perturbation–function relationships. ER studies have shown that ecosystem state (usually, species composition) can exhibit a threshold response to external environmental changes, and similar arguments can be made for responses of different 'ecosystem functions' to perturbations (Fig. 2b). Threshold responses of ecosystem functions to perturbations can be revealed by identifying abrupt changes over time (Andersen *et al.* 2009), although such changes can also occur with a smooth response function if the perturbation is large and abrupt. We can also use the changes in ecosystem function across space (i.e. in areas with different levels of perturbation) to reconstruct perturbation–function relationships (Sasaki *et al.* 2008). In the search for nonlinear patterns across space, variation in functions must be observed along the full range of perturbation levels; otherwise, we may fail to detect underlying critical thresholds.

Both the process- and pattern-based approaches described above have drawbacks. Predicting functional changes using the process-based approach that includes both direct and indirect pathways presents a massive empirical challenge. Likewise, it may be extremely difficult to extrapolate pattern-based knowledge from one ecosystem to another. Thus, we argue that integrated approaches are necessary to advance our understanding of the perturbation–function relationship. An important task is to characterize the form of perturbation–function relationships for a wide range of realistic scenarios and to draw connections between those patterns and the underlying ecological processes. While processes (e.g. complementarity in BDEF, feedback mechanisms in ER) feature in both lines of research, process-based inferences have largely relied on the post hoc interpretation and modelling of empirical patterns. Simultaneously, understanding response–effect trait dynamics and changes in ecosystem function along perturbation gradients should provide critical and complementary insights into the processes underlying abrupt functional changes. For example, if species groups with similar effect traits differ in their response traits, a perturbation might not result in a strong shift in ecosystem functions. The degree of decline in the range and variation in response traits (i.e. response diversity; Elmqvist *et al.* 2003) may be a key indicator of pending functional collapse in ecosystems. Below, we discuss several key directions that we believe should be integrated in future research.

Directions for future research

RESPONSE PATTERNS

By cataloguing and dissecting response patterns for different situations, we may be able to identify the conditions under which ecosystems and their functions follow gradual or threshold changes. Gradual responses of ecosystem functions may be more likely for the types of perturbations in which the direct influence of abiotic changes predominates and few changes in ecosystem state variables are involved. In contrast, threshold responses may be more likely in situations where complex changes in ecological interactions through trophic cascades are involved (Estes *et al.* 2011). On the basis of a literature review of ER studies, Didham, Watts & Norton (2005) argue that hysteresis may be most frequent in ecosystems that were historically subject to strong abiotic regimes. Case studies that document a lack of response to perturbations also offer important lessons. For example, Grime *et al.* (2000, 2008) found that an infertile, limestone grassland in UK was highly resistant to experimental climate change in terms of biomass and floristic composition, while more fertile, early-successional grassland was much more responsive. We lack a general understanding of what determines such difference in responsiveness of ecosystems. Studies that contrast ecosystems with different initial conditions will enhance our knowledge of how biotic and abiotic factors interact to govern responses to perturbations.

WARNING SIGNALS FOR CRITICAL TRANSITIONS

In contrast to the pattern-based detection of thresholds, recent studies also attempt to forecast such critical transitions. Theoretical work suggests the existence of some early-warning signals for threshold occurrence (Scheffer *et al.* 2009). A large-scale manipulative experiment using lake ecosystems detected statistical signals, as predicted by theory, more than a year before food web transition was complete (Carpenter *et al.* 2011). In arid ecosystems, local interactions among plants can develop characteristic spatial patterns of vegetation patches when the systems are close to transition to desertification (Kéfi *et al.* 2007). Studies on such signals are just emerging, and data limitations have largely prevented the application of early detection analyses to management. Generalized early-warning signals for critical transitions in real ecosystems are an important research priority, although data on the specific system of interest would much improve predictions of when critical transitions will happen (Boettiger & Hastings 2013).

RESPONSE-EFFECT TRAIT FRAMEWORK

The identification of key effect and response traits is an important research priority (Suding *et al.* 2008). In particular, removal experiments in natural ecosystems based

on the species loss order associated with response traits, coupled with better knowledge of relationships between response and effect traits, would provide more predictive knowledge for functional consequences of perturbations (Dangles, Carpio & Woodward 2012; Eklöf *et al.* 2012) and for scaling experimental results at local scales to the landscape scale (Cardinale *et al.* 2012). Nonetheless, the response-effect trait framework predicts functional changes based on the sum of independent species responses to a given perturbation, without considering interactive (i.e. diversity) effect between species that has been emphasized in BDEF research. Functional traits have been successful in distinguishing niche differentiation and may also be helpful to predict the extent of interactive effects. A pioneering work by Roscher *et al.* (2012) used a grassland biodiversity experiment to demonstrate that the variation in productivity and net diversity effects was largely explained by functional identity of dominant species, whereas functional trait diversity of the community explained little additional variation.

