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SPECIAL FEATURE: FUNCTIONAL DIVERSITY

Are differences in functional diversity among plant communities on Mediterranean coastal dunes driven by their phylogenetic history?

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Abstract

Question: Variability in species function is often studied by using phylogenetic relatedness as a surrogate for functional similarity between species, rather than by measuring functional traits directly. The phylogenetic-based method is far less data-intensive than trait-based methods. However, to what extent community-level variability in species function is driven by phylogenetic history has rarely been explored in terms of composition and diversity. In this paper we test this empirically by asking: do differences in the functional composition and diversity of species assemblages (i.e. plots) along an environmental gradient mirror differences in phylogenetic structure?

Location: Coastal dune communities of the Tyrrhenian coast of Italy.

Methods: We calculated fuzzy-weighted mean trait values and the Rao index for dominant species in 405 plots using 16 functional traits that were measured in the field or from other sources. Based on a phylogenetic distance matrix among species obtained from an aged phylogenetic supertree, we applied matrix correlation tested against appropriate null models to calculate how much of the plot-to-plot variability in functional composition (measured through fuzzy weighting) and diversity (measured with the Rao index) is predicted by the corresponding phylogenetic metrics.

Results: At the species pool level there was evidence for a phylogenetic signal in trait variation. Furthermore, we found that differences in species functional diversity among plots were closely related to their phylogenetic variability, but this was not true for functional composition.

Conclusions: The results show that even when there is evidence of phylogenetic trait conservatism at the species pool level, phylogeny may be unable to capture all aspects of functional community structure. This emphasizes the need for caution when interpreting measures of phylogenetic community structure as proxies of functional community structure.

Introduction

Understanding the mechanisms driving community assembly has been an important focus in plant ecology. Species co-existence within communities, and species sorting along environmental gradients, are thought to be regulated by the degree to which species share similar adaptations. Both functional and phylogenetic approaches have been used for testing these hypotheses. In the first approach, functional traits reflecting species adaptations and plant strategies are used to decipher the relative importance of different niche-based processes for community assembly (Stubbs & Wilson 2004; Cornwell et al. 2006; Kraft et al. 2008; Cornwell & Ackerly 2009; Pillar et al. 2009). Which traits most influence the processes governing community assembly is not always clear. Therefore, a second approach attempts to quantify the relative importance of species function by using phylogenetic relatedness as a surrogate for functional similarity (Webb 2000; Cavender-Bares et al. 2004a; Kraft et al. 2007; Vamosi

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et al. 2009). The underlying assumption is that traits of closely related species are more similar than traits of species more distant on a phylogenetic tree because of trait conservatism, which can be tested by searching for a 'phylogenetic signal' (Blomberg et al. 2001). Evolutionary trait divergence within lineages can also occur (Losos et al. 2003), but when traits exhibit a phylogenetic signal, then related species are also likely to share similar ecological requirements. When this is the case, the phylogenetic dispersion of a species assemblage should reflect its functional dispersion (Swenson & Enquist 2009), and composition in terms of phylogenetic lineages should reflect functional composition. Hence, the two approaches can be used to express community structure in terms of both composition and diversity.

The phylogenetic-based method is far less data-intensive than the trait-based method and has therefore been broadly applied to different communities and trophic levels and across different spatial and phylogenetic scales (for a review, see Vamosi et al. 2009). However, both methods have seldom been applied together (but see Cavender-Bares et al. 2004a; Ingram & Shurin 2009). Recently, Swenson & Enquist (2009) and Kraft & Ackerly (2010) applied both approaches to a Neotropical dry forest and an Amazonian forest, respectively. They both found that, taken together, the two methods can be complementary and give more insight into the processes that determine community assembly. Furthermore, new frameworks have been proposed for decoupling functional, phylogenetic and taxonomic diversity, with the aim of identifying the phylogenetic component of trait variation (Pillar & Duarte 2010; Diniz et al. 2011; Ives & Helmus 2011; Peres-Neto et al. 2012). However, to what extent plot-to-plot functional turnover along an environmental gradient is driven by phylogenetic history has rarely been explored in terms of both composition and diversity.

The aim of our paper is to test whether variation in the functional composition and diversity is driven by phylogenetic history in plant communities on sand dunes along the Tyrrhenian coast of Italy. These communities provide an ideal system to test this question because they occur along a clearly defined stress gradient that drives considerable turnover in species composition and physiognomy over short distances. We hypothesize that differences in the functional composition and diversity among distinct species assemblages along the environmental gradient should mirror differences in phylogenetic structure.

