REVIEW

Beyond species: functional diversity and the maintenance of ecological processes and services

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Summary

1. The goal of conservation and restoration activities is to maintain biological diversity and the ecosystem services that this diversity provides. These activities traditionally focus on the measures of species diversity that include only information on the presence and abundance of species. Yet how diversity influences ecosystem function depends on the traits and niches filled by species.

2. Biological diversity can be quantified in ways that account for functional and phenotypic differences. A number of such measures of functional diversity (FD) have been created, quantifying the distribution of traits in a community or the relative magnitude of species similarities and differences. We review FD measures and why they are intuitively useful for understanding ecological patterns and are important for management.

3. In order for FD to be meaningful and worth measuring, it must be correlated with ecosystem function, and it should provide information above and beyond what species richness or diversity can explain. We review these two propositions, examining whether the strength of the correlation between FD and species richness varies across differing environmental gradients and whether FD offers greater explanatory power of ecosystem function than species richness.

4. Previous research shows that the relationship between FD and richness is complex and context dependent. Different functional traits can show individual responses to different gradients, meaning that important changes in diversity can occur with minimal change in richness. Further, FD can explain variation in ecosystem function even when richness does not.

5. *Synthesis and applications.* FD measures those aspects of diversity that potentially affect community assembly and function. Given this explanatory power, FD should be incorporated into conservation and restoration decision-making, especially for those efforts attempting to reconstruct or preserve healthy, functioning ecosystems.

Key-words: biodiversity conservation, community assembly, ecosystem function, ecosystem services, functional diversity, restoration, species richness

(In) a description of the essential characters of individual birds…(it) is more difficult to furnish whether they resemble or are different from one another in the shape of the limbs, the movements they make, the way they feed, the care of their young, their mode of flight, and their style of defense. Let it, however, be remembered that, in general, their bodily conditions and their other peculiarities are due to definite cause.[Emperor Frederick II, quotation taken from Wilkins (Wilkins 2009), using the Wood and Fyfe translation (Frederick II of Hohenstaufen 1943)]

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Introduction

Throughout the history of biological thought, recognition of the importance of species' traits and ecologies has informed our understanding of speciation and how species interact with the world. For example, the heretic Holy Roman Emperor and naturalist, Frederick II (1194–1250), rejected the Aristotelian classification scheme based on species essences for one based on physical characters and behaviour (Wilkins 2009). In this tradition, community ecologists are increasingly realizing that

a trait-based, causal view of community diversity may be more meaningful than species richness or composition (McGill *et al.* 2006). Ecologists routinely lump species together according to similarities in function or in response to abiotic conditions (Grime 1973), but the use of traits in ecology has greatly expanded recently. Ecologically, a species is a collection of individuals with phenotypic and behavioural traits that determine when and where they can exist and how they interact with individuals from other species (McGill *et al.* 2006). This view of species as an assemblage of traits is reshaping how ecologists measure diversity, assess coexistence and restore habitats (Fukami *et al.* 2005). More importantly, though, is the emerging view that by measuring and understanding trait diversity, we can make better conservation and restoration decisions.

A trait is any measurable feature of an individual that potentially affects performance or fitness and can be physical (e.g. plant branching pattern, predator tooth morphology), biochemical (e.g. plant photosynthetic pathway, presence of secondary metabolites), behavioural (e.g. nocturnal vs. diurnal foraging, females cannibalizing males) or temporal or phenological (e.g. flowering time, pelagic duration of larval stage). Depending on the exact nature of the measured traits, traits can influence environmental tolerances and habitat requirements. Thus, traits determine where a species can live (Steneck & Dethier 1994; Lavorel *et al.* 1997); how species interact with one another, informing the strength and axes of competition or the consumption efficiency of a predator (Davies *et al.* 2007); or even the contributions of species to ecosystem function, for example, through differences in nutrient use and storage (Hillebrand, Bennett & Cadotte 2008; Mokany, Ash & Roxburgh 2008; Lavorel *et al.* 2011).

