

IDEA AND PERSPECTIVE

Phylogenetic diversity and the functioning of ecosystems

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Abstract

Phylogenetic diversity (PD) describes the total amount of phylogenetic distance among species in a community. Although there has been substantial research on the factors that determine community PD, exploration of the consequences of PD for ecosystem functioning is just beginning. We argue that PD may be useful in predicting ecosystem functions in a range of communities, from single-trophic to complex networks. Many traits show a phylogenetic signal, suggesting that PD can estimate the functional trait space of a community, and thus ecosystem functioning. Phylogeny also determines interactions among species, and so could help predict how extinctions cascade through ecological networks and thus impact ecosystem functions. Although the initial evidence available suggests patterns consistent with these predictions, we caution that the utility of PD depends critically on the strength of phylogenetic signals to both traits and interactions. We advocate for a synthetic approach that incorporates a deeper understanding of how traits and interactions are shaped by evolution, and outline key areas for future research. If these complexities can be incorporated into future studies, relationships between PD and ecosystem function bear promise in conceptually unifying evolutionary biology with ecosystem ecology.

Keywords

Biodiversity, ecosystem function, functional traits, niche conservatism, phylogenetic community ecology, phylogenetic signal.

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INTRODUCTION

All organisms, including humans, depend on the continued functioning of ecosystems, such as reliable fluxes of energy and nutrients through food webs and the movement of gametes and propagules by dispersal vectors. Recent 'biodiversity-ecosystem function' research has shown that reductions in species richness at the community level often compromise such ecosystem functions (e.g. Cardinale *et al.* 2006, 2011). Despite the overall signal of species richness on ecosystem functions (EFs), however, species richness explains only a fraction of the variance in EF, even in the most rigorously controlled experiments (Cardinale *et al.* 2006). Some of this unexplained variance is due to effects of species composition independent of species richness (e.g. Tilman *et al.* 1997). Furthermore, most species richness-EF experiments have precluded both the natural assembly of ecological communities and their disassembly through anthropogenic activity, and there is substantial debate about the importance of species richness-EF processes when membership in communities is not experimentally constrained (e.g. Sankaran & McNaughton 1999; Srivastava & Vellend 2005; Paquette & Messier 2011).

It may be that counts of species only describe some of the relevant biological variation in communities. There has been increasing evidence that the functionally important aspects of biodiversity are

better represented by the diversity of functional traits, niches and ecological interactions (Petchey & Gaston 2006; Diaz *et al.* 2007; Lavorel *et al.* 2011; Paquette & Messier 2011). Here and throughout this article we use 'functional traits' as shorthand for the traits that determine the role of a species in affecting EFs, also called functional effect traits (e.g. Suding *et al.* 2008). Related species often have similar functional traits (Box 1), niches (Wiens *et al.* 2010) and ecological interactions (Rezende *et al.* 2007; Bersier & Kehrli 2008; Gomez *et al.* 2010), suggesting that phylogenetic diversity may encapsulate many of the functionally important aspects of biodiversity. By phylogenetic diversity (PD) we mean the total amount of phylogenetic distance among species in a community, which is influenced both by how related species are to each other on average and by how many species are present. Many indices have been developed to describe PD (reviewed in Cadotte & Davies 2010), but for simplicity we do not consider these explicitly in this article; rather we consider PD as a general concept (Fig. 1a). Although the emerging field of community phylogenetics considers the processes responsible for patterns in the phylogenetic structure of communities (i.e. interacting species within a trophic level) and ecological networks (i.e. interacting species at multiple trophic levels), there has been surprisingly little consideration of how the phylogenetic structure of communities and networks might affect their functioning (Cavender-Bares *et al.* 2009; Wiens *et al.* 2010).

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Box 1 Do related species have similar traits?

Phylogenetic signal measures the extent to which close relatives have more similar trait values than distant relatives. Traits refer to phenotypic characteristics of individuals that impact their fitness. Strong phylogenetic signals can be generated when traits randomly deviate through time (Brownian motion) such that differences in traits between species are expected to accumulate in proportion to the time since divergence. In one of the most comprehensive attempts to test for phylogenetic signals, Freckleton *et al.* (2002) looked at a total of 103 'ecological traits' measured in 26 clade-level datasets. In this analysis, 60% of traits had a significant phylogenetic signal. Although this is encouraging for the PD-EF hypothesis, the details of which traits are conserved, and at what spatial and phylogenetic scales, will ultimately determine if changes in community PD affect EF.

Plants have been particularly well-studied in terms of functional traits, many of which turn out to be have significant phylogenetic signals, such as wood density (Swenson & Enquist 2007), growth forms and reproductive traits in trees (Chazdon *et al.* 2003), maximum height and seed mass of trees (Kraft & Ackerly 2010), nitrogen fixation (Flynn *et al.* 2011) as well a wide variety of leaf and root traits (Ackerly & Reich 1999; Swenson & Enquist 2007; Kraft & Ackerly 2010; Kembel & Cahill 2011). However, other traits show little conservatism (e.g. specific leaf area and root length in Canadian grasslands: Kembel & Cahill 2011), and in many cases phylogenetic signal is dependent on spatial scale (e.g. Kembel & Cahill 2011) or phylogenetic method (e.g. Flynn *et al.* 2011).

Animal clades also frequently show phylogenetic signals in traits that may influence EFs. In some predator clades, there seems to be a deep evolutionary signal to predation strategy, such as in spiders (Dias *et al.* 2010). Animal body size, which likely correlates with a number of ecological processes, also has a strong phylogenetic signal (Harmon *et al.* 2010). Conversely, animal behaviours, which are major determinates of how an organism interacts with other organisms and the environment, generally appear to be more labile than these morphological traits (Blomberg *et al.* 2003).