Methods

Study area, vegetation data and environmental gradient

The study was performed on recent holocenic dunes of the Central Tyrrhenian coast of Italy, within the Lazio region (ca. 250 km). The area has a mediterranean climate (Carranza et al. 2008) and the holocenic dunes generally occupy a narrow strip along the seashore. These dunes are not very high (usually <8–10 m) and are relatively simple in structure, with beaches varying in breadth from a few meters to ca. 40 m, low embryo dunes, generally only one mobile dune ridge, dune slacks and stabilized dunes. The main environmental gradient is due to varying wind intensity, sand burial, salt spray, drought and soil development in relation to distance from the sea (Carboni et al. 2011). The vegetation on the dune profile follows a compressed zonation along the sea–inland environmental gradient: from the pioneer communities of the upper beach to the woody communities (Mediterranean macchia and evergreen forests) of the inland fixed dunes (Acosta et al. 2003). These distinct coastal dune community types (or habitats) are reasonably homogeneous in composition along the entire Central Italian coast (Acosta et al. 2003).

Most of the remaining contiguous dune systems in this region are distributed within five sites spanning a total of ca. 50 km along the coast of Lazio and separated by rocky promontories, silty river outlets and totally urbanized littorals (Fig. 1). For this study, we used a vegetation database available for these dune sites (Carboni et al. 2011; Santoro et al. 2012). The database contains georeferenced plots of 2 × 2 m in size, which were randomly sampled during spring–summer (April–June) from 2004 to 2008 after restricting the sampling area to recent holocenic dunes identified on orthophotographs. In each plot, all vascular plant species were recorded and the cover of all species was visually estimated using a 10% interval rank scale. Based on the species assemblage recorded, each plot was assigned to a plant community type of the coastal

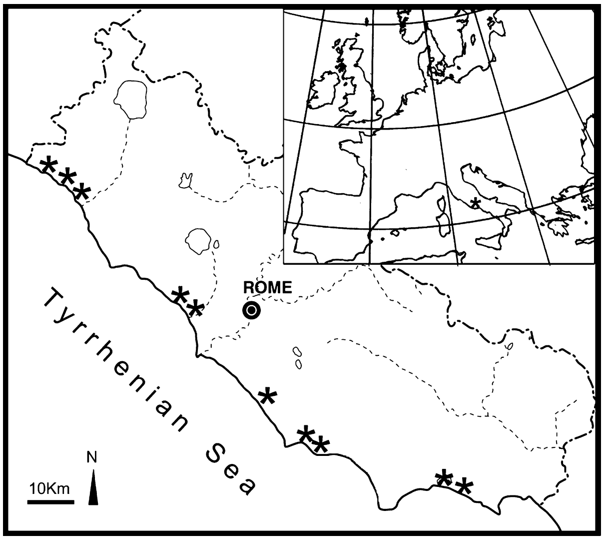

Fig. 1. Location of the study sites along the Tyrrhenian coast of Lazio (Central Italy).

dune zonation described for these areas. See Carboni et al. (2011) for more details on the sampling and database construction. In a previous study we measured environmental variables (pH, total organic matter, moisture and granulometry of the soil, as well as wind erosion, salt spray and sand burial) in a subset of plots and showed that all variables significantly correlated with distance to the sea (Carboni et al. 2011). In particular, values associated with higher environmental stress and disturbance were recorded in plots closer to the sea. Hence, here we used the distance to the sea as a single variable representing a proxy for the main environmental gradient. For the purpose of this study, we selected 405 plots distributed in the five study sites (Fig. 1), covering all community types of the zonation and at varying distances from the sea. This ensured that we could examine variation in species function in plots along the strong sea–inland environmental gradient. In the following, we refer to the plots as 'communities' or 'species assemblages' and to the community types of the coastal dune zonation as 'habitats'.

Traits

Traits were collected or measured on a subset of 46 dominant species. This subset of species was chosen by selecting the most common and abundant species within each habitat along the sea–inland gradient (Santoro et al. 2012) and of the complete vegetation database used in this study. We estimated that the selected species collectively made up at least 80% of the maximum standing live biomass of each dune habitat (estimated through the cumulative cover of all species available for the 4-m^2 plots). This threshold has been shown to ensure a satisfactory description of overall community properties (Pakeman & Quested 2007).

