Response diversity determines the resilience of ecosystems to environmental change

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ABSTRACT

A growing body of evidence highlights the importance of biodiversity for ecosystem stability and the maintenance of optimal ecosystem functionality. Conservation measures are thus essential to safeguard the ecosystem services that biodiversity provides and human society needs. Current anthropogenic threats may lead to detrimental (and perhaps irreversible) ecosystem degradation, providing strong motivation to evaluate the response of ecological communities to various anthropogenic pressures. In particular, ecosystem functions that sustain key ecosystem services should be identified and prioritized for conservation action. Traditional diversity measures (e.g. 'species richness') may not adequately capture the aspects of biodiversity most relevant to ecosystem stability and functionality, but several new concepts may be more appropriate. These include 'response diversity', describing the variation of responses to environmental change among species of a particular community. Response diversity may also be a key determinant of ecosystem resilience in the face of anthropogenic pressures and environmental uncertainty. However, current understanding of response diversity is poor, and we see an urgent need to disentangle the conceptual strands that pervade studies of the relationship between biodiversity and ecosystem functioning. Our review clarifies the links between response diversity and the maintenance of ecosystem functionality by focusing on the insurance hypothesis of biodiversity and the concept of functional redundancy. We provide a conceptual model to describe how loss of response diversity may cause ecosystem degradation through decreased ecosystem resilience. We explicitly explain how response diversity contributes to functional compensation and to spatio-temporal complementarity among species, leading to long-term maintenance of ecosystem multifunctionality. Recent quantitative studies suggest that traditional diversity measures may often be uncoupled from measures (such as response diversity) that may be more effective proxies for ecosystem stability and resilience. Certain conclusions and recommendations of earlier studies using these traditional measures as indicators of ecosystem resilience thus may be suspect. We believe that functional ecology perspectives incorporating the effects and responses of diversity are essential for development of management strategies to safeguard (and restore) optimal ecosystem functionality (especially multifunctionality). Our review highlights these issues and we envision our work generating debate around the relationship between biodiversity and ecosystem functionality, and leading to improved conservation priorities and biodiversity management practices that maximize ecosystem resilience in the face of uncertain environmental change.

Key words: biodiversity-ecosystem functioning, complementarity, ecosystem services, effect and response traits, functional compensation, functional diversity, functional redundancy, low multifunctional redundancy, regime shift, trait-based redundancy.

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I. INTRODUCTION

The relationship between biodiversity and ecosystem functioning has been the subject of numerous studies investigating whether biodiversity affects ecosystem processes, and aiming to elucidate the mechanisms by which biodiversity determines ecosystem properties. Although many controversies still exist and mechanisms often remain poorly understood, accumulated knowledge generally supports the idea that biodiversity promotes ecosystem functionality and stability, and thus contributes significantly to various ecosystem services (Tilman, Reich & Knops, 2006; Naeem et al., 2009). This evidence serves to highlight the dangerous possibility that loss of biodiversity may result in a decline or loss of crucial ecosystem services (Duffy, 2009; Cardinale et al., 2012; Hooper et al., 2012). The cumulative understanding emerging from this 'ecosystem services perspective' (Mace, Norris & Fitter, 2012) should be more extensively publicised in a bid to convince society at large, and particularly those parties responsible for policy development, that the safeguarding of biodiversity is of the highest priority if human well-being is to be sustained in the face of global change (Díaz et al., 2006; Loreau et al., 2006).

Recent syntheses (Balvanera et al., 2006; Cardinale et al., 2007) reveal that most studies of biodiversity-ecosystem functioning have used species richness as a diversity metric. These studies generally show that regardless of focal taxa, trophic level, and guild composition, mixtures of species (polycultures) contribute more, on average, to representative ecosystem functions such as primary production than do monocultures. However, such studies have often been criticized as having little practical relevance for management and conservation (Srivastava & Vellend, 2005; Thompson & Starzomski, 2006). Most have aimed primarily to clarify the mechanisms by which a mixture of species enhances the functional performance of ecosystems (e.g. the debate over sampling/selection effects versus complementarity effects; Cardinale et al., 2007, 2011; Fargione et al., 2007), rather than providing convincing evidence that biodiversity contributes to the stable, optimal provision of actual ecosystem services (but see Winfree & Kremen, 2009; Haas et al., 2011; van Elsas et al., 2012). Indeed, most available evidence to this effect is from experimental systems and theories in which the number and identity of species has been highly controlled. Newly emerged concepts based on measures of diversity other than species richness have aided practical application of knowledge about the effects of biodiversity on ecosystem functionality. These alternative measures include those based on functional traits and intraspecific (genotypic and phenotypic) variation (Reiss et al., 2009). Although it is difficult to determine which measure of diversity is most appropriate in a given context (because the different measures are context dependent), it is clear that species richness is not always the optimal measure at every level of biological organisation (McGill et al., 2006; Cadotte, Cardinale & Oakley, 2008; Hillebrand & Matthiessen, 2009).

Some researchers have suggested that functional diversity exerts a greater influence on ecosystem functioning than does taxonomic species richness or diversity, because it presupposes a mechanistic link between diversity and ecological processes (Díaz & Cabido, 2001; Cadotte, Carscadden & Mirotchnick, 2011; Díaz et al., 2011). Functional diversity concerns those components of diversity that affect ecosystem operation, and is measured by determining the range and values of 'functional effect traits' of species in a community (Díaz & Cabido, 2001; Hooper et al., 2005). Note that these traits can be measured at the level of the individual or at the level of sub-functional groups (and that within-species variability of traits over time and space is important for further understanding of community processes; e.g. Laughlin et al., 2012; Violle et al., 2012), but for simplicity we generally discuss functional traits measured as species-level averages. The practical importance of functional diversity is that a loss of any functional types will likely result in loss of some ecosystem functions. By contrast, whilst extinction of a species is serious when viewed from the 'conservation perspective', which regards biodiversity itself as an ecosystem service (Mace, Norris & Fitter, 2012), the extinction may not have marked functional consequences. This is because different species often have similar effects on ecosystem processes when a single function is considered under one set of environmental conditions (Walker, 1995; Walker, Kinzig & Langridge, 1999; Díaz & Cabido, 2001). This 'functional redundancy' plays an important role in sustaining the functionality of ecosystems during environmental perturbations (Naeem, 1998), since the extinction of a species performing a particular ecosystem role can be compensated for by growth or dominance of species that have similar functional effects. At this juncture, it is important to emphasize that these compensatory responses in no way justify anthropogenic erosion of biodiversity, even if this impact has no apparent effect on ecosystem

functioning. However, given the urgent need to halt and reverse the degradation of key ecosystem properties (UNEP, 2009), and given the inevitable conflicts between biological conservation and social and economic demands (Polasky *et al.*, 2008; Bullock *et al.*, 2011), restoration efforts will in practice have to be focused preferentially on 'crucial' ecosystem services. It would thus be prudent to characterize functional redundancy carefully for the incorporation of this concept into ecological management frameworks. If this redundancy is clearly understood and accurately defined then management decisions can be made for its active maintenance, thus safeguarding ecological resilience and increasing the likelihood that desirable ecosystem states will be sustained under changing environmental conditions (Walker, 1995; Naeem, 1998; Elmqvist *et al.*, 2003; Tscharntke *et al.*, 2005; Carpenter, Bennett & Peterson, 2006).

In particular, the idea of functional redundancy deserves careful attention because variation within a functional effect group is important to buffer against environmental fluctuations and to facilitate successful reorganisation of ecological systems following disturbances (Walker, 1995; Naeem & Wright, 2003; Hooper *et al.*, 2005). This follows from the notion of 'response diversity' (Elmqvist *et al.*, 2003), which suggests that an assembly of species with similar functional effect traits should respond differently to disturbances and environmental changes, otherwise even small disturbances could result in loss of the majority (or in extreme cases the entirety) of species constituting a particular functional type (Elmqvist *et al.*, 2003; Duffy, Richardson & France, 2005). A recent meta-analysis of 'functional response traits' in plant communities (i.e. species-specific traits related to disturbance response or post-disturbance regeneration: Díaz & Cabido, 2001; Hooper *et al.*, 2005), showed that intensification of resource extraction and land use can cause a global decline of response diversity, suggesting that anthropogenic pressures can increase ecosystem vulnerability to environmental change (Laliberte *et al.*, 2010).