We propose that our understanding of how and when biodiversity affects EFs may be improved by a more pluralistic approach that incorporates phylogeny and species traits. We will argue that biodiversity-EF theory is fundamentally based not only on the number of species but also on the total trait space encompassed by a community (Petchey & Gaston 2006) and one of the most synthetic estimates of community trait space may be phylogenetic diversity (Wiens *et al.* 2010). Accounting for differences between species – not just counting them – may explain some of the variance in EF that species richness cannot. Furthermore, by considering phylogenetic constraints on functional traits and species interactions in concert with the phylogenetic structure of different communities and ecological networks (Bersier & Kehrli 2008; Cavender-Bares *et al.* 2009; Vamosi *et al.* 2009; Gomez *et al.* 2010), we may better understand the circumstances under which species losses or gains will likely affect EFs. Certainly, several recent empirical studies suggest that examining effects of PD on ecosystem functions may be a rich area of inquiry (Maherali & Klironomos 2007; Cadotte *et al.* 2008, 2009; Cadotte & Strauss 2011; Flynn *et al.* 2011; but see Paquette & Messier 2011). For example, two re-analyses of 29 experiments that randomly assembled terrestrial plant communities with differing numbers of species found that PD was generally a better predictor of ecosystem function than species richness or the number of functional groups, and that PD complemented functional diversity in explaining species richness-EF relationships (Cadotte *et al.* 2008; Flynn *et al.* 2011).

We focus this article around four questions. (1) Why consider effects of phylogenetic diversity on ecosystem functions? We suggest three reasons why ecologists should consider the functional effects of PD. (2) What are the mechanisms and evidence for PD-EF relationships? We outline potential mechanisms and supporting evidence at three scales of ecological complexity, first for single trophic levels, then for plant-animal interactions and finally for ecological networks. (3) What might diminish the effect of PD on ecosystem functions? We consider how community assembly and natural selection can

weaken the community-scale phylogenetic signal of functional traits, and explore consequences for EFs. (4) What are the key areas for future research? We outline six research foci that would have the most impact on our understanding of PD-EF effects.

WHY CONSIDER EFFECTS OF PHYLOGENETIC DIVERSITY ON ECOSYSTEM FUNCTION?

Given that researchers are already explaining the functioning of ecosystems in terms of the contribution of particular species, genotypes or functional traits, why should we consider PD, yet another measure of diversity? There are several conceptual and pragmatic reasons why researchers should explore links between PD and function, and here we list six important reasons.

PD incorporates the evolution of species ecologies

The ecologies of species are shaped by their evolutionary history. We offer three examples of how an understanding of evolutionary origins can help explain when EFs will be affected by changes in species richness. (1) The order in which traits related to habitat and resource-use evolve may have profound implications for community structure (Ackerly *et al.* 2006; Kembel & Cahill 2011). For example, in *Ceanothus* spp. communities, species diversified into a broad range of specific leaf area values (an important functional trait) earlier than they diverged in traits related to habitat use, such that *Ceanothus* species within the same habitat represent more evolutionary history and functional trait space than expected through random assembly (Ackerly *et al.* 2006). As functional trait space is, as we show later, conceptually related to EFs, the evolutionary history of functional traits in this community suggests that associated EFs may be sensitive to species loss. (2) Sympatric species diversification involves a change in the total niche space occupied by a lineage that occurs concurrently with an increase in the number of species. For example, the repeated radiation of generalist stickleback ancestors

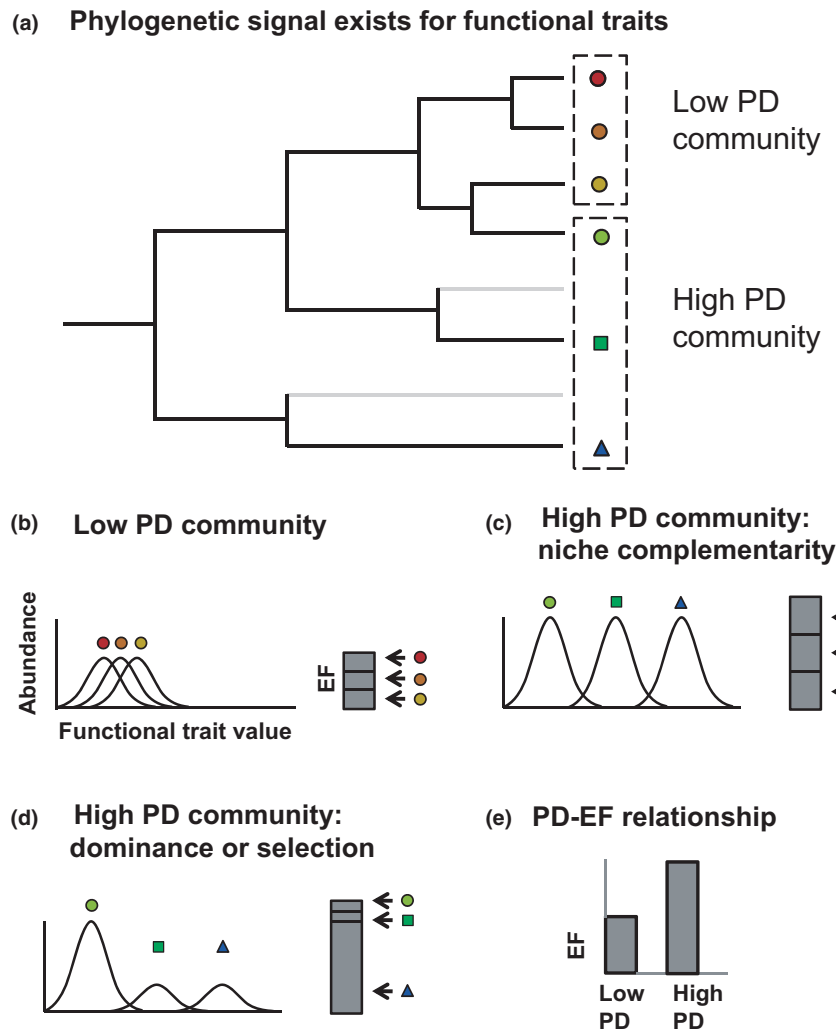


Figure 1 Consider a community (a) in which closely related species are more functionally similar (symbols differ only in colour) than distantly related species (symbols differ in shape). If this community has low phylogenetic diversity (PD), it will include species with high overlap in functional traits, perhaps also strong interspecific competition limiting abundances, and consequently low ecosystem functions (EF) (b). A high PD community will include species with less overlap in functional traits, potentially increasing the contribution of all species to EF via niche complementarity (c) or increasing the likelihood of including a dominant species with a functionally important trait (d). Either of these mechanisms will result in a positive correlation between PD and EF (e).

into benthic and limnetic specialists (Schluter & McPhail 1992) results in profound changes in EFs of ponds, both through an increase in trophic specialisation and complementarity between the specialists in their ecosystem engineering effects (Harmon *et al.* 2009). As sympatric speciation often involves a generalist ancestor and specialist derived species, these results have broad relevance. If the evolutionary history of sticklebacks is ignored, we miss the potential to generalise the results of Harmon *et al.* (2009) beyond the three species of sticklebacks involved in their experiment. (3) The effect of species invasions on EFs may depend on the phylogenetic relatedness of the colonising species to the recipient community. We develop the argument later in this article that colonising species from allopatric species pools are often distantly related to the recipient community, and so can increase both phylogenetic and trait dispersion of the community (Cadotte *et al.* 2010; Gerhold *et al.* 2011), leading to an expectation of larger changes in EFs through exotic than native species colonisation.