For each species we collected data on 16 functional traits that are related to plant responses to the environment (Table 1). We measured seven continuous traits (Table 1) related to the leaf–height–seed (LHS) plant strategy scheme (Westoby 1998). Each trait was obtained by measuring at least ten replicate samples on different individuals per species and averaging. Only individuals growing on well-conserved coastal dunes at one of the study sites were sampled (Fig. 1). For each species, individuals were measured within the habitat of the coastal zonation where the species was most abundant/dominant. The different leaf traits tend to be inter-correlated and are mostly indicators of leaf life span, but do not always capture the same functions. For example, higher specific leaf area (SLA) is associated with shorter leaf life span, higher leaf nitrogen, higher photosynthetic capacity, shorter nutrient residence times

Table 1. Description of the functional traits used in this study. Sources: Pignatti (1982), Tutin et al. (1964–1993). Seed shape is calculated according to Thompson et al. (1993).

Trait	Description	Data Type	Attribute	Source
Plant height	Plant height at maturity	Quantitative	[cm]	Measured
Seed mass	Weight of air dried dispersules	Quantitative	[mg]	Measured
SLA	Specific leaf area (leaf area/dry weight)	Quantitative	[mm^2·mg^{-1}]	Measured
LDMC	Leaf dry matter content (dry weight/fresh weight)	Quantitative	[mg·g^{-1}]	Measured
Leaf size	Leaf area	Quantitative	[cm^2]	Measured
Leaf thickness	Leaf thickness	Quantitative	[mm]	Measured
Seed shape	Variance of the three main dimensions	Quantitative	variance	Measured
Flowering phenology	Flowering phenology	Ordinal	1. April and before 2. May 3. June 4. July and after	Literature
Clonality	Vegetative propagation	Binary	0. Clonal; 1. Non-clonal	Literature
Leaf persistence	Leaf phenology	Binary	0. Deciduous 1. Evergreen	Literature
Life span	Plant life span	Binary	0. Annual 1. Biennal-Perennial	Literature
Pollination	Pollination system	Binary	0. By wind or non-specialized 1. By insects or birds	Literature
Life form	Raunkiaer life form	Nominal	1. Phanerophyte 2. Chamephyte 3. Hemicryptohyte 4. Geophyte 5. Therophyte	Literature
Growth form	Growth form	Nominal	1. Short basal 2. Long-semibasal 3. Erect leafy 4. Cushions, tussocks and dwarf shrubs 5. Shrubs, trees and climbers	Literature
Dispersal	Dispersal mode	Nominal	1. Anemochorous 2. Barochorous 3. Zoochorous	Literature
Leaf texture	Leaf texture	Nominal	1. Succulents 2. Malacophyllous 3. Semi-sclerophyllous 4. Sclerophyllous	Literature

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and higher relative growth rates (Westoby et al. 2002). Leaves with high leaf dry matter content (LDMC) tend to be relatively tough and more resistant to herbivory and decomposition (Cornelissen et al. 2003; Garnier et al. 2007). Plant height (height of flowering shoot) relates to both competitive ability and tolerance of disturbance (Westoby et al. 2002). Finally, the two seed traits are a proxy of dispersal ability and germination.

Furthermore, we collected information for nine categorical traits that relate to species growth form, phenology, dispersal ability and pollination from regional and national floras (see Table 1 for a full description and sources).

Phylogeny and phylogenetic signal at the species pool level

For the 46 dominant species we constructed an aged phylogenetic tree using the Phylomatic and Phylocom software (Webb et al. 2008). We assigned branch lengths by using a branch length adjustment algorithm (BLADJ), based on the minimum age of nodes estimated from the fossil record (Wikstrom et al. 2001). We next calculated a matrix of pair-wise phylogenetic distances between all species (summed branch lengths separating pairs of species). Although the phylogenetic tree constructed by the software Phylomatic contains many polytomies at the species and genus level, Phylomatic is virtually the sole freely available operational tool that enables ecologists without deep knowledge of evolutionary biology to reconstruct a meaningful community phylogeny. Accordingly, due to its simplicity, we consider it an acceptable tool for the integration of phylogenetic information into studies of community ecology (Ricotta et al. 2012a).

We next quantified the degree of phylogenetic signal at the species level for the traits used in this study. First, we calculated a multivariate matrix of pair-wise functional dissimilarities between species using the Gower distance Gower (1966) for mixed variables proposed by Pavoine et al. (2009b). Then, we used standard Mantel statistics to test whether this functional distance matrix was significantly correlated with the matrix of pair-wise phylogenetic distances between species. Although the Mantel test has been criticized because of its poor statistical performance in terms of low power and high type-I error rates (Harmon & Glor 2010), this method allowed us to deal with the categorical traits used in our study in a relatively simple manner. Furthermore, the species functional performances are expected to be driven by complex interactions among traits that are not fully independent from each other (e.g. Milla et al. 2009). In this framework, combining single trait differences between species into a multivariate pair-wise dissimilarity matrix, the Mantel test is essentially the sole approach that allows testing for phylogenetic signal for the entire set of traits used (Pillar & Duarte 2010; Hardy & Pavoine 2012).