In light of the above, it seems likely that high response diversity is essential to ensure ecosystem functionality, providing a means to cope with uncertainties and ecological surprises (Elmqvist *et al.*, 2003). However, current understanding of response diversity is still poor (see online Fig. S1), and our focus on this concept is thus amply justified. This poor understanding stems from a variety of factors. First, there is a rudimentary understanding of functional redundancy, especially regarding its relationship to the insurance effects of biodiversity. Second, there is considerable subjectivity inherent in defining functional traits, because there is no fixed basis for determining effect and response traits. Third, response diversity has been only rarely quantified experimentally, observationally, or theoretically. And fourth, there is little knowledge of the mechanisms by which response diversity determines 'ecological resilience', i.e. the capacity of a system to absorb disturbance so as to retain the same controls on fundamental functions (Holling, 1973; Berkes, Colding &

Folke, 2003; Chapin, Kofinas & Folke, 2009; Gunderson, Allen & Holling, 2009), notwithstanding extensive research on complex adaptive systems by the Resilience Alliance (www.resalliance.org; Walker *et al.*, 2002), through which the concept of response diversity originated (Elmqvist *et al.*, 2003). In this review we provide some crucial insights and future directions based on key literature. Clearly, a proper understanding of the biodiversity-ecosystem functioning relationship is an essential basis for response to the escalating (and sometimes conflicting) demands for conservation and restoration of different ecosystem services (Walker, 1995; Duffy, 2009). Current species loss is not random and could potentially result in critical loss of vital ecosystem functionality (Zavaleta & Hulbey, 2004; Bracken *et al.*, 2008; Selmants *et al.*, 2012). We anticipate that our perspectives will be useful for the development of strategies to adapt to the current situation and mitigate this risk (note that related concepts and glossaries are listed in Table 1).

II. QUESTIONS AND DIRECTIONS

(1) What is a functionally redundant community?

Is a community with high functional redundancy always stable in terms of generating and maintaining ecosystem functionality? Existing studies provide clear evidence that this is not the case (Elmqvist *et al.*, 2003; Laliberte *et al.*, 2010). It is possible for a functional group with high redundancy to be more vulnerable to environmental fluctuations than groups with lower redundancy (Fig. 1). In Fig. 1, low levels of external pressure cause extinction of highly vulnerable species (black), eliminating functional groups FG2 and FG6. Moderate levels of pressure also remove species with medium vulnerability (grey), eliminating FG3, FG4 and FG5. Thereafter, only the species with high stress tolerance (white) in FG1 and FG7 remain. Thus, high redundancy does not necessarily ensure high response diversity and the consequent preservation of functionality in the face of environmental fluctuations. At this juncture we must consider the issue of functional compensation and its contribution to ideas about redundancy. Here, we disentangle and clarify different concepts of redundancy and the insurance effects of biodiversity.

(a) Low redundancy

According to the insurance hypothesis of Yachi & Loreau (1999), the greater the variance of species responses to environmental fluctuations, the lower the species richness at which the temporal mean of an ecosystem process saturates and the ecosystem becomes redundant. Subsequent theoretical developments suggest that an assembly of species with different responses to environmental fluctuations can stabilize an ecosystem function (e.g. process rate) in the face of environmental change, through compensatory dynamics among species (reviewed by Gonzalez & Loreau, 2009).

Table 1. Glossary

Alternative stable states: Multiple (alternative) basins of attraction within an ecological system (Carpenter & Gunderson, 2001; Scheffer & Carpenter, 2003). This concept predicts that ecosystems can persist under multiple states (such as sets of particular biotic and abiotic conditions). An ecosystem can abruptly shift from one state to another, the phenomenon referred to as 'regime shift'.

Complementarity: Niche differences among species, such as interspecific differences in resource use, lead to more efficient acquisition of available resources and therefore a higher rate of an ecosystem function. This has been discussed well in the relationship between biodiversity and productivity (e.g. Cardinale *et al*., 2007; Fargione *et al*., 2007).

Density compensation: This is said to occur when the total density or biomass of a community maintains the same level following species loss (Gonzalez & Loreau, 2009). This does not necessarily assure the persistence of ecosystem function that the community provides (see main text).

Ecological resilience: The capacity of a system to absorb shocks and disturbances and retain the same level of fundamental functions (Berkes, Colding & Folke, 2003; Folke *et al*., 2004; Chapin, Kofinas & Folke, 2009).

Ecosystem function: The changes in energy and matter over time and space occurring through biological activity, such as primary production, nutrient uptake, decomposition, and evapotranspiration. The rates of such functions are often positively associated with higher levels of biodiversity (e.g. Balvanera *et al*., 2006; Cardinale *et al*., 2007).

Ecosystem process: This is synonymous with 'ecosystem function' (Reiss *et al*., 2009).

Ecosystem services: Humanity benefits from a multitude of resources and processes supplied by ecosystems. Ecosystem services are grouped into four categories: provisioning (such as providing food and water); regulating (such as climate regulation and pest control); supporting (such as carbon and nutrient dynamics); and cultural (such as recreational and educational use).

Functional compensation: Under environmental perturbations, species in a community may be lost or become functionally less important or even dormant. However, the aggregate of an ecosystem process can nonetheless be maintained, because the remaining species can compensate functionally for the loss (Walker, 1992, 1995; Naeem, 1998; Díaz & Cabido, 2001). This does not necessarily accompany density compensation (see main text).

Functional diversity: The variation or dispersion of functional traits in an assemblage (e.g. Díaz & Cabido, 2001; Hooper *et al*., 2005; Petchey & Gaston, 2006; Hillebrand & Matthiessen, 2009; Laliberté & Legendre, 2010; Cadotte, Carscadden & Mirotchnick, 2011).

Functional redundancy: The number of species contributing in a similar way to an ecosystem function (Laliberte *et al*., 2010).

Functional trait: Component of an organism's phenotype that determines its effect on ecosystem processes, called a functional effect trait (e.g. Hooper *et al*., 2005; Petchey & Gaston, 2006; Suding *et al*., 2008; Lavorel *et al*., 2011) and its response to environmental changes, called a functional response trait (Naeem & Wright, 2003; Suding *et al*., 2008; Suding & Hobbs, 2009). Some define effect and response traits as those influencing biogeochemical processes and regenerative traits, respectively (e.g. Laliberte *et al*., 2010).

Insurance hypothesis: The idea that species-rich communities are less likely to lose ecosystem functionality during environmental fluctuations (Yachi & Loreau, 1999).

Low multifunctional redundancy: Effects of species identity on ecosystem functions increase when functional contexts (such as locations, functions, time or environmental-change scenarios) are considered at multiple dimensions (e.g. Isbell *et al*., 2011). In this context, the number of species promoting ecosystem functions increases monotonically with functional dimensions (see main text).

Regime shift: Crossing a threshold point brings about a sudden, sharp, and dramatic change in the structure and function of an ecosystem; for example, standing water can become overgrown by floating plants, shrubs can rapidly encroach into savannahs, and lake systems can experience a sudden shift from clear to turbid water (reviewed by Scheffer & Carpenter (2003) and Folke *et al*. (2004)).

Response diversity: The diversity of species that can perform similar ecosystem functions but have different capacities to respond to disturbance, imparting greater resilience to the entire system (Walker, 1995; Elmqvist *et al*., 2003; Suding & Hobbs, 2009). Note: while this can be evaluated at the level of the individual or at the level of functional groups, this synthesis describes it only at the species level.

Trait-based redundancy: This idea presupposes that when multiple species have similar contributions to a focal function (that is, they have similar functional effect traits that are of interest), an ecosystem is able to maintain its key functionality (see main text).

Experiments also indicate that species asynchrony (i.e. the dominance of different species at different points in time) is a key component of these compensatory dynamics (e.g. Isbell, Polley & Wilsey, 2009; Hector *et al*., 2010). This enables a community steadily to generate the aggregate of ecosystem properties, leading to the concept of low temporal redundancy. This concept considers that species that are functionally redundant at a given point in time may no longer be redundant at a later juncture (Loreau *et al*., 2001; Reich *et al*., 2012). Recent expansion of this idea has produced the notion of 'low multifunctional redundancy', which suggests that the number of species that promote ecosystem functioning increases with the number of functional contexts considered (Hector & Bagchi, 2007; Zavaleta *et al*., 2010; Isbell *et al*., 2011; Lohbeck *et al*., 2012; Maestre *et al*., 2012).