PD represents ecological differences better than traits

The use of PD has been justified as a 'stand-in' for traits that have not or cannot be measured or adequately captured in multivariate metrics (Cadotte *et al.* 2008, 2009). Pragmatically, PD may summarise information on multiple traits into a simple index of ecological, phenotypic and functional similarity. For example, consider that for a meta-analysis of the effect of plant traits on herbivory, Carmona *et al.* (2010) needed to compile 178 different traits, including information on primary chemical composition, secondary metabolites, physiology, leaf and stem physical traits, gross morphology, plant size, and life history. However, herbivores tend to prefer closely related plant species (Weiblen *et al.* 2006), so the single metric of plant PD may permit estimation of variance in herbivory rates without measuring large numbers of traits for each plant species. Recent studies have also emphasised the need to consider multiple functions when assessing effects of diversity on function (Hector &

Bagchi 2007), which further increases the number of traits to measure as different traits often contribute to different EFs (Petchey & Gaston 2006; de Bello *et al.* 2010). It is also not simply a matter of concentrating on the traits most related to the EF(s) of interest, such as prey capture traits for predation rate. For example, two predators with identical prey capture traits may differ in their microhabitat use, leading to synergistic effects of the predators on total prey capture. As we discuss later, EFs can be influenced by niche complementarity, and species' niches are determined by a wide range of individual traits (we use 'niche' in the Hutchinsonian sense, referring to the range of environmental and biotic conditions within which a species can persist). A sensible way forward may be to look first for an effect of PD on EFs, and then to use a process of elimination to determine which phylogenetically conserved traits are responsible for this PD effect (e.g. Flynn *et al.* 2011), rather than attempt *a priori* to guess the relevant traits.

Phylogenetic diversity may also capture unknown interactions that affect ecosystem function. For example, interspecific interactions between plants can be explained in part via soil pathogen effects (Petermann *et al.* 2008), but current studies that relate plant traits to EFs do not attempt to identify, let alone measure, traits that could mediate pathogen effects (e.g. de Bello *et al.* 2010). Even if these other players in an interaction remain unknown, PD measured in a single trophic level may still represent their effects as long as there is a phylogenetic signal (defined in Box 1) for both antagonistic and mutualistic interactions (Rossberg *et al.* 2006; Rezende *et al.* 2007; Bersier & Kehrli 2008).

In summary, community composition likely influences EFs through determining functional traits, niches and species interactions. The common denominator here is phylogeny, given evidence for phylogenetic signals for each of functional traits (Box 1), niches (Wiens *et al.* 2010) and ecological interactions (Rezende *et al.* 2007; Bersier & Kehrli 2008; Gomez *et al.* 2010). Thus, phylogeny is not just a statistically useful predictor of EF, but underlies the reasons why species are ecologically different and thus have complementary effects on EFs.

PD is a simpler and more accurate measure of variation

Phylogenetic diversity turns the explanatory variable into a continuous measure. Traditional species richness-EF studies assess the ability of count-based measures (number of species and functional groups) to explain variation in EF (e.g. Tilman *et al.* 1997). This approach is unable to explain variation in EF among different combinations of species that represent the same number of species or functional groups. Distance-based diversity indices, such as PD and functional diversity, convert binned measures of diversity into a continuous measure that can account for both the species richness and compositional aspect of diversity (Petchey & Gaston 2006; Cadotte & Davies 2010). If related species are ecologically similar (Box 1; Gomez *et al.* 2010; Wiens *et al.* 2010), then PD can represent the increase in ecological roles when communities increase both in the number and average evolutionary distinctiveness of species. In essence, this view of communities as occupying continuous trait space represents a shift in how ecologists measure and understand the consequences of diversity.

In addition, PD can be measured even when functional traits cannot. Although the choice of methods to infer phylogenetic relationships is not trivial, the information to estimate these relationships

can be more readily available for large numbers of taxa than trait values. This may be particularly true for taxa like bacteria, whose genetic information can now be relatively easily sequenced to identify species (or, more precisely, molecular operational taxonomic units), but whose functional traits remain difficult to measure due to challenges in culturing most bacteria. Conversely, despite recent advances in compiling trait information, such information may be only as available as gene sequences for certain plant taxa in particular locales (e.g. Center for Tropical Forest Science plots). Even if information on relevant functional traits is available, integrating this trait information into a predictive index of functional diversity and species difference is complicated by the fact that traits differ in their importance for EFs, their units of measurement, their individual variances and their covariances with other traits, and there is considerable debate about the best way to overcome these problems (Petchey & Gaston 2006; Poos *et al.* 2009).

PD compliments conservation prioritisation

Phylogenetic diversity is an important measure of diversity because it is linked to the valuation of species for conservation (Cadotte & Davies 2010). The argument to conserve evolutionarily distinct taxa (Vane-Wright *et al.* 1991; Faith 1992) because they collectively harbour a greater amount of evolutionary history (Redding *et al.* 2008; Cadotte & Davies 2010) is strengthened if loss of such species from communities reduces EFs. Otherwise, there needs to be greater discussion about whether to prioritise conservation of evolutionarily distinct species or functionally important species.

WHAT ARE THE MECHANISMS AND EVIDENCE FOR PD-EF RELATIONSHIPS?

