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update

Beyond taxonomical space: large-scale ecology meets functional and phylogenetic diversity

Community ecology traditionally focuses on hypothetical-deductive and experimental approaches and often is criticized for narrowing our understanding of nature to local idiosyncrasies, ignoring the importance of historical explanations. On the other hand, approaches taken by macroecologists and biogeographers have been excessively exploratory and correlative, with limited success in elucidating the mechanisms responsible for many of the large-scale patterns we observe in nature (see Gaston & Blackburn 1999, Ricklefs 2008 and references therein). Recognizing that both approaches can learn from each other is pivotal in the challenge of integrating data from different scales in order to unravel the ecological and evolutionary mechanisms that influence current patterns in biodiversity and ecosystem functioning.

Species richness has been the most common metric used to represent all aspects of biological diversity (from genetic and taxonomic to phenetic diversity). However, species richness alone cannot describe the processes involved in species coexistence and ecosystem functioning and also does not describe properly the differences in community structure. In contrast, phylogenetic and functional diversities allow us to understand the relative importance of species composition in terms of evolutionary history and ecological similarities. Phylogenetic diversity (PD) is a biodiversity measure that accounts for the phylogenetic relationship (hence evolutionary history) among species, whereas functional diversity (FD) represents how species are distributed in a multidimensional niche space defined by ecological traits.

Phylogenetic and functional approaches to community ecology emerged as prominent fields of research in the last decade (Fig. 1), but somehow independently and without much crossover in the first years. Early PD measures were proposed as a tool to select conservation areas, but later the idea was extended to understand how communities are assembled from a regional pool. FD, which initially was considered the holy grail of the biodiversity-ecosystem functioning agenda, also was rapidly applied as a metric for investigating assembly rules (see Pavoine & Bonsall 2011). How could macroecology and biogeography benefit from these two approaches? The answer lies in understanding what FD and PD should represent and how they relate to each other: while phylogenetic community ecology links evolutionary and biogeographic history to present-day ecology, functional diversity (as any trait-based approach) links niche theory to large-scale approaches, such as macroecology, biogeography or phylogeography. Therefore, combining ecological and phylogenetic frameworks to explain large scale patterns of biodiversity is an important step, taken recently.

Large-scale studies involving PD and FD seems to be increasing at similar rates (Fig.1). Recently, it was shown that both measures can be decomposed into gamma (regional), alpha (local) and beta (turnover) components. Whereas large-scale studies and any-scale studies follows a similar trend for beta-PD, there were few studies with beta-FD (none at large-scale). This is perhaps because biogeographers and macroecologists were more aware of evolutionary and historical hypotheses, so the conceptual framework of beta-PD was likely to be absorbed first. Also, this could reflect the assumption that closely related species should be ecologically more similar than distant related species and, thus, PD should be a good surrogate for FD (in fact this is what most large and local-scale PD studies used to assume). This traditional assumption is now debated (e.g. Losos 2008), and these two measures may be viewed as complementary, rather than competing, approaches (Gómez et al. 2010, Diniz-Filho et al. 2011, Meynard et al. 2011, Pavoine & Bonsall 2011, Safi et al. 2011).

While some large-scale studies involving PD and FD are exploratory (e.g. Meynard et al. 2011) others have presented hypotheses and predictions. Safi et al. (2011) investigated global patterns of mammal PD and FD and found that when controlling mammal assemblages for their evolutionary history the tropics were characterized by a FD deficit. This suggests that more species can be closely packed into the ecological space in tropical than in temperate regions (see figure 3 in their paper), a paradoxical situation in which competition seems to limit trait evolution in a group, but does not decrease the co-occurrence of species with similar trait values (Wiens 2011). There are several non-mutually exclusive mechanisms that could be responsible for this pattern (see Figure 1 in Safi et al. 2011). In temperate regions, for example, if resources are limited, species need to occupy wider ecological niches in order to secure their energy demands and therefore communities would show signs of overdispersion in functional traits. In addition, high environmental heterogeneity could also result in an overdispersion in FD because coexisting species could adapt and specialize to the different environmental conditions.