These studies propose that redundancy should be evaluated using multiple factors in addition to functional effect traits (including spatial and temporal variation of environmental conditions) to ensure a more accurate multifunctional characterization of ecosystems at large spatio-temporal scales. The ideas of low redundancy, the non-equilibrium nature of multispecies communities and species-specific responses to environmental fluctuations all point to high spatio-temporal complementarity of species (Loreau, 2004), resulting in long-term stability of multifunctional ecosystems.

(b) Trait-based redundancy

Traditional definitions of functional redundancy are based solely on similarity in the effect traits of different species (e.g.
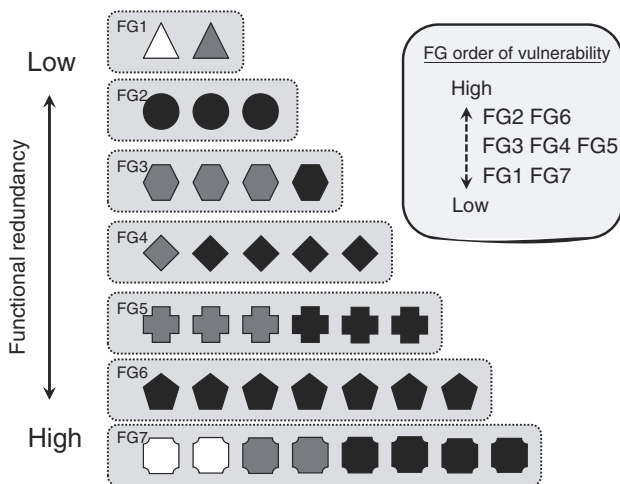
Fig. 1. Illustration of the difference between functional redundancy and response diversity. Each instance of a symbol represents a different species, where symbol shape indicates functional effect traits and symbol shading indicates functional response traits. Each functional group (FG) is composed of species with identical effect traits, and the number of species in a FG determines its functional redundancy. Vulnerability to environmental pressures is determined by response traits, with black/gray/white representing high/medium/low levels of vulnerability. See the text for further explanation of this figure.

biogeochemical attributes; Naeem, 1998), and these trait-based definitions do not usually consider spatial or temporal variability in the functional effects of species. Functional traits comprise the phenotypic characteristics of an organism that affect its performance and fitness (Hooper *et al.*, 2005; Petchey & Gaston, 2006; Suding *et al.*, 2008; Cadotte, Carscadden & Mirotchnick, 2011). Whilst some traits such as phenological or behavioural differences among species may be useful to infer spatial and/or temporal complementarity that leads to a community-level aggregate of ecosystem properties, most functional traits (such as those based on morphological and physiological characteristics) are not strong indicators of niche specialization in a community. In other words, although functional effect traits are useful for identifying a group of species with similar functional roles (e.g. nitrogen fixation and non-fixation), they reveal little about whether and how within-group species asynchrony and spatio-temporal complementary occur.

(c) Synthesis

To illustrate the difference between these two concepts of redundancy, we use a hypothetical group of eight species that each contributes to the long-term maintenance of an ecosystem function (Fig. 2). Suppose that the number of active species within the group fluctuates over time, where active species are those that promote functionality at any given juncture. Six of the eight species are active each year, though each species contributes to a different degree. Relative contributions vary from year to year,
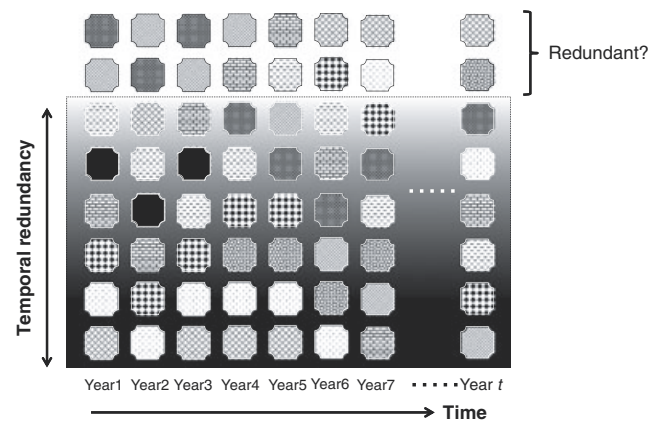

Fig. 2. Temporal fluctuation of redundancy in one functional effect group. Each instance of a symbol represents a different species; shape indicates functional effect traits and pattern indicates functional response traits. All species have similar effect traits. In any year, the top two species are inactive (functionally dormant), whilst the six species enclosed within the rectangle all contribute in varying degrees to the overall functioning of the group in that year. Their relative contribution (high–low) is indicated by their position along the background gradient of the rectangle (dark–light). Resulting from different responses of species to environmental conditions at different times, this group can steadily perform complementary resource use and maintain overall functioning in the face of environmental fluctuations (functional compensation). Note that for simplicity we describe annual variation in each species' dominance and dormancy (such as those seen in annual plant communities); however, similar asynchrony among species can be observed at different temporal scales.

and the set of active species also varies annually. Possible explanations causing such interspecific asynchrony in dominance under environmental fluctuations (i.e. temporal niche differentiation) include the storage effect (Caceres, 1997; Angert *et al.*, 2009) and intraspecific trait variation (Violle *et al.*, 2012). In a given year, the two inactive species would be considered functionally redundant according to the trait-based definition, but not so under the concept of low multifunctional redundancy. Nonetheless, both views would consider all eight species in Fig. 2 to be important despite the intermittent functional contributions of some species; those that are functionally dormant in a given year will respond to different future conditions and once again contribute to ecosystem functioning. This response diversity constitutes the insurance effect of biodiversity.

Some authors consider the two views of redundancy (low redundancy and trait-based redundancy) as allied. For example, Walker, Kinzig & Langridge, (1999) and Gonzalez & Loreau (2009) consider functional redundancy to be the compensatory responses to environmental fluctuations among functionally similar species. However, a real conceptual divide exists regarding the insurance effects of biodiversity, and it is necessary to assess critically the different views based on key findings emerging from research on response diversity. We recommend that future studies

considering functional redundancy should be explicit in the expression of functional context. That is, it is important to specify a focal set of environmental conditions when considering whether species are functionally active or dormant.

The only meta-analysis to date that deals with response diversity showed that for all 18 existing datasets, functional redundancy and response diversity were both significantly reduced by land-use intensification such as biomass removal and fertilization (Laliberte *et al.*, 2010). In agreement with the insurance hypothesis (Yachi & Loreau, 1999), this finding supports the importance of conserving higher number of species that respond differently to external pressures, if key ecosystem functions are to be conserved. However, the synthesis of Laliberte *et al.* (2010) depends on the assumption that species with similar effect traits are always functionally redundant. This simplification, which reflects the trait-based concept of redundancy, may preclude careful consideration of resource use and niche differentiation to detect subtle functional variation, and the synthesis may thus be at odds with the idea of low redundancy. We think that the critical factor complicating the concept of redundancy is the issue of 'functional dormancy', whereby certain species in a community temporally lose their functional roles as a result of environmental change (Fig. 2).

It is well known that the competitive balance between species often shifts according to changes in biotic and abiotic factors (e.g. Hartley & Amos, 1999). As a result of such changes, species in a community may occasionally become functionally less important or even dormant. However, the aggregate of ecosystem processes (such as annual biomass production of a plant community) can nonetheless be maintained by shifts in the dominance of other species in the community (functional compensation). Although poorly understood, this species asynchrony in response to environmental fluctuations (e.g. MacArthur, 1955; Chapin & Shaver, 1985; Leary & Petchey, 2009) appears to be the key point of departure of the low redundancy concept (which proposes that a species-rich assembly with niche differentiation is less likely to lose ecosystem functionality under spatio-temporal environmental fluctuations) and the trait-based redundancy concept (which proposes that a group of species with similar effect traits is resilient to environmental change and is able to maintain functionality). The major difference between these views is that the former considers each species as belonging to a different functional context, while the latter considers species with similar effect traits to be functionally identical, though with varying degrees of stress tolerance and different magnitudes of response (Fig. 2). Notwithstanding their differences, both redundancy views regard high response diversity as a buffer against loss of ecosystem functioning.

(2) How are effect traits and response traits functionally different?