With the increasing awareness that species' traits influence coexistence and ecosystem function, ecologists now quantify trait variation or multivariate trait differences within a community, generically referred to as 'functional diversity'. Functional diversity (FD) is measured in a multitude of ways (see Appendix S1 Supporting Information). Technically, it represents the diversity of traits but is taken to represent the diversity of species' niches or functions (Petchey, Hector & Gaston 2004; McGill *et al.* 2006; Petchey & Gaston 2006; Villeger, Mason & Mouillot 2008). As a representation of niches or functions, FD has been used to understand how species richness or diversity relates to ecosystem function (Petchey, Hector & Gaston 2004; Cadotte *et al.* 2009; Flynn *et al.* 2011) and how diversity responds to environmental stress or disturbance (Norberg *et al.* 2001; Suding *et al.* 2008). The power of FD is that unlike traditional measures of species richness or diversity, it presupposes a mechanistic link between diversity and the ecological phenomena in question. This intuitive link is attractive, and FD is appearing in the literature with increasing frequency (Fig. 1).

To advocate for the use of FD measures assumes mechanistic links with niche and functional aspects of species diversity. Here, we review the literature to determine how FD differs from traditional measures of diversity (with a primary focus on richness given its widespread use) and what FD can tell us about ecosystem function.
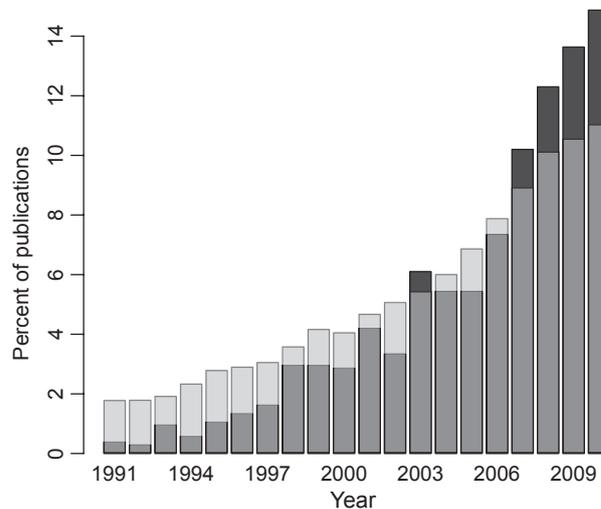

Fig. 1. The yearly percentage of publications found using ISI Web of Science using the keywords 'functional diversity' and 'ecology' (dark bars), compared with the yearly percentage of publications found using 'community ecology' (transparent light bars) for all papers published 1990–2010.

Are richness and FD correlated?

Covariance between species richness and functional richness creates challenges in discerning the dynamics generating patterns and their relative impacts on ecosystem processes (Naeem 2002). The justification for the use of FD measures as a pragmatic representation of potential niche differences rests on the assumption that variety of functional trait values is likely to give insight into ecosystem function beyond that provided by species diversity measures (e.g. Diaz & Cabido 2001; Petchey & Gaston 2002b). Still, several biodiversity-ecosystem function (BEF) studies have manipulated species richness and then deduced FD trends, presuming a positive correlation between these two diversity measures (Naeem & Wright 2003). It is useful, then, to evaluate the validity of species richness as a proxy for FD. Species richness and functional richness are inherently linked. Monocultures fall into one functional group, whereas polycultures are usually sampled from a pool of species representing multiple functional traits; therefore, the correlation between species richness and functional richness theoretically ranges from negligible to a one-to-one relationship. Beyond this, the precise relationship between species richness and functional richness remains unresolved for most natural systems (Naeem 2002).