The functional role of PD within a trophic level

A number of mechanisms have been proposed to explain why increases in species richness within a trophic level often lead to increases in EFs (Loreau 2010; Carroll *et al.* 2011). Many of these mechanisms involve an increase in the range of occupied niches in the community as the number of species increases. Such niche-based mechanisms should apply even more to PD-EF relationships than species richness-EF relationships, given that PD can potentially (if certain conditions are fulfilled, as described shortly) capture the increase in community niche space resulting from increasing either the number of species or their evolutionary distance from each other (Fig. 1). For example, coexistence theory predicts that niche differentiation between species reduces interspecific competition, permitting both a greater number of coexisting species and more efficient utilisation of the full range of available resources (Loreau 2010). The problem in using this mechanism to universally explain correlations between species number and EFs is that we must assume that the only explanation of high diversity is niche differentiation, whereas equivalence between species in their fitness is also a potential explanation (Chesson 2000) and may have opposing effects on EFs (Carroll *et al.* 2011). By contrast, high PD communities may exhibit niche differentiation not only through coexistence mechanisms but also by phylogenetic conservatism of ecological niches (Fig. 1a–c and e). For example, we might predict that detrital decomposition by aquatic insects increases with insect PD, given a modest phylogenetic signal for detrital processing mode amongst

lotic insects (Poff *et al.* 2006). A particularly compelling example of how PD can affect EFs via niche differentiation is a mycorrhizal inoculation experiment whereby a gradient in mycorrhizal PD was created by holding colonising species richness constant, but increasing the number of families represented (Maherali & Klironomos 2007). The authors explained the resultant increase in plant productivity with mycorrhizal PD as a consequence of niche differentiation: different mycorrhizal families provide different advantages to their plant host in terms of pathogen resistance and phosphorus uptake (Maherali & Klironomos 2007).

Niche differentiation between species can also lead to facilitation. There is emerging evidence that distantly related species are more likely to exhibit facilitation. For example, in semi-arid habitats, facilitation is primarily between evolutionarily distant plant species, suggesting that the functional traits that distinguish nurse species from facilitated species are phylogenetically conserved (Valiente-Banuet & Verdú 2007). Facilitation can increase EFs. For example, plant productivity increases when plant species in symbiotic relationships with N-fixing bacteria co-occur with plant species without such relationships (e.g. Tilman *et al.* 1997). There is a strong phylogenetic signal to N-fixing symbioses in vascular plants (one family, Fabaceae, contains most species), and in a meta-analysis of 29 plant experiments this signal explained much of the effect of PD on community productivity (Flynn *et al.* 2011). However, we caution that high community PD may be a necessary, but not sufficient, condition for facilitation, as facilitation requires certain trait combinations to be represented in the community (Valiente-Banuet & Verdú 2007). For example, in detrital processing chains, families of aquatic invertebrates that shred or scrape detritus into fine particles (e.g. detritivores within Scirtidae, Tipulidae) facilitate resource capture by families that collect or filter fine particulate organic matter (e.g. most Chironomidae, Culicidae). For the processing chain to contribute fully to EF, communities must contain both benefactors (shredders, scrapers) and beneficiaries (collectors, filterers).

Diverse communities can also have higher EFs when relative abundances shift towards species with the highest per capita rates of the function, notably when high rates of function are linked to a competitive advantage (this mechanism is included in calculations of 'dominance' by Fox (2005) and 'positive selection' by Loreau (2010)). Such shifts in relative abundance are contingent on the likelihood of including the competitive dominant in the community. If the competitive dominants in the community are restricted to certain clades (Ricciardi & Atkinson 2004; Mayfield & Levine 2010), then increasing PD would increase the likelihood of including at least one member of such a clade (Fig. 1a,b,d and e). We caution here that there is contradictory evidence about the relationship between competitive dominance and evolutionary uniqueness (Ricciardi & Atkinson 2004; Maherali & Klironomos 2007; Cahill *et al.* 2008; Jiang *et al.* 2010). We also caution that any PD dominance/selection mechanism implicitly requires traits related to competitive ability and functional traits to be phylogenetically correlated, a key point that we consider in more detail later.

So far, we have argued that, if functionally important traits are conserved, PD is more likely than species richness to describe the functional trait space represented by a community, and therefore more likely to explain how community function is affected through various mechanisms. This hypothesis is supported by two meta-analyses of random-assembly plant experiments (Cadotte *et al.* 2008; Flynn *et al.* 2011). In the experiments analysed, species richness was correlated

with aboveground biomass in large part due to covariance of species richness with PD ($r^2 = 0.84$) (Flynn *et al.* 2011). Such strong and linear covariance between species richness and PD is expected when species are randomly selected from a limited species pool. However, ecologists are ultimately interested in explaining EFs in natural communities, which typically have non-random species compositions and consequently non-random patterns in phylogenetic structure (Vamosi *et al.* 2009; Kraft & Ackerly 2010). Although the reasons for these phylogenetic patterns is still under debate (Cavender-Bares *et al.* 2009; Vamosi *et al.* 2009; Mayfield & Levine 2010), the consequence is that the relationship between PD and species richness is often variable, as evidenced by recent studies on woody plants in the Mediterranean (power function: Morlon *et al.* 2011), bird communities in France (no congruence: Devictor *et al.* 2010) and vascular plants along an urbanisation gradient (inverse relationship: Knapp *et al.* 2008). If, as we argued earlier, key mechanisms determining EFs are more closely aligned with PD than species richness, then we would expect that species richness would often be a poorer predictor in natural communities than random-assembly experiments, due to the more variable covariance between species richness and PD in natural communities. This is consistent with the observation of variable strengths of species richness-function relationships in nature (examples of negative correlation: Sankaran & McNaughton 1999; no correlation: Schumacher & Roscher 2009; positive correlation: Paquette & Messier 2011). So far, we know of only two studies that have compared the ability of PD and species richness to predict EFs in natural communities, one of which suggests that PD is a better predictor (Cadotte & Strauss 2011), and one that suggests that neither is as useful a predictor as functional diversity (Paquette & Messier 2011).

The relationship between PD and species richness may be particularly pertinent to understanding the functional consequences of contemporary changes in local diversity, through local extinctions (species loss) or species introductions (species gain). At regional scales, extinction risk has a measurable phylogenetic signal (e.g. Purvis *et al.* 2000). At community scales, both contemporary climate change (Willis *et al.* 2008) and urbanisation (Knapp *et al.* 2008) have been shown to reduce phylogenetic dispersion. In other words, anthropogenic stress can serve as a filter through which only certain closely related groups of species can pass, presumably because of particularly conserved traits. If functional traits are also conserved, we would predict that local extinctions would initially cause little change in function, as remaining close relatives may be able to functionally compensate for extirpated species due to shared traits. When most members of the susceptible clade have been extirpated, however, there may be large and abrupt changes in function. Such a situation may already exist for the world's primates, where the most endangered species are both evolutionarily distinct and ecologically unique (Redding *et al.* 2010).