Some light has been shed on beta-PD patterns by Gómez et al. (2010), studying Neotropical Forest antbirds at different spatial scales. If speciation occurred mainly among ecoregions, there is a lower probability of sister species co-occurring in the same ecoregion, resulting in phylogenetic evenness at this smaller scale. If so, we would expect high species turnover (taxonomic beta diversity) and low phylogenetic turnover (beta-PD) among ecoregions, because species would tend to be close relatives. An alternative scenario is when phylogenetic structure at the regional scale is a product of limited dispersal of lineages. In this case we would expect both high species turnover and high beta-PD among regions, because each

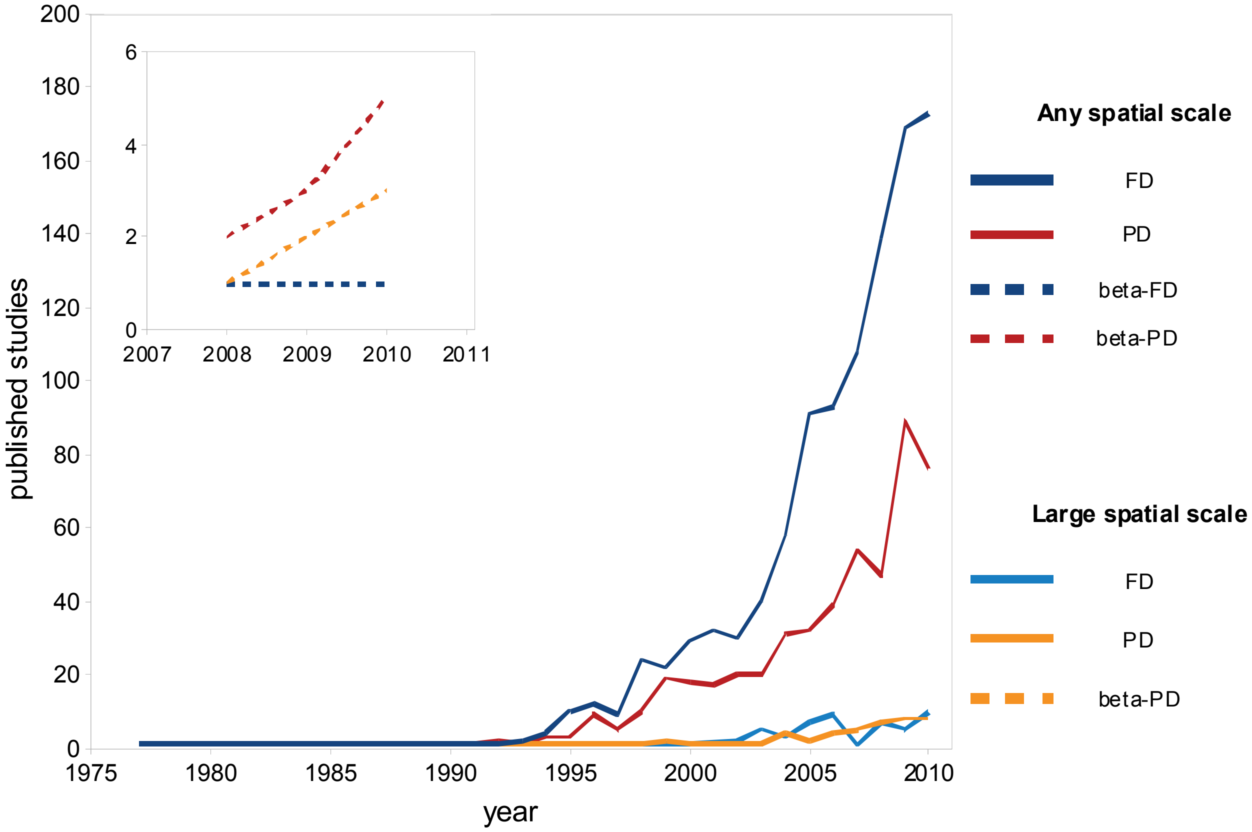

Figure 1. The number of articles published in peer-reviewed journals indexed by ISI with functional and phylogenetic diversity in the title, abstract or key-words from 1976 to 2010. Any spatial scale means all studies published in all sub-disciplines of ecology and evolutionary biology, irrespectively of scale. Large spatial scale are those studies constrained by the search expression Topic=(geograph* OR macroecol* OR biogeogr*), that is, those studies most likely to be related to macroecology and biogeography. FD = any study with topic “functional diversity”; PD = any study with topic “phylogenetic diversity”; beta-FD = any study with topic “functional beta diversity” or “functional turnover”; beta-PD = any study with topic “phylogenetic diversity” or “phylogenetic turnover”. The inset is provided to show currently starting publication trends concerning beta-PD and beta-FD. There was no large-scale study involving beta-FD up to 2010; but a few were published in 2011 or are in press.

region would contain distinct clades, with independent diversifications. Finally, if observed values of species turnover and beta-PD do not differ from what would be expected by chance (using null-models where random assemblages are built from the species pool), phylogenetic structure at the regional scale is unlikely to be the result of historical processes. In that case using FD should be better because niche-based processes are more likely to explain the pattern. For example, along a strong environmental gradient where species are sorted from the regional pool according to their traits, we expect both species and functional turnover. However, if the species pool is composed of ecologically similar species – an indication that species were sorted according to their traits at a higher spatial scale (for example, due to a climatic filter or historical processes) – we should expect low functional turnover because the pool already contains very similar species. Also, in the absence of environmental filters, species turnover should occur independently of functional turnover (Mouchet *et al*. 