A study of ant diversity along a successional gradient revealed that the increase in ant species richness and diversity with forest age was mirrored by functional richness and FD measures (Bihn, Gebauer & Brandl 2010). Similarly, Heino (2008) noted a strong correlation between species richness and functional richness in littoral macroinvertebrate communities. One explanation for a strong positive correlation between FD and richness is the selection effect as defined by Mayfield and colleagues (Mayfield *et al.* 2010). This selection effect occurs when the likelihood of capturing the range of functional trait

values in a regional species pool increases with local species pool size (Huston 1997). A random or uniform distribution of species along a functional dissimilarity spectrum would support a proportional relationship between species richness and functional richness; however, this distribution is atypical in natural systems (Diaz & Cabido 2001). Where species converge into relatively discrete functional strategies, Diaz & Cabido (2001) propose a positive linear relationship, with species richness exceeding functional richness.

Despite these examples of positive linear relationships between species richness and FD, this trend is not universally supported. Functional redundancy, trait inclusion in measures of FD, the FD metric used (see Appendix S1) and environmental filters can all shape the relationship between species diversity and FD.

Treating species richness as a proxy for FD implies that every added species increases FD by an identical amount (Petchey, Hector & Gaston 2004). However, in assemblages with functionally redundant species, random species loss is unlikely to decrease FD much, and an influx of species is unlikely to contribute different functional traits to the assemblage, especially when local and regional environmental conditions permit the same values and variety of functional traits (Mayfield *et al.* 2010). Fonseca & Ganade (2001) calculated that 75% of species could be lost from an Argentinean plant community by random extinction before functional group richness would decrease, illustrating the divergence between species richness and functional group richness in functionally redundant systems. If, instead, species diversity remains static because colonization matches species loss, FD may fluctuate fairly independently of species diversity. This pattern could be seen if functionally unique species colonize an area following loss of functionally redundant species, or *vice versa* (Mayfield *et al.* 2010).

Different functional traits have different levels of redundancy within an assemblage, and there are many possible permutations of the species diversity–FD relationship within a single community (Fonseca & Ganade 2001; Naeem & Wright 2003). When assessing FD, a large number of functional traits increase the ability to detect functional differences between species (it increases the 'trait space' in which they can vary), reducing the impact of species identity and the likelihood of classifying species as functionally redundant (Petchey & Gaston 2002b). Only traits related to the function of interest should be included in the FD metric; excessive incorporation of neutral or positively correlated traits will cause artificial convergence of FD and species diversity (Naeem & Wright 2003), while negatively correlated traits will inflate FD values. However, *a priori* determination of the functional impacts of traits is not likely to be known, but traits used in FD measures should be uncorrelated.

The relationship between species diversity and FD is also influenced by the sensitivity of the FD metric to functional differences between species. While Fonseca & Ganade (2001) found high redundancy in functional groups, other measures of FD typically reveal less redundancy (Petchey & Gaston 2002a). Species richness will be greater than measured

functional richness when broad functional groups subsume subtle variation between functionally clustered species. In other words, use of functional groups overestimates functional redundancy, distorting the relationship between measured FD and species diversity and probably masking important functional consequences of some traits (Wright *et al.* 2006).

When modelling plant diversity patterns, Kleidon *et al.* (2009) employed plant growth strategy richness as a surrogate for species richness after confirming that functional richness and species richness patterns corresponded. Without this verification, it is difficult to know the actual relationship between species diversity and FD in a given community. Because the species diversity–FD relationship is dependent upon community functional redundancy, the number and identity of the functional traits evaluated, the actual functional implications of particular traits and the FD metric used, use of species richness as a stand-in for functional richness is ill advised.

The key to understanding the relationship between species diversity and FD, and how they affect ecosystem function, is determining how abiotic factors influence these diversity measures. The influence of abiotic variables on community composition and species abundance is expected to affect the relationship between species diversity and FD (Naeem & Wright 2003). Reported trends between species richness or functional richness and environmental gradients can be confounded by the interaction between abiotic factors and by the span of the gradient examined. Turnover of functional groups along a resource axis may be more informative than total species richness in examining biodiversity patterns along environmental gradients (Pausas & Austin 2001). Surprisingly, few studies have assessed overall FD trends in relation to abiotic factors; here, we review how nutrient availability, disturbance, light availability, water availability and temperature affect both species richness and FD.