Some studies have confused response traits with effect traits and their results may thus be of little use for deducing the functional consequences of environmental change in terms of both process rate and ecosystem stability. One of the acceptable means of measuring response is, using the best available information, to evaluate the multivariate within-group dispersion in response trait space after categorization into effect groups. However, there are some difficulties associated with this method. The first is that it corresponds to the evaluation of functional richness (i.e. a discontinuous metric representing the number of groups with similar functional effect traits). Although this may ease investigations of response diversity (e.g. Laliberte *et al.*, 2010; Karp *et al.*, 2011), functional diversity is more often expressed as continuous gradients of different effect traits (e.g. Díaz & Cabido, 2001; Hooper *et al.*, 2005; Petchey & Gaston, 2006; Hillebrand & Matthiessen, 2009; Laliberté & Legendre, 2010). The second is the subjectivity inherent in the definition and categorization of functional traits. For example, Laliberte *et al.* (2010) classified plant height as an effect trait, while Duffy *et al.* (2009) treated it as a response trait, highlighting the constant challenge of distinguishing functional effect traits and functional response traits (Hooper *et al.*, 2005; Suding *et al.*, 2008). Actually, some traits can act as both effect and response traits (Laliberte *et al.*, 2010). In practice, identification and prioritization of crucial functions in each ecosystem enables realistic decisions about which effect traits are of concern, and subsequent consideration of the dominant disturbance factors in each system facilitates selection of important response traits.

Below, we describe an approach for how functional traits should be conserved for the maintenance of crucial ecosystem functionality. Realistic decisions about which effect traits are of concern are related to realistic threats to ecosystem functionality that biodiversity provides. For example, human activity can threaten the diversity of natural avian communities, affecting ecologically and economically important functions such as seed dispersal, seed predation, pollination, and pest control (Tscharntke *et al.*, 2008; Karp *et al.*, 2011). Suppose conservation priority is given to these functions, because of their value as regulating services (Sekercioglu, 2006). In this case, primary attention should be paid to guild structure, because these processes are supported by different dietary guilds (i.e. frugivores, granivores, nectarivores, and insectivores, respectively; Sekercioglu, 2006). In the light of this focus, the study of Karp *et al.* (2011) is noteworthy. They recently investigated a possibility of compensatory species dynamics within each guild, and found that response diversity contributes to guild resilience (Fig. 3); however, because avian communities were less resilient and stable during high-intensity land-use (Fig. 4), they claimed that a need exists to decrease land-use intensity as a way to promote avian diversity and potentially augment and stabilize ecosystem service provision. Non-random loss of species may cause losses of diversity for specific groups that have a relatively greater contribution to ecosystem functioning. These groups include dominant species (Bracken *et al.*, 2008), subordinate species (Bracken & Low, 2012), and specific guilds (Tscharntke *et al.*, 2008). Thus, the
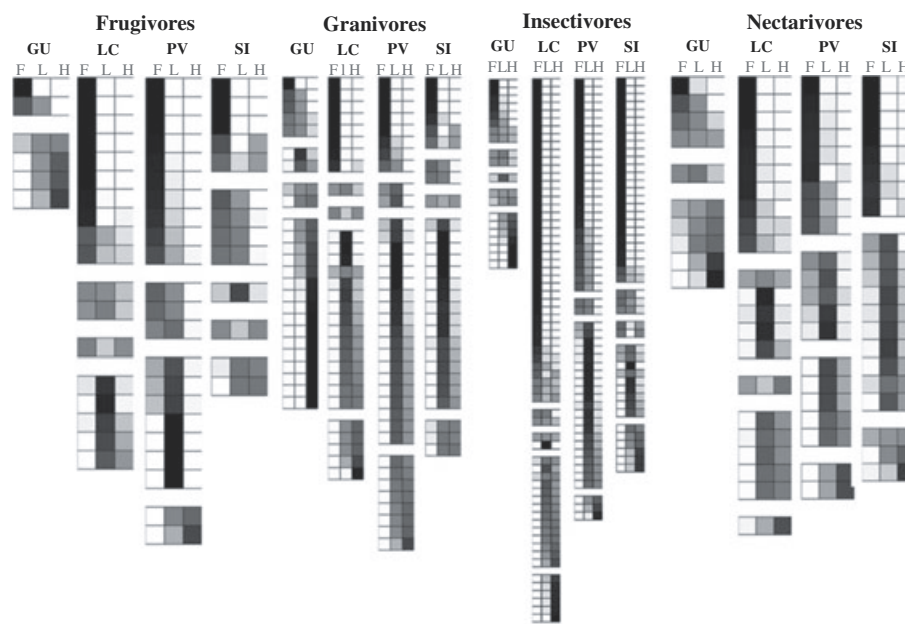
Fig. 3. Response diversity of avian communities in Costa Rica (Karp *et al.*, 2011). The figures represent cluster analyses based on relative abundances of species in forest (F), low-intensity land use (L), and high-intensity land use (H). Rows are individual species, and columns are study regions: Guanacaste (GU), Las Cruces (LC), Puerto Viejo (PV), and San Isidro (SI). Dark-filled boxes indicate higher relative abundance. Species are grouped together by similar responses to land-use intensification (all species within the same group have >0.25 correlation coefficients). Groups of species are separated from each other by empty rows. Because multiple groups are present for each guild and region, it is clear that species within each guild respond differently to land-use intensification and thus, exhibit response diversity. Reproduced with permission from Karp *et al.* (2011).

approach of Karp *et al.* (2011) may indicate an important direction; it implies that the evaluation of response diversity after identifying the key effect traits (in terms of their functional contributions and vulnerability to disturbance) helps to improve the ability of an ecosystem to sustain the functional and service roles biodiversity provides. This view is based on the view of trait-based redundancy and functional richness, and so may not be sufficient to take a larger number of functional contexts into account. However, considering realistic limitations, such as physical limits, financial costs and protection efforts, this approach is rationally operational in restoring and conserving naturally functioning ecosystems.

Another important issue is involved with phenotypic plasticity of species traits. There is now a growing body of literature that demonstrates the importance of intraspecific variation of traits in considering community processes (e.g. Laughlin *et al.*, 2012; Violle *et al.*, 2012). Traditionally, ecologists have long recognized that the traits of an organism may change according to environmental conditions (acclimation). For example, trees acclimate to changing light conditions *via* corresponding morphological changes (Horn, 1971; Küppers, 1989; Poorter & Werger, 1999; Mori, Mizumachi & Sprugel, 2008). In addition to overall changes in tree morphology, individual leaves are also able to respond to their local light conditions through appropriate adjustment of leaf traits such as lifespan, nitrogen content, size, and dry matter content (Reich *et al.*, 1991; Niinemets

& Lukjanova, 2003; Mori & Takeda, 2004). Under a particular set of environmental conditions, the ecological fitness of the whole tree is the cumulative result of changes in these morphological and physiological characteristics at various organ levels (Mori & Takeda, 2004). This phenotypic plasticity clearly indicates that responses (e.g. light acclimation) and performance (e.g. photosynthesis) are the outcomes of interactions of numerous traits within an individual. Yet, in scaling up from individual functional traits to community-level processes, traits are generally averaged for each species (Reiss *et al.*, 2009), making it difficult to evaluate functional traits. Most studies have regarded leaf traits as functional effect traits, since community-average leaf traits influence the rates of biogeochemical processes such as primary production, litter decomposition and nutrient cycling. Note that in the example above, traits of each leaf vary in response to variations in local light availability, and all leaves contribute to the overall functionality of the whole tree. This is comparable to the cumulative responses of species leading to an overall community response (Hillebrand & Matthiessen, 2009). In summary, effect traits always respond in some way to extrinsic changes, and cumulatively determine community-level performance (Suding *et al.*, 2008). Thus, actually, many functional effect traits are nested within functional response traits (Díaz & Cabido, 2001; Suding *et al.*, 2008).