2010). Nevertheless, species traits should have – at least to some extent – some phylogenetic signal and, therefore, partitioning the relative contribution of evolutionary history to trait dissimilarities among species may be important. A potential, and unexplored, solution is to decouple functional diversity into “phylogenetic structured” and “specific (ecological)” components. This would help us to better understand historical and recent processes on biodiversity patterns and assembly rules (Diniz-Filho et al. 2011).

The ground is reasonably well settled to start “rebuilding community ecology from functional traits” (McGill et al. 2006) and “merging community ecology with evolutionary biology” (Cavender-Bares et al. 2009). Yes, there are some methodological challenges – how to properly define the species pool and null models, which traits should be used, what is the most suitable measure of PD and FD, and so on (see Pavoine & Bonsall 2011), but we should avoid becoming locked into a blinkered debate about methodological issues. For example, in the last decade more than two measures of PD or FD were proposed, each year! This may come at the expenses of the more important (and exciting) steps of doing science: how can we move forward the theory by using novel approaches?

All existing hypotheses that have been applied to taxonomic diversity can be extended to phylogenetic and functional diversity (Meynard et al. 2011). However, PD and FD can be used to create more rigorous and direct predictions for most of the hypotheses in macroecology and biogeography, such as attempts to explain latitudinal patterns of biodiversity (Willig et al. 2003). These metrics also present an opportunity to formulate new hypotheses about how species evolutionary history and trait diversity are distributed across communities at different scales. For example, Wiens et al. (2011) showed situations where after a major evolutionary radiation within a region, the region can still be invaded by ecologically similar species from another clade, challenging the paradigm that communities are ‘saturated’. Large-scale phylogenies and trait databases are currently becoming available for a wide range of taxonomic groups, facilitating estimates of FD and PD. Including these two aspects of biological diversity will be crucial if we want to advance from exploratory studies which report interesting relationships between biodiversity and environment to also identifying their causal mechanisms.

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