NUTRIENT AVAILABILITY

Species richness is commonly linked to nutrient availability, but positive, negative and unimodal trends have all been reported (Pausas & Austin 2001). Kleinebecker, Holzel & Vogel (2010) found positive linear correlations between total species richness in peat bogs and availability of N and NH_4Cl-soluble Ca. This trend collapsed when species richness of particular functional groups was investigated. The identity of the dominant functional group varied along gradients of resource availability. In contrast, N addition reduced species richness in alpine meadows, but alteration to community composition with nutrient supplementation depended upon levels of functional evenness and identity of functional dominants (Wang *et al.* 2010). Functionally diverse communities were prone to composition shifts and increased dominance with nutrient addition because they were more likely to contain a species with functional traits suited to exploitation of the added resource (Wang *et al.* 2010). In fertilization experiments, it is common to find negative relationships between nutrient (N, P and K) addition and species richness (Critchley *et al.* 2002). High FD in nutrient uptake and utilization strategies could

explain the tendency for nutrient poor soils to foster high species diversity (Lambers *et al.* 2010). Quantifying the levels of multiple nutrients may elucidate limiting factors and clarify confounding interactions when exploring the impact of a nutrient on diversity patterns.

DISTURBANCE

Mayfield *et al.* (2010) proposed a wide variety of relationships between species diversity and FD as communities respond to land-use change. Biswas & Mallik (2010) reported that plant species richness, species diversity, functional richness and FD were all maximized at intermediate disturbance intensity in temperate upland and riparian systems. However, they discovered a disconnect between measures of diversity moving from moderately to greatly disturbed riparian sites: species diversity and species richness increased while FD and functional richness dropped. Comparing forested and deforested (heavily disturbed) sites, Mayfield *et al.* (2005) found that functional richness for certain traits increased more rapidly with species addition in forested areas, but this trend was reversed for other functional traits. Disturbance altered the link between species richness and functional richness, and the relationship observed depended on the traits considered.

LIGHT, WATER AVAILABILITY AND TEMPERATURE

Light limitation can reduce species richness and species diversity, but once again the impact depends upon functional identity and functional evenness in the community (Wang *et al.* 2010). Light attenuation precludes seedling establishment of photophilic plants (Wang *et al.* 2010). Plants with erect growth forms or that allocate a large proportion of their resources to early shoot growth should be better competitors in low light conditions (Hautier, Niklaus & Hector 2009). As environmental filters (such as light) act on functional traits, understanding the correspondence between abiotic factors and particular functional traits would help predict which species from a regional pool could colonize and survive in area (Keddy 1992). Reductions in light, precipitation or temperature restrict the pool of viable growth habits, lowering species richness (Kleidon *et al.* 2009).

In a natural system in New South Wales, Australia, rainforest and eucalypt tree species richness were both greatest at high temperature and moderate rainfall (Austin, Pausas & Nicholls 1996; Pausas & Austin 2001). However, these two functional types diverged in their tolerance of insolation. Both total tree species richness and rainforest tree species richness decreased as light levels increased. Eucalypt species richness, in contrast, exhibited a unimodal response. This highlights the importance of examining multiple abiotic gradients in conjunction before making conclusions about biodiversity patterns.

Pausas & Austin (2001) reasoned that the variety of response curves might be an artefact of the range in resource availability examined; a broader gradient could reveal a unimodal relationship (Grime 1973). Peat bog plants of the Kleinebecker, Holzel & Vogel (2010) study must cope with stressful environmental conditions: low nutrient levels and waterlogged soils. The positive linear relationship between species richness and nutrient supply (Kleinebecker, Holzel & Vogel 2010) suggests that the entire nutrient gradient studied fell below optimal levels. Species richness decreased linearly with water level, indicating that water levels exceeded that which would support peak species richness. In other words, unimodal trends best describe the changes in diversity along many environmental gradients; other response curves reported may represent a segment of the encompassing unimodal trend (Pausas & Austin 2001).