Human activity can also increase local diversity, for example when colonisation by introduced species is not offset by extirpation of resident species. Exotic introductions in particular can result in substantial increases in phylogenetic dispersion (Cadotte *et al.* 2010; Gerhold *et al.* 2011). Furthermore, the species in allopatric assemblages (i.e. mixtures of native and non-native species) have not coevolved together for long periods of time, and so should exhibit stronger phylogenetic signals than sympatric assemblages that have undergone divergent selection (Cadotte *et al.* 2010). Thus, we would predict that exotic introductions could result in larger changes in EFs than expected from simply examining trends in species richness.

By combining the above predictions for extinctions and colonisations, we speculate that asymmetric effects of species losses and gains on PD can lead to similar asymmetries in EFs. For example, Cadotte & Strauss (2011) tracked temporal changes in plant communities differing in initial composition and diversity, and found that changes in PD were driven more by colonisations than extinctions, and such changes in PD – unlike changes in species richness – were positively correlated with changes in biomass production.

PD and interactions between two groups of organisms

Many EFs involve interactions between two trophic levels (e.g. rates of herbivory, predation, parasitism and disease) or mutualist partners (e.g. pollination, seed dispersal).

Effects of plant diversity on herbivory have been particularly well studied. High plant diversity seems to reduce rates of consumption by herbivores (Hillebrand & Cardinale 2004; but see Cardinale *et al.* 2011). One explanation of such patterns is the dilution (also called resource concentration) hypothesis (Root 1973), which suggests that predators are inefficient at finding preferred prey species at high prey diversities because their preferred species are at relatively low densities. This classic species richness dilution effect (Fig. 2a) will be most effective when predators specialise on a single prey species, but can also apply to predators that specialise on any subset of the available prey species. In the latter case, we would predict that the consumption of the preferred prey species increases as the PD of the prey community decreases, because closely related prey species may support consumers that can also attack the focal prey species (Fig. 2b). For example, in plant-herbivore systems, consumers tend to feed on closely related prey (Weiblen *et al.* 2006). Fungal pathogens are also often unable to infect plant species that are distantly related to their host species, suggesting that the dilution effect can extend to a positive effect of plant PD in reducing risk of infection (Gilbert & Webb 2007). It has been proposed that such a PD dilution effect (Fig. 2c) could explain why seedlings that are less related to neighbouring species or the forest dominant have higher survival (Webb *et al.* 2006; Bagchi *et al.* 2010).

A particularly interesting case of the PD dilution effect involves pollination. Closely related plant species also tend to share pollinators (e.g. Rezende *et al.* 2007) and so their presence may attract higher abundances of potential pollinators, resulting in greater pollination rates (Moeller 2004). The opposite effect may occur, however, if pollinator numbers are limited: closely related plants may also directly compete for visits by shared pollinators (Schuett & Vamosi 2010), and shared pollinators can transfer heterospecific pollen which often impairs reproductive success of the focal plant. Researchers have just started to examine this question, but so far pollination of a focal species can be both positively (Schuett & Vamosi 2010) and negatively (as predicted by a PD dilution effect: Moeller 2004; Sargent *et al.* 2011) correlated with its phylogenetic distance to co-occurring plants.

It should be noted that most studies have measured effects of community PD on herbivory, infection or pollination of a single focal species, rather than of the whole community (Cardinale *et al.* 2011), whereas the latter is the relevant scale for understanding impacts of PD on ecosystems. Now that we are starting to understand the mechanisms by which plant PD influences the functioning of individual species, the next priority is to examine the functioning of the entire plant community.

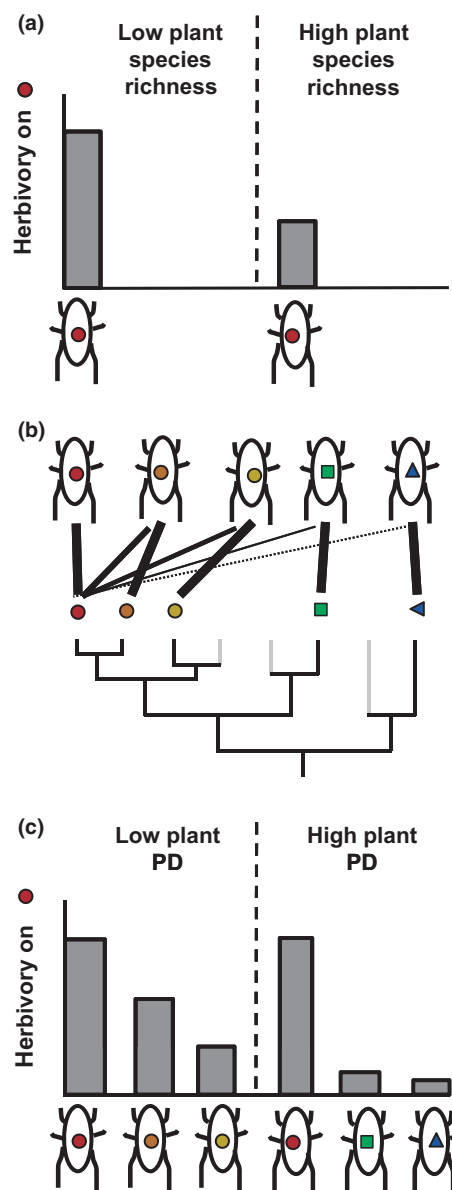


Figure 2 Species richness dilution effects occur when specialist herbivores (beetle icon) feeding on a focal plant species (red circle) are less efficient in locating their host plant as plant species richness increases (a). Phylogenetic diversity (PD) dilution effects occur when herbivores that prefer one plant species (indicated by symbols on beetles) will also consume other species, with herbivore preference (width of lines; subset shown) declining with phylogenetic distance from host plant (b). If the focal plant species occurs in a low PD plant community, it will therefore experience herbivory not only from its primary herbivore but also from herbivores of closely related plant species. By contrast, a higher PD plant community will contain herbivores with less secondary impact on the focal plant species (c).

PD and EFs within ecological networks

So far we have considered how the PD of one group of species affects the flow of energy, nutrients or services (like pollination) to another group of species. This second group of species can also be characterised by PD, however, and an intriguing question is how the PDs of multiple interacting groups affect EFs. Although we emphasise that there are as yet no direct tests of PD-EF relation-

ships in ecological networks, recent advances in network theory and analyses give us tantalising glimpses of why phylogeny might matter to EFs affected by entire ecological networks.