MULTITROPHIC COMMUNITY DYNAMICS

Ecological resilience studies have emphasized changes in feedbacks and biotic interactions as key underpinnings of shifts to alternative states. As in the example of shallow lakes, positive feedbacks can cause abrupt shifts to alternative states by magnifying even small changes in ecosystems. Well-known ER studies have also emphasized factors such as the loss of consumers, compensatory dynamics through trophic cascades, mutualistic interactions and altered disturbance regimes (Scheffer *et al.* 2001; Folke *et al.* 2004; Estes *et al.* 2011). For example, the shift from coral to macroalgal dominance in some Caribbean reefs was triggered by the loss of herbivorous fish by fishing and herbivorous urchins by disease (Mumby, Hastings & Edwards 2007). Such modifications of predator-prey interactions (antagonistic interactions) have historically been thought to have the greatest impact on community structure, and ecosystem function and stability (MacArthur 1955). As such, species interaction network structure is generally vulnerable to external perturbations such as habitat modification or top predator extinction (Tylianakis, Tscharntke & Lewis 2007). Nonetheless, some observed structural attributes of empirical networks (e.g. nestedness, compartmentalization) appear to enhance community persistence (Fontaine *et al.* 2005; Thébault & Fontaine 2010) and resilience (Thébault & Fontaine 2010; Stouffer & Bascompte 2011) in the face of external perturbations. For example, mutualistic interactions (e.g. plant-pollinator interaction networks) have been shown to play an important role in maintaining biodiversity, and thereby in promoting long-term stability in ecosystem functioning (Fontaine *et al.* 2005). Network approaches can therefore provide a key tool for integrating BDEF and ER perspectives, as they integrate the complexity of ecological interactions with the mechanisms behind the responses of ecosystem functions to perturbations.

ABIOTIC CONTROLS

Despite some ongoing attempts to quantify the direct vs. indirect influences of environment on ecosystem functions using comparative meta-analyses as well as experimental approaches (Cornwell *et al.* 2008; Hooper *et al.* 2012), our understanding of this issue is still quite rudimentary. Structural equation modelling of observational data provides a promising way to test the BDEF relationships, including both direct and indirect effects, along realistic perturbation gradients. For example, Laliberté & Tylianakis (2012) employed generalized multilevel path models to test multivariate causal hypotheses for a 27-year grassland experiment simulating intensification of fertilizer use and grazing pressure. They demonstrated that resource availability exerted the dominant control over above-ground primary productivity, both directly and indirectly through changes in plant functional composition and altered impacts of grazing. Additional studies are needed identifying the conditions under which indirect effects of environmental change on ecosystem functions are most important.

EVOLUTIONARY PERSPECTIVES

Given the increasingly recognized potential for rapid evolutionary trait change, evolutionary perspectives should be integrated into future studies of ecosystem function. Both theoretical (Abrams 2000; Kondoh 2003) and experimental studies (Yoshida *et al.* 2003; Jones *et al.* 2009) demonstrate that evolutionary responses of component species in an ecological network can influence community dynamics. Furthermore, genetic variation in traits affecting ecological networks, and therefore community and ecosystem properties, can be substantial (Whitham *et al.* 2006; Lavandero & Tylianakis 2013). Further study is necessary in order to understand the conditions under which evolutionary responses of a given species have significant ecological consequences. In addition, because individual species can have huge effects on ecosystem function, it is crucial to assess the adaptability of key focal species – via either evolutionary or plastic change – and the degree to which this differs among lineages. For example, change in the abundance of plants over the past ~150 years was found to be strongly correlated with the ability of species flowering time to track climate change (Willis *et al.* 2008). Identifying the factors that influence rates of adaptation will be of critical importance to understanding the response and reorganization of communities to sustained perturbations.

Management Implications and Conclusions

The integrated framework is broadly applicable to a range of systems, from management of (semi-)natural ecosystems to that of domesticated (e.g. agricultural or forest) ecosystems. While the framework basically consid-

ers single-ecosystem functions, we should also acknowledge that perturbations can affect different functions in the opposite directions. Another key task to make research to be informative for management is therefore to understand how the trade-offs between functions are mediated by abiotic and biotic processes. Ecological research can and should play an important role in ecosystem management by providing basic knowledge about how abiotic and biotic perturbations will affect ecosystem functioning. These links have traditionally been pursued under multiple, and largely independent, frameworks. We argue that the integration of relevant disciplines, including both BDEF and ER research, is necessary. Recognizing how the different lines of research relate to one another and contribute to the same overarching goal will be crucial not only for ecologists in further advancing research, but also for managers in deriving practical implications for management from academic literature.

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