The above examples illustrate that (i) an assortment of response curves of biodiversity measures to abiotic factors (even within the same abiotic factor) is possible; (ii) abiotic factors interact, and the quantification of multiple abiotic factors should clarify diversity-environment patterns; and (iii) different functional types often respond in different ways to environmental gradients, resulting in species richness trends within certain functional groups counter to the overall species richness trend. Logically, an organism's ability to cope with extremes in resource availability should be a reflection of its corresponding functional trait values.

How well does functional diversity explain ecosystem function?

Since it was first introduced to the field in the 1990s, FD has revolutionized BEF research (Tilman *et al.* 1997). Before they were first empirically tested, theories about the effects of biodiversity on ecosystem function incorporated FD in explanations of causation (Chapin, Schulze & Mooney 1992), recognizing that species' functional traits were probable determinants of ecosystem function. When the early experiments were designed, however, they defined biodiversity as species richness, probably for the ease of manipulation (Naeem *et al.* 1994; Tilman & Downing 1994).

Research was initially motivated by accelerating rates of biodiversity loss that became increasingly apparent over the last several decades (Tilman & Downing 1994). To determine the impact of these extinctions, researchers created communities containing different numbers of species and compared ecosystem function among these communities. The focus on species richness was thought to reflect real-world biodiversity loss scenarios, where species were affected uniformly by extinction (Naeem *et al.* 1994).

One of the strongest explanations for the BEF relationship is that as biodiversity increases, so too does the diversity of functional traits. These traits determine how an organism extracts resources from its environment (McGill *et al.* 2006). Thus, as FD increases, a community increases its partitioning of the total available resources. Griffin *et al.* (2009) found that the inclusion of highly productive species largely explained total productivity in macroalgal communities, but for plots that exhibited overyielding, the additional yield of mixtures relative to monocultures, FD provided a better explanation of productivity. In cases where overyielding increases with FD, especially when the assemblage productivity is greater than the most productive monoculture, it is difficult to postulate a

better mechanistic explanation than the partitioning of resources along axes represented by the chosen traits.

Griffin *et al.* (2009) cautioned that FD does not necessarily isolate a precise mechanism for overyielding. They were referring, however, to the fact that FD can provide evidence for resource partitioning, but it does not specify along which niche axis resources are being partitioned (Griffin *et al.* 2009). A FD–productivity relationship invites the conclusion that resource partitioning explains the BEF relationship, but it does not indicate what the resources are. Nonetheless, when data for several traits are available, model selection methods can clarify the relative contribution of each trait to overyielding (e.g. Cadotte *et al.* 2009; Flynn *et al.* 2011).

Functional trait-based approaches can also help identify selection effects. The idea that certain species contribute disproportionately to ecosystem function rests on the premise that those species possess particular functional traits that allow them to capture a greater proportion of the total available resources than other species. Functional trait measurements can reveal whether or not species with similar trait values are contributing the most to ecosystem function. While trait values may elucidate the degree of selection effects in an experiment, multivariate FD measures would not be much use for singling out species because they are community-level metrics.

WHY FUNCTIONAL DIVERSITY IS IMPORTANT FOR ECOSYSTEM FUNCTION

Theory predicts that greater differences in resource use lead to increased ecosystem function. The key differences should therefore be in the traits that determine how organisms utilize resources. There are ample theoretical predictions that ecosystem function increases with FD (Diaz & Cabido 2001). These predictions are often found in studies that manipulated species diversity and assumed that FD was being simultaneously manipulated (Petchey & Gaston 2006).

In a theoretical study, Loreau (1998) hypothesized that if species have complementary functional traits, such as root geometry, they will occupy nonoverlapping spatial niches and as species diversity increases, so too will the total occupied niche space. In their review, Diaz & Cabido (2001) found that one of the best explanations for the effects of FD on ecosystem function was that higher diversity of functional traits increases resource-use efficiency in heterogeneous environments.