In ecological networks, initial species extinctions might cascade through multiple links, resulting in secondary extinctions and larger than anticipated changes in EFs (Thebault *et al.* 2007). Analyses of both food webs (Bersier & Kehrli 2008; Gomez *et al.* 2010) and mutualistic interaction webs (Rezende *et al.* 2007; Gomez *et al.* 2010) have found a phylogenetic signal to species interactions (i.e. related species tend to interact with the same partner species). This has contrasting implications for how extinction cascades might affect EFs. On the one hand, if species loss triggers secondary extinctions in another trophic level or mutualist group, these secondary extinctions will tend to be phylogenetically correlated, because each species in the network tends to interact with a group of related species (Rezende *et al.* 2007). This implies that a few secondary extinctions might cause an entire clade of species to be lost from a community, resulting in a simultaneous drop in PD and EF (assuming the clade of species was functionally distinct from the rest of the community). On the other hand, phylogenetic constraints on network structure (Rossberg *et al.* 2006; Bersier & Kehrli 2008) might lessen these secondary extinctions. For example, compartmentalisation tends to buffer food webs against cascading extinctions and permits recovery from perturbations (May 1972; Thebault & Fontaine 2010). The compartmentalised structure of food webs may reflect, in part, the fact that related prey tend to share the same predator whereas related predators have less overlap in their diet (Rezende *et al.* 2007; Bersier & Kehrli 2008). It is an open question whether phylogeny also explains the predominance of nested structure in mutualist networks, of interest as nestedness also buffers mutualist networks from secondary extinctions (e.g. Thebault & Fontaine 2010). Of course, the above is only relevant if extinction cascades are common, and ecologists are just starting to supplement anecdotal evidence and model predictions with experimental tests for extinction cascades (e.g. Srivastava & Bell 2009).

The strength of the phylogenetic signal to species interactions is often asymmetrical between groups. Recall that in food webs, there is a stronger phylogenetic signal for prey (related prey share the same predators) than for predators (related predators do not necessarily share the same prey) (Rossberg *et al.* 2006; Bersier & Kehrli 2008). In plant-animal mutualism webs, related animals tend to facilitate the same plant species, but the reverse is less often true (Rezende *et al.* 2007). Given that many EFs are affected by species interactions, this asymmetry in phylogenetic signal suggests that effects of PD on EFs may be greater for prey than predators, and for animal than plant mutualists. There are also asymmetries in the phylogenetic signals for the number of interaction partners and a tendency for signals to strengthen with host use specialisation (Rezende *et al.* 2007; Gomez *et al.* 2010), and the implications of these patterns for the flow of energy and services in ecological networks have not yet been explored.

WHAT MIGHT DIMINISH THE EFFECT OF PD ON ECOSYSTEM FUNCTION?

Any attempt to understand variance in EFs in terms of community or network PD must consider that the explanatory power of PD will breakdown when (1) the important functional traits do not have a strong phylogenetic signal, (2) the strength of the phylogenetic signal

is reduced by community assembly processes, (3) the traits important for competitive dominance are not correlated with the traits important for function and (4) we are unable to accurately measure PD.

Caveat 1: Not all functional traits have a strong phylogenetic signal

Although some functional traits in plants and animals have strong phylogenetic signals, other functional traits seem much more labile (Box 1). Natural selection is continuously acting on those traits, so in some ways it is surprising that ecological traits ever have strong phylogenetic signals. Simulations show that phylogenetic signal can be reduced by many forms of natural selection, including stabilising, constrained, fluctuating and divergent selection (Revell *et al.* 2008). Adaptive radiations provide some of the best counter examples to trait conservatism. For example, stickleback species are found in sympatric pairs of benthic and limnetic species that appear to have diverged from a generalist ancestor less than 13 000 years ago (Schluter & McPhail 1992). Recent work has shown that benthic and limnetic stickleback species, although closely related, have dramatically different effects on EFs like primary production, light transmission and prey abundance (Harmon *et al.* 2009). In a second example, lab experiments show that marine bacterial strains exhibit a relationship between PD and EF, but when they are selected – independent of ancestry – to use new carbon sources, this relationship disappears, while a species richness-EF relationship remains (Gravel *et al.* 2011 and Gravel D. & Mouquet N., personal communication). In general, under sympatry, traits are expected to diverge at a much faster rate than under allopatry, and an extremely high rate of divergence would result in an inability for patterns of common ancestry to explain the present day distribution of traits.

Caveat 2: The strength of phylogenetic signals is affected by community assembly

All mechanisms by which PD affects EF, including complementarity and selection, require a substantial phylogenetic signal of key functional traits and ecological interactions *at the scale of the community*. Although there is evidence for relevant phylogenetic signals at the level of entire phylogenies or regional species pools (Box 2), this does not guarantee that this signal will be preserved at the smaller spatial scales – and often reduced phylogenetic scope – of a natural community (Cahill *et al.* 2008).

If there is a significant phylogenetic signal in the regional pool, this signal is generally expected in communities that are randomly assembled from that regional pool, although sampling effects can induce variability in the phylogenetic signal found in any particular assemblage (Fig. 3a). However, there is accumulating evidence that natural communities are not randomly assembled, and show phylogenetic patterns that are distinct from random subsets of the regional pool (reviewed by Cavender-Bares *et al.* 2009; Vamosi *et al.* 2009). There is some evidence to suggest that closely related species interact strongly (e.g. Jiang *et al.* 2010; Gerhold *et al.* 2011) and so do not co-exist at small spatial scales (Webb *et al.* 2006; Maherali & Klironomos 2007; Kraft & Ackerly 2010), potentially explaining patterns of phylogenetic overdispersion at the community level. Such communities lack information on trait similarity of closely related species, reducing the power to detect a phylogenetic signal for traits, especially those recently derived (Fig. 3b).