It should be noted that if strong overlaps exist between effect and response traits, effect traits alone are useful
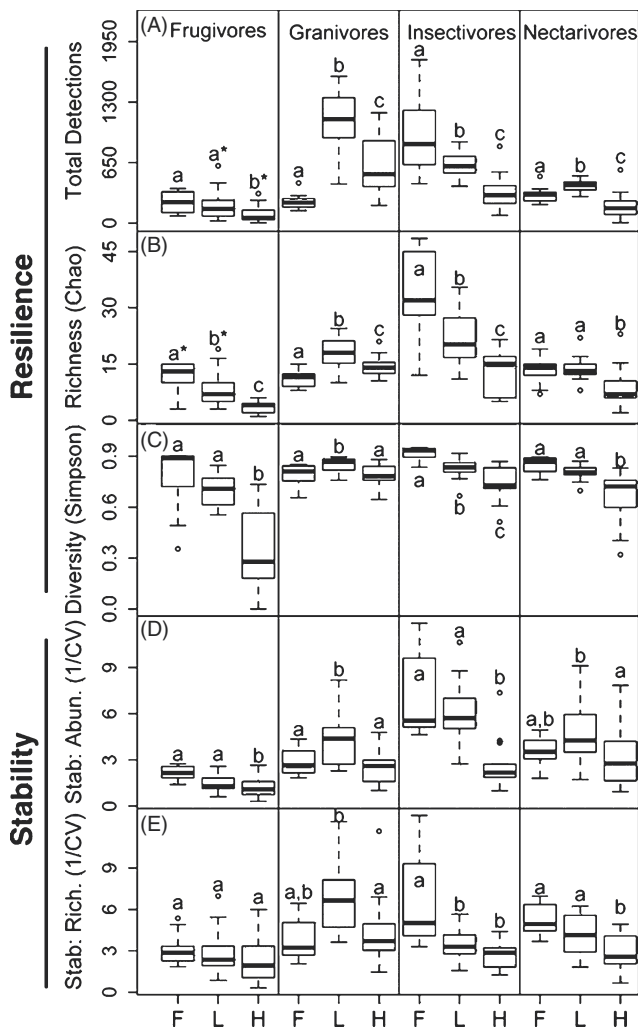
Fig. 4. Resilience of guild structure [(A) total detections, (B) species richness, and (C) diversity] and stability [the inverse of 10-year variation in (D) total detections and (E) species richness] along a land-use gradient (F, forest; L, low intensity; H, high intensity) in avian communities in Costa Rica (Karp *et al.*, 2011). Letters denote significance under Tukey *post-hoc* or Wilcoxon signed rank tests ($P < 0.05$). Asterisks denote significance of $0.05 < P < 0.1$. Whiskers represent minimum and maximum values without outliers (circles) defined as two times the interquartile range subtracted and added from the first and third quartile (the bounds of boxes). Box and whisker plots show that birds were more resilient and stable in low- than high-intensity land use. Reproduced with permission from Karp *et al.* (2011).

as a marker for the maintenance of ecosystem functions (e.g. Lavorel *et al.*, 2011). However, the two are not always correlated, and thus the consideration of response diversity in addition to effect diversity is often important and practical. In fact, it would be interesting for future studies to quantify the extent to which functional effects and responses are correlated across species, and it is important to determine which types of ecosystem functions could be threatened if sufficient attention is not paid to functional responses.

(3) How does response diversity change with increasing environmental pressure?

Species with high sensitivity to environmental stress are often preferentially lost in response to environmental pressures such as habitat fragmentation and altered disturbance regimes (Smith & Knapp, 2003; Gonzalez & Loreau, 2009). In the presence of interspecific interactions, such non-random extinctions can ultimately decrease the compensatory capacity of a community (Ives & Cardinale, 2004). This anthropogenic erosion of community resilience may result from changes in response diversity, because it is response diversity that ensures functional compensation (Leary & Petchey, 2009).

In theory, non-random loss of species is expected to decrease response diversity, ultimately leading to a loss of some ecosystem processes. However, in reality, the meta-analysis of Laliberte *et al.* (2010) showed that response diversity (measured for each individual effect group in each of the 18 studies) can increase, sometimes dramatically, with land-use intensification. Mayfield *et al.* (2010) also found numerous response trajectories of functional traits after land-use change. One possible reason for such variability in response diversity is that, in addition to external pressures, response diversity is influenced by internal factors such as changes in interspecific competition, facilitation, and food-web structure. For example, if a dominant species sensitive to anthropogenic pressures became extinct and the newly available resource was then partitioned among multiple species sourced from outside the community, the total number of functionally similar species would increase as a result of complementary resource use by these new colonizers. This would in turn increase the response richness and probably also the response diversity of the community. This example assumes that a competitively dominant species can be more vulnerable to environmental changes than are other subordinate species (Sasaki *et al.*, 2009b), and also assumes an open system. Most theoretical and experimental studies assume a closed system in which compensatory dynamics can involve only the original members of a local community (e.g. McGrady-Steed & Morin, 2000; Wohl, Arora & Gladstone, 2004). In reality, however, ecosystems are open systems (Mori, 2011) in which meta-community dynamics (Wilson, 1992; Leibold *et al.*, 2004) are commonplace. Indeed, in real natural ecosystems the effects of species loss on response diversity are often complex; some observations suggest that changes in response richness associated with realistic species addition or loss do not necessarily alter ecosystem functionality.

Here, we describe the consequences of realistic species addition or loss on functional diversity using an example from a rangeland ecosystem. In rangelands, livestock grazing selectively affects those plant species that have relatively high palatability (Pakeman, 2004). A typical example is that grazing often suppresses competitively dominant but highly palatable grasses and thus favours diversity by allowing the increase of subordinate grasses and forbs (Bakker & Olff, 2003; Sasaki *et al.*, 2009b). For instance, Sasaki *et al.* (2009b)
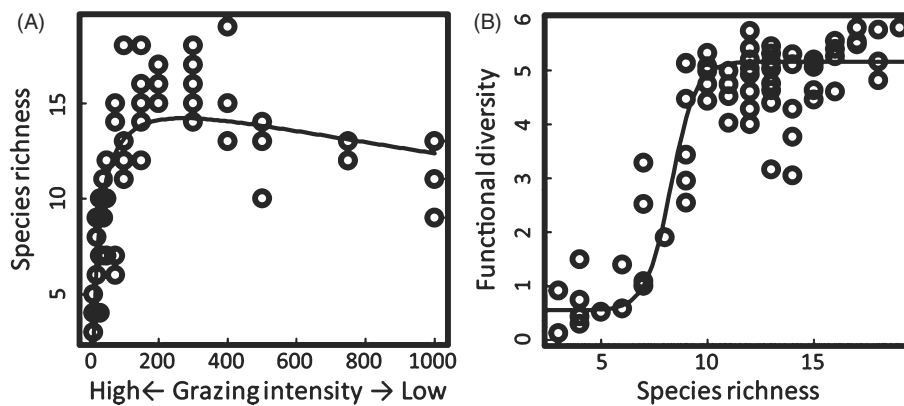
Fig. 5. Observational evidence for the consequences of realistic species addition or loss on functional diversity. (A) The maximization of species richness by certain intermediate levels of grazing, taken from Sasaki *et al.* (2009*b*). The axis of grazing intensity represents the distance (m) from livestock camps or water points, which form the source of grazing gradients. Smaller values are thus indicative of higher grazing intensity. (B) The relationship between species richness and functional diversity along a gradient of grazing intensity, taken from Sasaki *et al.* (2009*a*). The maximization of species richness at certain intermediate levels of grazing does not lead to a proportional increase in functional diversity, as a surrogate for grassland functionality. Reproduced with permission from Sasaki *et al.* (2009*a*,*b*).

showed that species richness in Mongolian grasslands can be maximized by certain intermediate levels of grazing (Fig. 5A). Determining the relationship between species richness and functional diversity along a gradient of grazing intensity could therefore have important implications for predicting the effects on ecosystem functionality that may result from realistic species addition or loss in response to grazing regimes. Because species differ in their inherent responses to a given disturbance (Yachi & Loreau, 1999), the addition or loss of any species would lead directly to a respective increase or decrease in response richness. Sasaki *et al.* (2009*a*) demonstrate that maximization of species richness at certain intermediate levels of grazing apparently does not produce a proportional increase in functional diversity, as a surrogate for grassland functionality (Fig. 5B). Their results also indicate that below a certain level of species richness, loss of species caused by grazing has no effect on functionality (Fig. 5B). They suggest that two factors are responsible for these patterns: non-random species loss (dominant and palatable grasses are affected first), and intrinsic similarities in the functional trait space of different species. Regarding the latter, theory and empirical evidence suggest that in rangeland ecosystems with a long history of grazing and aridity, traits for grazing resistance evolve convergently in multiple taxa (Adler *et al.*, 2004; Cingolani, Noy-Meir & Diaz, 2005). An additional study (Sasaki *et al.*, 2012) indicates that whilst species richness changes in response to grazing pressure (Sasaki *et al.*, 2009*b*), ecosystem services of particular importance in the rangeland context (e.g. herbage nutritive value) remain relatively constant below a certain level of grazing intensity.