In practice, direct tests of the mechanistic relationship between FD and ecosystem function are more difficult to perform. In one of the earliest such tests, Tilman *et al.* (1997) planted grassland communities containing varying numbers of functional groups and measured several ecosystem functions. They found that functional richness and composition explained ecosystem function better than species richness. Petchey, Hector & Gaston (2004) reanalysed six BEF experiments and found that multivariate FD metrics explained variation in ecosystem function better than functional richness or species richness. FD can explain variation better than richness because it includes a magnitude (Fig. 2a). For example, if communities in one ecosystem have higher FD than communities in
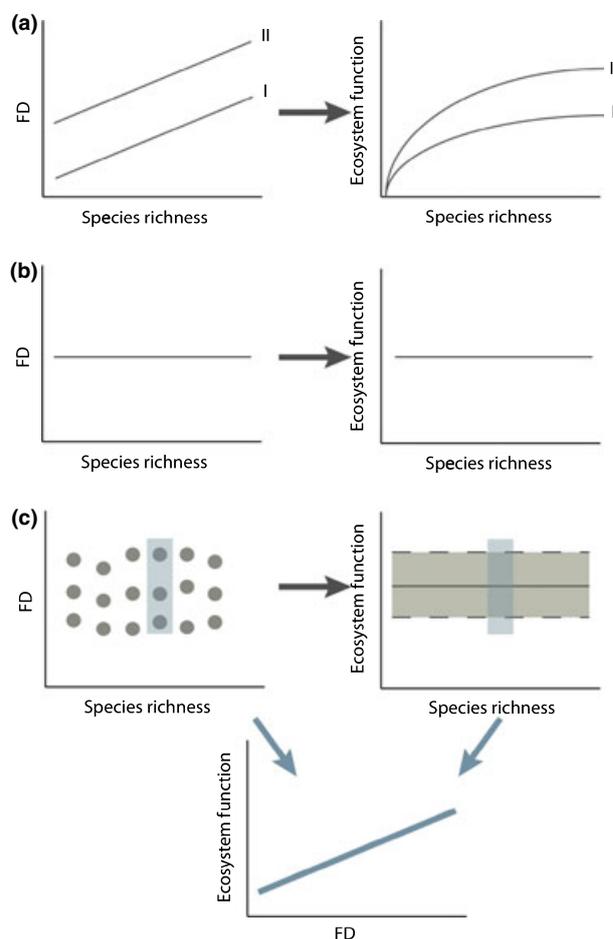

Fig. 2. The relationship between species richness and functional diversity (FD) will influence the shape and magnitude of biodiversity-ecosystem function (BEF) relationships. Positive richness–FD correlations will result in positive BEF relationships, but the magnitude will depend on the amount of FD (a). A lack of variation in FD means species are functionally redundant, and diversity does not impact ecosystem function (b). A lack of a correlation between species richness and FD can result in differing amounts of ecosystem function as long as there is variation in FD (c). Even when there is a lack of a species richness–ecosystem function relationship, FD can still explain significant variation in ecosystem function.

another, that ecosystem should have greater functioning even if FD is strongly correlated with richness in both. If FD lacks variation (i.e. high redundancy), then BEF relationships should be negligible (Fig. 2b), but if there is variation in FD, it could still explain variation in function even if richness does not (Fig. 2c).

FUNCTIONAL DIVERSITY IS SPECIES BLIND

Recently, a paradigm shift has begun in BEF; researchers have started including intraspecific variation in their definitions of biodiversity (Bolnick *et al.* 2011). Driving this shift is an increasing awareness that many of the functional traits known to influence ecosystem function can vary approximately as much within species as they do between species (Albert *et al.* 2010; Hulshof & Swenson 2010; Messier, McGill & Lechowicz

2010). Furthermore, a large body of literature has emerged showing effects of genetic diversity within species on ecosystem function. These effects are analogous to the effects of species diversity on ecosystem function, and they provide indirect evidence that FD within species can affect ecosystem function (Kotowska, Cahill & Keddie 2010). This recent work suggests that it is the diversity of functional traits at all biological scales that is behind the BEF relationship; species richness, per se, is probably not driving ecosystem function. In particular, Messier, McGill & Lechowicz (2010) explicitly concluded that their detection of substantial intraspecific functional trait variation merited a shift from species-based to trait-based ecology.