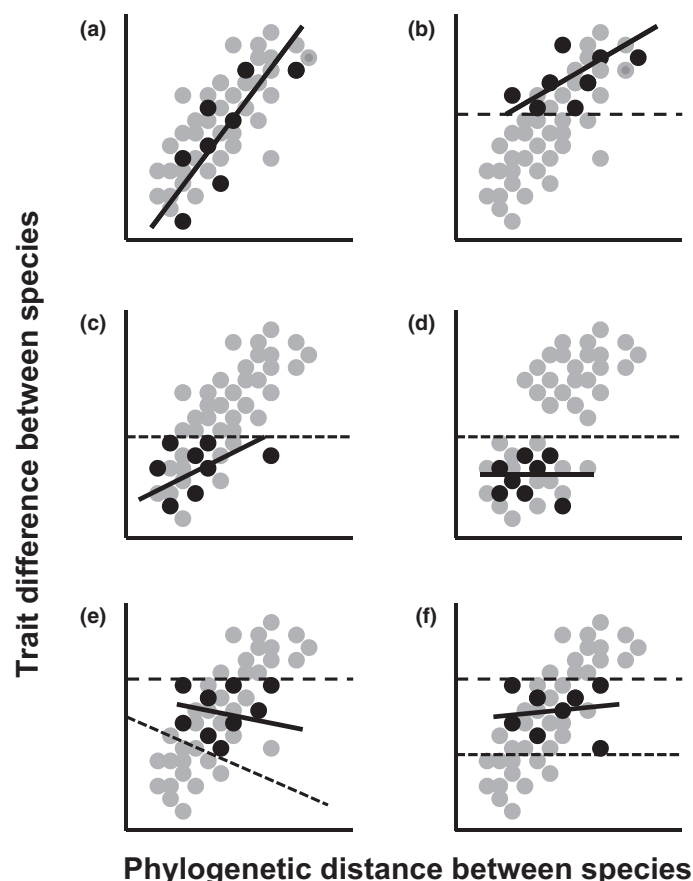


Figure 3 Phylogenetic signal, the correlation between trait differences and phylogenetic distance, is contrasted between a regional phylogeny (each grey circle represents a pair of species) and a community (black circles, correlation shown with solid line). The community will most closely reflect the regional signal when community assembly is trait neutral (a). The community signal may weaken when species co-occurrence requires a minimum trait difference (long dashed line, b) or species co-occurrence requires similar traits (short dashed line, c), and disappear or reverse when an entire clade is absent from the community and clades diverge basally in the trait (d), when coexistence of closely related species requires divergence in the measured trait (e), or when maximum and minimum thresholds occur simultaneously (f).

On the other hand, communities often contain species that are more related than predicted by chance ('phylogenetic clustering', supported in 23 of 39 studies reviewed by Vamوسي *et al.* 2009), as expected when species co-occurrence is primarily determined by conserved environmental tolerances, although Mayfield & Levine (2010) argue such patterns are also likely when coexistence is achieved through fitness equivalence. In either case, the outcome is restriction of the species able to persist in a community to particular clades with particular traits, resulting in phylogenetic and trait clustering and reducing the power to detect phylogenetic signal (Fig. 3c). If major divergences in functional traits occur early in the phylogeny, such phylogenetic clustering could further result in a reduction in the *community-level* phylogenetic signal for these traits (Fig. 3d). Phylogenetic clustering also predicts intense interspecific competition if related species have similar niches, although this hypothesis has received mixed support (Ricciardi & Atkinson 2004; Cahill *et al.* 2008; Jiang *et al.* 2010; Gerhold *et al.* 2011). Such intense competition among related species may create selection leading to

divergence along particular trait axes (Prinzing *et al.* 2008), reducing phylogenetic signal at the community level for such traits (Fig. 3e).

Given that ecologists expect communities to be simultaneously affected by multiple processes (e.g. habitat filtering, competitive exclusion), then patterns between community PD and functional diversity will ultimately depend on the relative strengths of these processes. When both habitat filtering and competitive exclusion are strong, coexisting species are expected to be neither very similar nor very different in traits, reducing the potential for a community level phylogenetic signal (Fig. 3f). Further complexity is added when traits responsible for habitat filtering and those responsible for species interactions differ in their phylogenetic signal (Kembel & Cahill 2011). For example, evidence from tropical dry forest trees and temperate sunfish communities suggests that habitat filtering affects the phylogenetic signal of certain traits, but other traits may be affected by competitive exclusion, with the net effect of no overall relationship between PD and trait diversity (Helmus *et al.* 2007; Swenson & Enquist 2009). Ultimately, the utility of PD will depend on whether the functional traits of particular importance for ecosystem functioning happen to be the same as those whose phylogenetic signal is preserved at the community scale.

Caveat 3: The traits important for function may not correlate with those important for competitive dominance

In single trophic communities, dominance/selection mechanisms require covariance between functional traits and traits responsible for competitive dominance. This may not always be the case. For example, tropical tree communities show clustering in functional effect traits like leaf area, leaf succulence and wood specific gravity, but are overdispersed in other traits that may be more closely linked to ecological coexistence, like maximum height and seed mass, indicating divergence in these two trait types (Swenson & Enquist 2009). More generally, Kembel & Cahill (2011) report that correlations between plant traits are highly dependent on the spatial scale at which traits are measured.

Caveat 4: Current levels of phylogenetic resolution may prevent us from accurately measuring PD

Although the availability of phylogenetic information has greatly increased in recent years, researchers need to be aware of the quality of the phylogenetic information and how assumptions about phylogenetic methods can impact ecological inference. One commonly used method to construct phylogenies for angiosperms is to attach taxa with arbitrary branch lengths to a backbone megatree. Trees produced by this method generally include polytomies (unresolved sets of species or internal branches with three or more lineages originating from a node) below the family level. These polytomies can produce uninformative measures of PD if the community phylogeny includes only a few diverse clades of closely related species. For example if one clade contains a number of very young taxa (e.g. grass genera, within Poaceae) vs. species that originated much earlier (e.g. Fabaceae), then community PD will generally only reflect the number of families (one or two) represented, rather than the smaller differences in branch length within families. Conversely, for communities with representation from many different clades, there is likely only a minor effect from such a tree (e.g. Flynn *et al.* 2011).

WHAT ARE THE KEY AREAS FOR FUTURE RESEARCH?

Research focus 1: Test for mechanisms

We have outlined a number of mechanisms by which PD can affect EFs, but these remain largely untested. For example, although two meta-analyses of random-assembly plant experiments have shown that PD is useful in predicting EF (Cadotte *et al.* 2008; Flynn *et al.* 2011), the precise mechanisms behind these patterns remain unknown. Additive partitioning approaches (reviewed by Fox 2005; Loreau 2010) have frequently been used in species richness-EF experiments to separate the effects of niche complementarity on function from other effects. Although we caution that additive partitioning is only a first step towards identifying mechanism (see also Carroll *et al.* 2011), such statistical methods could help determine which general class of mechanisms underlie these PD-EF relationships. Such an analysis could also help us understand why PD and functional diversity have orthogonal effects on plant productivity (Flynn *et al.* 2011).