In fact, the above example does not illustrate fully the long-term consequences for ecosystem services; it is possible the decline of species richness may make the community vulnerable to different types of subsequent environmental change (e.g. drought and biological invasion;

Tilman & Lehman, 2001). However, the incongruity of change pattern between species richness and functional diversity may potentially have significant implications for ecosystem functioning (Flynn *et al.*, 2009; Sasaki *et al.*, 2009*b*). Future research such as long-term experiments including the manipulation of other drivers would benefit a deeper understanding of possible effects of the actual loss of species on functional response diversity. Considering that some experimental evidence shows a non-random loss of diversity may lead to a substantial decline in a process rate (e.g. Zavaleta & Hulbey, 2004; Bracken *et al.*, 2008; Isbell *et al.*, 2008), the example illustrated above has important implications. Because meaningful decisions about biological conservation should consider realistic threats on ecosystem functionality (Perrings *et al.*, 2011), additional studies which quantify actual capacity of real ecological communities through response diversity (e.g. Karp *et al.*, 2011) are required (Tscharntke *et al.*, 2012).

Another possible explanation for observed variability in response diversity is the wide variety of causal anthropogenic pressures, such as fertilization and nitrogen loading (substance input), biological invasion (community alteration), clear-cut and slash-and-burn practices (resource overuse), and land abandonment (resource underuse). Although detailed quantifications are lacking, heterogeneous responses of species to different pressures lead to complex changes in response diversity when these pressures intensify. In addition, real ecosystems are likely to experience the simultaneous effects of multiple sources of change; for example, the impacts of climate change on certain threatened species are further complicated by habitat loss and fragmentation, leading to the ongoing debate about assisted colonization (e.g. Lawler & Olden, 2011). Tilman & Lehman (2001) also speculated that, since the impact of multidimensional environmental changes is likely multiplicative, a series of relatively small changes may be as important as a single

major change. If so, focusing on a narrow range of response diversity (that is, focusing exclusively on a single major driver) may lead to undesirable management outcomes. Most anthropogenic pressures on ecological systems interact with other co-existing stressors. In the current context of global change (Sala *et al.*, 2000), predicting the future trajectories of response diversity in real ecosystems is extremely challenging (Mayfield *et al.*, 2010).

Notably, the evaluation of response diversity based on species-level attributes needs reconsideration. Whilst much of the established theory assumes equal abundance of all species, Hector *et al.* (2010) suggested that the stabilizing effects (insurance effects) of species diversity are, in reality, strongly influenced by abundance. Changes in population abundance within a community should therefore be taken into consideration when evaluating community resilience. This is especially so because extinction of only a single species could result in significant or even irreversible consequences should this species contribute greatly to ecosystem functioning by virtue of its high abundance (e.g. foundation species; Ellison *et al.*, 2005). Dominant species may often play a crucial role in maintaining ecosystem processes (Smith & Knapp, 2003; Hillebrand, Bennett & Cadotte, 2008), though the contention surrounding this issue is illustrated by the differing perspectives on Grime (1998)'s mass ratio hypothesis (e.g. McLaren & Turkington, 2010; Sasaki & Lauenroth, 2011). Traditional theory involving density compensation predicts that species loss will have little effect on ecosystem functioning because of the expected community-wide increases in mean population abundance (Gonzalez & Loreau, 2009). However, in reality, Winfree & Kremen (2009) showed that in agricultural fields of the western and eastern United States, crop pollination is steadily maintained in the absence of density compensation among species, by high response diversity of native bees (measured as variability in the density of each bee population in response to changes in native vegetation cover). Similar findings were reported for a large dataset of bird communities in Costa Rica (Karp *et al.*, 2011). These studies suggest that density compensation is not a ubiquitous mechanism by which ecosystem services are stabilized and maintained in real systems, and further studies are thus necessary quantitatively to separate functional compensation from density compensation. We suspect that the tight control and unrealistic levels of species evenness in many experimental systems designed to investigate the diversity-stability relationship may make the resultant knowledge difficult to incorporate into real conservation strategies. Actually, a recent meta-analysis found a strong effect of evenness on diversity-functionality relationships (Zhang, Chen & Reich, 2012), although several studies have found no major influences of evenness in stabilizing ecosystem functioning (e.g. Isbell, Polley & Wilsey, 2009). Therefore, further studies on the interactive effects of species richness and evenness (or dominance) on ecosystem functioning are required to understand how response diversity is stabilized or endangered under environmental fluctuations.

(4) How do declines in response diversity lead to a shift in ecosystem states?

A functionally diverse community (i.e. an assemblage with high effect trait diversity) can perform various ecosystem processes simultaneously because of the complementarity between different groups of species. Response diversity is important for the long-term maintenance of this multifunctionality. According to the resilience theory, changes are ubiquitous in ecological systems and the resilience of a system determines its capacity for reorganization while undergoing change (Berkes, Colding & Folke, 2003; Chapin, Kofinas & Folke, 2009; Gunderson, Allen & Holling, 2009). This is consistent with the insurance concept of biodiversity; the self-organisation capability of a system in the face of environmental stresses and disturbances is generally considered to be proportional to diversity. However, although several studies have suggested that response diversity is equivalent to ecosystem resilience (Peterson, Allen & Holling, 1998; Elmqvist *et al.*, 2003; Laliberte *et al.*, 2010; Karp *et al.*, 2011), to date there has been no robust explanation of the link between the two.

To sustain optimal ecosystem functionality (especially in the face of environmental change) it is necessary to preserve functional groups of species that will be able to contribute to system renewal and reorganization. Response diversity is known to safeguard ecosystems against functional degradation and collapse (e.g. Elmqvist *et al.*, 2003). To the best of our knowledge, our conceptual model shown in Fig. 6 is the first proposal that explains a mechanism by which a drop in response diversity can erode the ecosystem resilience of a naturally functioning ecosystem, increasing the likelihood of critical ecosystem degradation.