In at least one study, significant functional trait variation was found within organs of plants. Hulshof & Swenson (2010) partitioned the variation in leaf traits across a range of scales of measurement, from organs to species. They found that in certain cases, traits such as specific leaf area could vary more among the leaflets of compound leaves than among species. They also detected significant trait variation among leaves within individual plants and among individuals of the same species. This study demonstrates a lack of evidence for natural breaks in functional trait values at the species level. Functional trait variation is more likely to be distributed continuously along a range of biological levels.

In cases where the relevant functional traits are not known or are difficult to measure, species richness may serve as a surrogate for FD. Perhaps more useful than richness, studies linking phylogenetic diversity to ecosystem function also provide indirect evidence that functional traits vary continuously along phylogenies and do not cluster at a particular taxonomic level (e.g. Cadotte, Cardinale & Oakley 2008). It may partly be the ability of phylogenetic diversity to encompass trait variation above the species level that makes it a better predictor of ecosystem functioning than species diversity.

THE STATE OF THE FIELD

Experiments, reviews and meta-analyses have shown that FD is one of the best predictors of ecosystem function available (Petchey & Gaston 2006; Hoehn *et al.* 2008; Griffin *et al.* 2009). Studies are increasingly defining biodiversity as the variety of functional traits in a community or ecosystem rather than the number of species (Reiss *et al.* 2009). Underlying this trend is the mounting evidence that taxonomic richness often only weakly influences ecosystem function, particularly at relatively large geographical scales, and universal relationships have mostly eluded ecologists (Thompson & Starzomski 2007). Evidence for the effects of species richness on ecosystem function is equivocal, and FD is increasingly recognized as a more appropriate metric of biodiversity. In their 2005 'Consensus of Current Knowledge' on BEF, Hooper *et al.* proclaimed with certainty that functional characteristics have a strong effect on ecosystem function.

In spite of FD's promise, the vast majority of BEF studies continue to use species richness (Feld *et al.* 2009). Some researchers have tried to incorporate FD into their experiments using a manually and computationally less intensive version of FD: functional richness. Functional richness provides some of the ease of manipulation of species richness while theoretically capturing more functional variation. Nonetheless, species richness and functional richness are both known to explain less variation in ecosystem function than FD (Petchey, Hector & Gaston 2004), with functional richness performing the worst out of all measures of biodiversity (Flynn *et al.* 2011) and no better than when the functional groups were assigned at random (Wright *et al.* 2006). Most remarkable, however, is not how poorly traditional diversity metrics perform, but how slow ecologists have been to adopt the more powerful FD metrics. A recent review of 446 BEF studies to date revealed that nearly all (94%) focused on either species or functional group richness (Balvanera *et al.* 2006). For a number of reasons, FD has been met with resistance by ecologists. In some cases, measuring traits may be more difficult than counting species. In other cases, however, measuring a small number of traits may be more efficient than identifying every species in a community. In any case, researchers need to start incorporating FD into BEF studies if they are to accurately define the mechanisms linking biodiversity and ecosystem function.