Research focus 2: Manipulate PD independently of species richness

So far, PD-EF relationships have primarily been determined by re-analysing experiments that were designed to examine species richness-EF relationships, with the study by Maherali & Klironomos (2007) being a notable exception. Although path analyses can attempt to account for covariance between PD and other metrics of diversity (Flynn *et al.* 2011), a more straightforward test for PD effects would be to assemble communities of identical species number but differing in relatedness. We point out that absence of a fully resolved phylogeny should not deter such experiments, as taxonomic relatedness often provides enough information to rank experimental treatments in terms of PD (Maherali & Klironomos 2007). This approach is also amenable to a meta-analysis approach, given numerous studies in both the competition and predation literature that compare EF of two-species polycultures with monocultures (Cahill *et al.* 2008 use a similar approach for a different question).

Research focus 3: Examine the functional role of animal PD

Empirical tests of PD-EF relationships have so far been constrained to plants, fungi and bacteria, with a notable lack of study on animals. Even when the function measured concerns a plant-animal interaction (e.g. herbivory, pollination), research so far has concentrated on the effect of PD within the plant community, not the animal community. In part, researchers have not studied the functional role of animal PD because we still lack well-resolved phylogenies for many animal taxa. However, in the absence of fully resolved molecular phylogenies for all species, a rough approximation might involve adding species as polytomies to a known backbone phylogeny representing relatedness among higher taxonomic orders (e.g. Rezende *et al.* 2007). Some authors have used taxonomic distinctiveness indices with Linnean classifications (e.g. Bersier & Kehrl 2008). A concerted effort to examine PD effects of both partners in plant-animal interactions would help unite the rich literature on evolution of interactions (e.g. coevolution, predator-prey arms races, chemical ecology) with ecosystem ecology (Loreau 2010).

Research focus 4: Use phylogeny to deepen understanding of functional diversity effects

Phylogenetic diversity has often been contrasted with functional diversity in terms of explaining ecosystem function, but these need not be competing explanations. Instead, PD may help us understand the role of functional diversity. For example, in natural landscapes, functional diversity can explain substantial amounts of the variance in EFs and predict effects of land use changes (Díaz *et al.* 2007; Schumacher & Roscher 2009; Lavorel *et al.* 2011; Paquette & Messier 2011). In these types of statistical models, the effects of environmental drivers on EF are maximised by positive correlations between functional response traits (i.e. traits that predicts species' response to a particular environmental factor) and functional effect traits (i.e. traits that predict species' effects on functions) (Suding *et al.* 2008). Phylogenetic analyses may help understand such trait correlations. For example, if both functional response and effect traits are highly conserved, they may covary simply by originating simultaneously in the phylogeny. Alternatively, there might be evolutionary constraints such that the value of one trait (e.g. the functional response trait) constrains the range of possible values of the second trait (e.g. the functional effect trait). Traits may also be much more labile, and their correlation may reflect a particular ecological strategy. Phylogenetically independent contrasts could be used to determine which of these scenarios result in observed correlations between functional response and effect traits (Ackerly & Reich 1999). The phylogenetic scenario matters, for if trait correlations in a particular phylogeny are simply a chance result of simultaneous evolutionary origin then there is no reason to expect such correlations in other phylogenies. Strategies and trade-offs, by contrast, represent fundamental ecological and evolutionary constraints that may apply to many different phylogenies.

Research focus 5: Compare and integrate the functional effects of genetic variance within and between species

In this article, we have argued that PD may efficiently summarise the total functional trait space occupied by a community, and so predict EF. However, intraspecific variation can explain a significant fraction of community functional diversity (e.g. Kembel & Cahill 2011) and have substantial consequences for EFs (Hughes *et al.* 2008). A broader framework would be to examine the functional consequences of genetic variation between individuals in a community, regardless of the source of that variation (phylogeny or population genetics). A key question is the relative importance of intraspecific and interspecific diversity for understanding EFs. One of the challenges here is the development of metrics that synthesise the variation within species (genotypic diversity) with between-species variation (PD) given the impossibility in genotyping all individuals in a community.

Research focus 6: Examine PD and ecosystem function within focal ecological networks

So far, we have only been able to speculate on the potential functional role of PD within ecological networks by uniting separate lines of evidence. There is a clear need for a concerted effort on a focal network to test these ideas. There is also a need for studies to

examine which groups in ecological networks exhibit the most change in PD, either in response to an anthropogenic stressor or to a natural environmental gradient. We predict that asymmetry in PD change between groups will have complex interactions with asymmetries in phylogenetic signal between these same groups. As a hypothetical example, if a stressor happened to particularly reduce the PD of insect pollinators, this loss of unrelated pollinator species will affect the pollination success of numerous plant clades (given conservatism of host plants among pollinators), and subsequent shifts in the composition of the plant community may have weak rebound effects on the phylogenetic structure of remaining pollinators (as weak conservatism of pollinators among plants). A further question here is the cascading effects of reduced pollinator PD for EFs moderated by the plant community, such as carbon uptake. Pollinator-plant and parasitoid-leaf miner networks may be particularly promising for such focused study of PD-EF effects. Both types of network are well characterised in terms of taxonomy and have obvious measures of ecosystem function (pollination rate and parasitism rate respectively).

SUMMARY

There are three important messages from this article. First, we demonstrated that a phylogenetic perspective can provide important insights into understanding how community composition affects ecosystem functions, in a multitude of communities: single-trophic, bi-trophic or multi-trophic networks of either antagonistic or mutualistic interactions. Second, we demonstrated that although the links between PD and EF are potentially important, there are few studies that have explicitly examined such links, and ample opportunities exist for focused tests of our proposed hypotheses. Third, we cautioned that any hypothesised links between PD and EF assume that the relevant traits have a measurable phylogenetic signal detectable at the scale of communities. These caveats suggest that rather than using PD simply as an alternative to understanding trait diversity, ecologists must consider how phylogenetic relationships both influence trait representation in communities (e.g. Prinzing *et al.* 2008) and constrain correlations between traits (e.g. Ackerly & Reich 1999). A synthetic approach will bring us to a deeper, more integrated understanding of the interplay between community structure and ecosystem function. If these complexities are incorporated into future studies, research on the effects of PD on EFs has the potential to conceptually unify the divergent fields of community ecology, evolutionary ecology, conservation biology and ecosystem ecology.

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AUTHOR CONTRIBUTION

All authors contributed substantially to the concepts and writing, in the order indicated.

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