Suppose functional diversity (effect diversity) is positively correlated with the number of ecosystem functions considered (Fig. 6A) (for simplicity, we treat functional diversity and functional richness as synonymous). With increasing anthropogenic pressures (driver intensification), functional effect diversity may show an abrupt decline at a certain ecological threshold (Fig. 6B), resulting from aggregated extinctions and the consequent loss of response diversity (Fig. 6C). The initial slow decrease in functional effect diversity (Fig. 6B) is caused by loss of sensitive functional groups (such as FG3 in Fig. 6C). With driver intensification, additional extinctions occur of groups that are less sensitive, leaving behind only the tolerant groups (such as FG1 and FG2). Aggregation of these extinctions (such as FG4 to FGi) may result in a sharp decline of functional effect diversity which leads to major loss of ecosystem functionality (Fig. 6D), inducing a critical regime-shift of the system (from Position b to c, Fig. 6E). In this ball-and-cup model of ecosystem resilience (Fig. 6E), the ball (ecosystem) is continually vibrating in response to external pressures. Resilience of the ecosystem is represented by the width of the right basin of attraction (desirable attractor). Anthropogenic pressures gradually shrink the basin of this desirable attractor while the basin of the undesirable attractor (left cup) hardly changes (transition from Position a–b). Eventually the cumulative loss of response diversity results in the ecosystem dropping
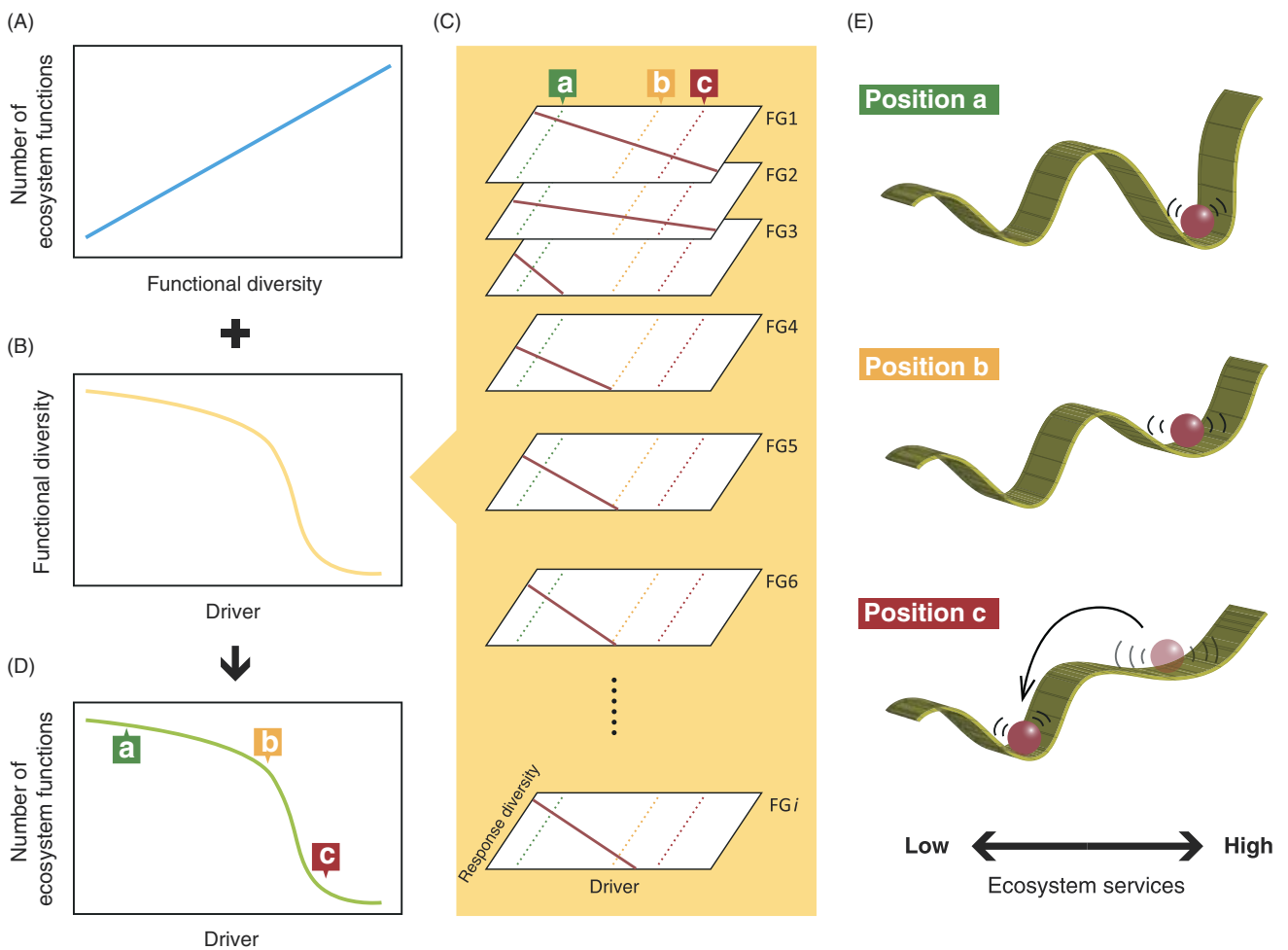
Fig. 6. Relationship between anthropogenic pressures (driver), functional diversity, response diversity, and ecosystem state, showing that accumulated loss of response diversity mediates an abrupt shift in ecosystem state triggered by decreased functional diversity. (A) Relationship between functional diversity and number of ecosystem functions. (B) Non-linear change in functional diversity with increasing pressures. (C) Relationships between response diversity and driver intensity for a series of functional groups (FG). (D) Non-linear change in number of ecosystem functions with increasing pressures. (E) Basic ball-and-cup model of ecosystem resilience. Cups represent attractors (right, desirable; left, undesirable) into which the ball (ecosystem) is drawn. Positions a–c in E correspond with the same letters in panels (C) and (D).

into the undesirable attractor (transition from Position b–c). In summary, the decline of response diversity as a buffer against environmental fluctuations shrinks the state basin of the multifunctional ecosystem (i.e. reduces resilience) and may eventually lead to loss of essential ecosystem services (i.e. ecosystem degradation).

Our model clearly shows that the sudden shift to an alternative ecosystem state, coinciding with rapid loss of functional diversity, results from the aggregated loss of response diversity. This emphasizes the importance of the trajectories of response diversity with progressive driver intensification. It is noteworthy that under the assumption of a gradual decline of response diversity with increasing anthropogenic pressures (Laliberte *et al.*, 2010), earlier studies have focused exclusively on the initial state of response diversity (the intercept of the driver *versus* response diversity relationship). However, it is clear that more attention should

be paid to the rate of change (slope) of this relationship. In Fig. 6, FG2 has a relatively low diversity of responses to environmental fluctuation, but because of its slow decline with increasing extrinsic pressures it is able to persist in the community even under strong anthropogenic impact. By contrast, most species groups (e.g. FG3 to FG*i*) are seemingly more diverse and stress-tolerant initially, but they are eventually pushed to extinction by progressive driver intensification. Meaningful evaluation of response diversity is therefore necessary. For a given functional group, a proxy for the slope of the driver *versus* response diversity relationship is the dispersion of species in response-trait space. Thus, it is more important to know the degree of variation among species with respect to their responses to environmental change, than to know the number of species with dissimilar responses. Rapidly developing trait databases such as TRY (http://try-db.org; Kattge *et al.*, 2011) could provide the

raw data for determination of dispersion, perhaps using multivariate analyses such as one proposed by Laliberté & Legendre (2010) that can calculate between-species distances for multiple response traits. Note that for simplification, our model (Fig. 6) assumes that changes in response diversity with driver intensification are linear; real relationships are perhaps more complex (Mayfield *et al.*, 2010). This reinforces the importance of focusing on the shape of the driver *versus* response diversity relationship, rather than simply evaluating the response richness at a given time.

This model clearly demonstrates that for conservation of ecosystem resilience, the specific relationship between response diversity and increasing anthropogenic pressure is substantially more important than the initial state of response diversity. Response diversity decreases with increasing anthropogenic pressures (e.g. forest conversion, habitat fragmentation, logging, grazing, and fertilization; Laliberte *et al.*, 2010). Notably, when the species in a given functional group vary widely in their responses to environmental change (i.e. have a high dispersion in response-trait space), even if the number of species in the group (i.e. functional effect redundancy) is low, it may be possible to avoid a drastic decline of response diversity under intensified pressures (Fig. 6).

Our simple model does not incorporate internal biotic interactions that may affect the trajectories of response diversity. Ives & Cardinale (2004) demonstrated mathematically that food-web interactions can reshuffle the order of species with regard to their tolerance of environmental stresses, suggesting that between-species distances of response traits within a community are also highly variable. Given the influences of pre-existing stressors, this variability leads us to conclude that the trajectory of response diversity in response to anthropogenic pressure is not always linear but may rather constitute some form of non-linear dynamic relationship. van Nes & Scheffer (2004) showed mathematically that gradual environmental change results in a gradual response in community composition followed by a sharp shift to an alternative attractor. These theoretical implications impose further complexity and uncertainty upon attempts to predict the pattern of driver-biodiversity-ecosystem services relationships. It is therefore important to determine which types of anthropogenic pressures can drive the ecosystem state rapidly beyond the threshold point *via* alteration of biological properties. To avoid undesirable ecosystem regime shifts, future studies should be directed towards elucidating how species interactions and abiotic factors synergistically determine the trajectory of response diversity.

III. MANAGEMENT IMPLICATIONS

Human activities gradually transform natural disturbances from pulses with characteristic magnitude and frequency, into press (or chronic) disturbances (Bengtsson *et al.*, 2003). Such chronic pressures are expected significantly to erode ecological resilience by shrinking the basin of the desirable attractor and making ecosystems more vulnerable to environmental perturbations (Carpenter & Gunderson, 2001; van Nes & Scheffer, 2004). Given this situation, there is an urgent need for ecological restoration. This study demonstrates that restoration priority should not always be given to functional groups that currently have low response richness and thus appear to be at highest risk of extinction. In reality, groups of species with high response richness at a given time may be more vulnerable to future extinction (in that case, the FGs have larger slopes of the driver-response diversity relationship illustrated in Fig. 6C).

Currently, we have only limited understanding of response diversity (inferred by Tscharntke *et al.* (2008)). However, a focus on response diversity is one of the most effective approaches for preservation of the particular aspects of functional diversity that benefit humans. Using various ecological tools to quantify effect and response traits, it is possible to assess response diversity for ecosystems across the globe. For instance, based on a global data base, Tscharntke *et al.* (2008) found that bird and insect communities are biased to specific functional types (guilds) as a result of responses to agricultural habitat transformation, thereby altering critical functionalities such as seed dispersal, pollination, and biological control. Furthermore, Cumming & Child (2009) found considerable spatial variation of response richness in relation to taxonomic richness in South African birds. This illustrates that species-rich communities are not necessarily diverse in terms of their responses to environmental fluctuations. Therefore, although most previous studies have focused on species richness, it is often more important to describe biodiversity based on functional characteristics (Díaz *et al.*, 2007, 2011; Cadotte, 2011). So, it would be worth requantifying many earlier works for the insurance effects of response diversity. Once available, this information (especially from re-evaluation of observation studies focusing on real ecosystems) will contribute significantly to our search for ways to conserve and rebuild ecosystem resilience, which is a property essential for the survival of our global ecosystems (and thus our global society) in the face of looming anthropogenic pressures on biodiversity and ecosystem services.