In the last few years, a promising new tool has emerged for explaining the effects of biodiversity on ecosystem function; the amount of phylogenetic diversity in an ecosystem has proven to be a better predictor of ecosystem function than species richness, functional richness or FD (Cadotte *et al.* 2009). Although the specific reasons behind this link have yet to be established, phylogenetic diversity is presumably correlated with ecosystem function because it encompasses most of the functional trait variation in a community, even when it is not known which traits are important, and is therefore a good proxy for FD (Cadotte, Cardinale & Oakley 2008). Our current understanding of which functional traits are most important for different ecosystem functions and how they should be measured is rudimentary. Consensus is also lacking as to how FD should be calculated (e.g. Podani & Schmera 2006; Petchey & Gaston 2007; Villeger, Mason & Mouillot 2008; Poos, Walker & Jackson 2009; Laliberte & Legendre 2010; Mouchet *et al.* 2010). What we usually refer to as FD is an approximation, based on a subset of traits, of the total FD of a community. Phylogenetic diversity, on the other hand, is a well-established tool that has benefitted from a wealth of molecular methods and data and sophisticated statistical techniques (Pagel 1999). The two metrics were recently found to provide extremely similar predictive powers for ecosystem function (Flynn *et al.* 2011). Ecologists generally believe that phylogenetic diversity is simply a stand-in for FD while FD methodologies are being refined (e.g. Cadotte, Cardinale & Oakley 2008). In other words, phylogenetic diversity does a better job of approximating true FD than our current FD metrics do. If phylogenetic diversity metrics, which are relatively advanced, are unlikely to greatly improve in the future and FD metrics still require much development, then in the coming years, FD should emerge as a significantly more powerful tool for predicting ecosystem function.

FD in conservation and applied ecology

Conservation and restoration strategies that explicitly account for community FD are ones that prioritize ecosystem function or stability. Increasingly, the goal for restoration projects is to create stable, functioning ecosystems (Thorpe & Stanley 2011). Given that the aspect of ecosystem function that is prioritized can change through time or with human valuation, and the precise aspects of the biology of species that contribute to ecosystem function are either not known, sufficiently complex or not generalizable across species, FD offers a methodology to integrate disparate traits and data with limited *a priori* valuation or knowledge about the precise functional consequences of particular traits. FD attempts to quantify overall similarities and differences in species' phenotypes or ecologies. Greater FD in managed or restored ecosystems should result in greater stability through time as multiple functional traits can help buffer ecosystems against abiotic variation (Walker, Kinzig & Langridge 1999).

By quantifying FD in natural communities, researchers gain an additional understanding of the spatial and temporal distribution of biodiversity, which can inform conservation prioritization (Petchey & Gaston 2002a; Devictor *et al.* 2010). Studies examining the effect of extinction on FD reveal that communities generally contain limited redundancy and that even the random extinction of a few species can result in significant loss of FD (Petchey & Gaston 2002a). Using high-resolution bird abundance data in France, Devictor *et al.* (2010) showed that there were significant spatial mismatches in the distribution of FD and species richness. Further, they found that existing reserves seem to protect many of the most speciose sites, but high FD sites were actually under represented. Future reserves should attempt to maximize the protection of FD.

There is little doubt that ecosystem functions are a top conservation priority because human survival depends on the ecosystem services they provide (Chapin *et al.* 2000; Palmer *et al.* 2004; Millennium Ecosystem Assessment 2005). These services range from storing carbon (e.g. Bunker *et al.* 2005) to producing food (e.g. Clough *et al.* 2011), and there are strong economic incentives to conserve them (Costanza *et al.* 1997). Here again, FD offers the ability to understand how diversity relates to these functions.

Biodiversity conservation efforts have thus far focussed almost exclusively on species (Mace, Gittleman & Purvis 2003). There is evidence, however, that FD is under even greater threat from human activities than is species richness. In a study of the effects of land-use intensification on species richness and FD, agricultural development caused significant reductions in both measures of diversity, but FD declined the most (Flynn *et al.* 2009). This discrepancy is likely to be caused by the differences we have highlighted in this review. Diaz & Cabido (2001) pointed out that conserving species richness alone will not maintain crucial ecosystem services in the face of continuing global change. They argued that because the contributions of different species to ecosystem functions vary so widely, conservation efforts should focus directly on traits and FD rather than on species richness.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Measuring functional diversity.

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