Given the serious threat of human-induced species extinction, response diversity is clearly an important point of focus. It is therefore necessary to evaluate how ecological communities respond to various anthropogenic drivers. However, despite the availability of copious trait information, it is still not feasible to quantify response diversity for biological communities in each conservation and management area. Nevertheless, the current knowledge about response diversity is beneficial since it helps to disentangle and clarify various different ideas about species singularity and redundancy. In summary, there is no canonical definition of redundancy. The original meaning derives from the notion that it is not possible to conserve all species in a region by means of reserves so prioritization is essential with considerations of legitimate competing demands for resources (Walker, 1992, 1995). That is,
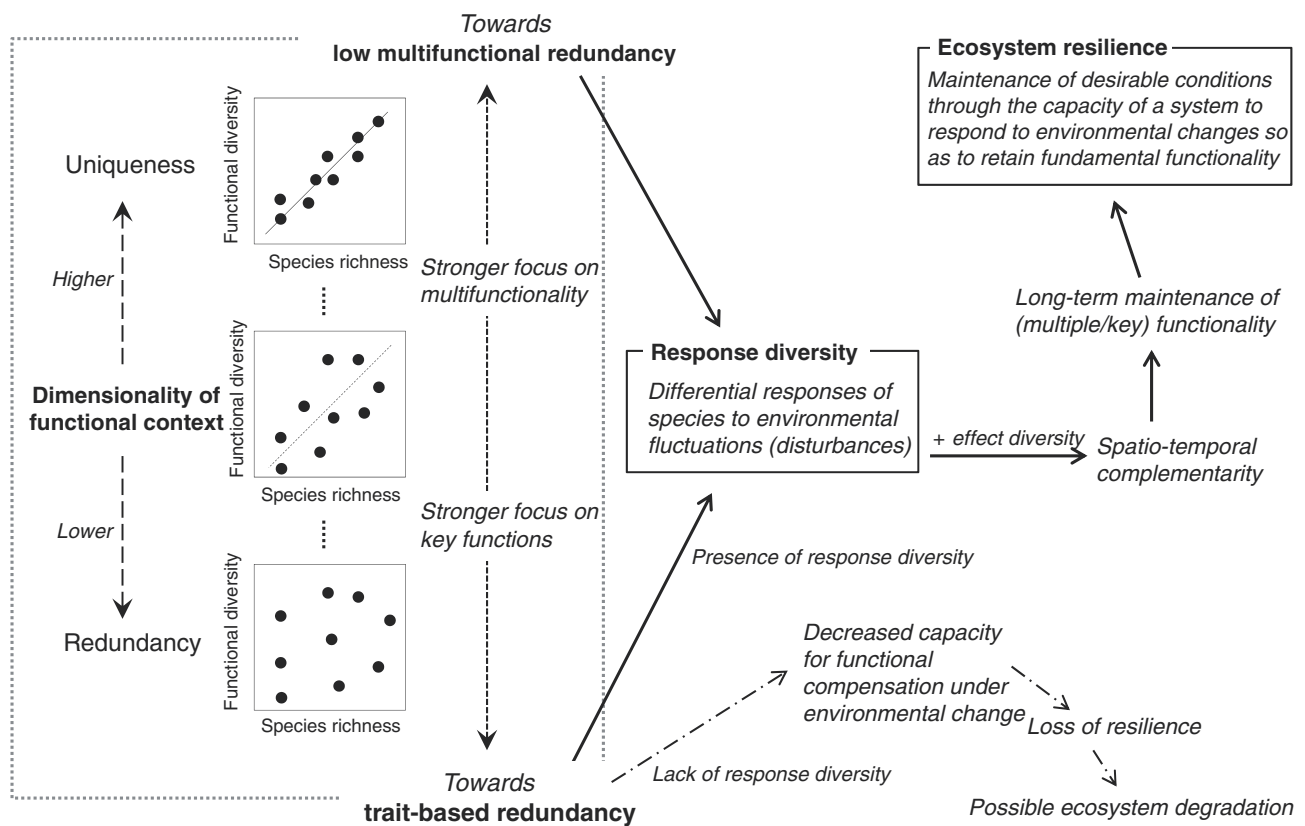
Fig. 7. A conceptual flow diagram relating functional redundancy to ecosystem resilience. We assume here that functional diversity reflects the dimensionality of the functional context. The three panels on the left show three possible relationships between species richness and functional diversity, from close linear correlation (top) to no correlation (bottom) depending on the functional contexts (species singularity or redundancy). Variable patterns of species diversity-functional redundancy have been reported (see Micheli & Halpern, 2005; Petchey *et al.*, 2007; Hoey & Bellwood, 2009; Sasaki *et al.*, 2009*b*; Joner *et al.*, 2011; Zhang, Chen & Reich, 2012).

it is often necessary to prioritize species with functional singularity (e.g. Hoey & Bellwood, 2009). In this context, redundancy does not mean 'unnecessary'; it never implies that no concern exists related to functionally redundant species (Walker, 1995). Practically, fruitful understandings of redundancy therefore rely on the management objectives. As illustrated in Fig. 7, the focus may vary from 'uniqueness' of each species to 'key functionality' supported by diversity. At this juncture, the core message from our synthesis is that response diversity is the key linking the fundamentally analogous but somewhat disjunctive concepts of functional redundancy and the insurance effect of biodiversity.

In particular, the focus on response diversity provides a deeper, process-orientated understanding and recognition of the functional consequences of biodiversity that goes beyond a focus on maximizing species richness and diversity as the ultimate insurance against environmental change. These functional consequences are also essential for the continued survival of humanity, which needs numerous ecosystem services. Ecosystem management plans should at least ensure long-term monitoring to infer the resilience of systems sustained by biodiversity, regardless of their current state of response diversity. This will equip managers to recognize

which ecosystem functions and services are threatened and to undertake the necessary preventative measures before the onset of serious ecosystem degradation and its undesirable consequences.

IV. CONCLUSIONS

(1) Studies on the relationship between biodiversity and ecosystem functioning have led to a significant paradigm shift in our understanding of the way in which biological diversity should be safeguarded (Naeem *et al.*, 2009; Cardinale *et al.*, 2012; Hooper *et al.*, 2012; Naeem, Duffy & Zavaleta, 2012; Tilman, Reich & Isbell, 2012).

(2) Biodiversity conservation should no longer be viewed as the sole ultimate 'objective', but rather as an effective and essential means of ensuring the long-term provision of ecosystem services that depend upon biodiversity and that are required for human well-being. In this regard, it is important to select crucial ecosystem services as priorities for conservation and management, and then to specify which ecological properties of these systems are priorities for restoration and conservation.

(3) To ensure key ecosystem functioning, the greatest attention should be focused on those elements of diversity that respond most strongly to environmental fluctuations, and in turn, most strongly influence the environment. Based on the emerging view of response diversity, it is important to reevaluate critically the present situation, in which species richness is prioritized strongly among the various aspects of biological diversity. The functional ecology view that treats biodiversity as both cause and effect enables us to face uncertain environmental changes adaptively without losing the multifunctionality of ecological systems.

(4) Thus, although the concept of response diversity is not new, we expect and recommend further studies on the insurance effects of response diversity, as well as a focus on effect diversity. Such studies will provide the requisite knowledge about biodiversity-stability and biodiversity-functionality relationships for informed, meaningful and successful ecosystem management to be achieved.

V. ACKNOWLEDGEMENTS

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VII. SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

Figure S1. Temporal publication trends in three related research fields, based on papers in the ISI *Web of Science* database. BEF, biodiversity-ecosystem functioning studies, located using the key words 'biodiversity', and 'ecosystem functioning' or 'ecosystem functionality' or 'ecosystem functions' or 'ecosystem processes' or 'ecosystem properties'. FD, studies of functional diversity, located using the key words 'functional diversity' and 'biodiversity'. RD: studies of response diversity, located using the key words 'response diversity' and 'biodiversity'. Despite the drastic increase in BEF studies since 1991, the rise of FD studies has been relatively slow, and very few RD studies have been published to date.