Analysis

Various indices have been proposed to measure relevant aspects of community trait variability. Among these, the 'community-weighted mean trait value' (CWM) and the Rao coefficient have been widely used in ecological research for summarizing different facets of functional composition and diversity (e.g. Lavorel et al. 2008). While CWM represents the average functional traits within a species assemblage, the Rao coefficient can be seen as a measure of trait dispersion (diversity) within the assemblage. Together, these two complementary measures can be used to effectively describe two different aspects of the functional turnover along environmental gradients (Ricotta & Moretti 2011). While shifts in mean trait values within communities can be ascribed to environmental selection for certain functional traits, shifts in trait dispersion are related to patterns of trait convergence or divergence in response to assembly mechanisms. Recently, Pillar & Duarte (2010) proposed using phylogenetic-weighted species composition to compare communities in terms of their phylogenetic resemblance along environmental gradients. Hence, to examine to what extent phylogenetic history drives variability in within-plot functional composition and diversity in the coastal dune communities studied (community level), we used two complementary approaches. All analyses were carried out in the R statistical environment (R Foundation for Statistical Computing, Vienna, Austria)

Method1: phylogenetic composition vs. functional composition

To summarize the influence of phylogenetic history on the community functional composition, we adopted the general analytical approach described in detail by Pillar & Duarte (2010). Briefly, this procedure allows estimation of the degree of correlation between phylogenetic and functional composition (termed phylogenetic signal at the metacommunity level in Pillar & Duarte 2010). First, a matrix P containing species compositions for each plot after fuzzy weighting by phylogenetic similarities is generated (expressing clade composition in each plot). The corresponding matrix T is generated with a similar procedure and in essence contains the trait averages in each community or community-weighted mean values (CWM). Phylogenetic similarities were calculated as pair-wise phylogenetic distances between species in million years, while for calculating multivariate functional similarity, we used the Gower functional distance (Gower 1966, Pavoine et al. 2009b). We consider as evidence of phylogenetic signal at the metacommunity level a significant Mantel correlation between the distance matrices derived from P and T (DP and DT, respectively), which is tested against a null model predicting that phylogenetic structure described in matrix P is independent from structure present in matrix T (details in Pillar & Duarte 2010). A strong correlation is expected when communities that are more similar in terms of phylogenetic structure are also similar regarding their average trait values. Furthermore, this framework also allows us to estimate the relationship between variation in phylogenetic/functional composition (DP and DT) and the main environmental gradient (matrix DE; here obtained based on the Gower distance) through matrix correlations tested against appropriate null models. Analyses were performed using the R-based package 'syncsa' (Debastiani & Pillar 2012).

Method2: phylogenetic diversity vs. functional diversity

To investigate the effects of the phylogenetic dispersion within communities on the corresponding functional dispersion, we first calculated the phylogenetic and functional diversities (Q) of single plot as (Rao 1982):

$$Q = \sum_{i,j}^{S} d_{ij} p_i p_j \tag{1}$$

where d_{ij} is any uni- or multivariate distance of choice between species i and j with $d_{ij} = d_{ji}$ for all $i \neq j$, and $d_{ii} = 0$. For calculating the Rao phylogenetic diversity, we used pair-wise phylogenetic distances between species, while for calculating the functional diversity we used the Gower functional distance (Pavoine et al. 2009b). The Rao index is defined as the expected dissimilarity between two individuals of a given species assemblage selected at random with replacement; as such it represents an analogy of variance that summarizes the amount of trait dispersion in multivariate space (Ricotta & Moretti 2011; Pavoine 2012).

Based on the decomposition of Q into additive alpha, beta and gamma components (de Bello et al. 2010; Ricotta et al. 2012b), we next calculated the pair-wise phylogenetic and functional distances (J) for each pair of plots as:

$$J_{ab} = \sqrt{Q_{ab} - \tfrac{1}{2}(Q_a + Q_b)} \tag{2}$$

where Q_a and Q_b are the Rao diversities for plots a and b, respectively and Q_{ab} is the Rao diversity for the pooled pair of plots (for details see Champely & Chessel 2002; de Bello et al. 2010). For calculation of the pair-wise functional distances J, we used the function 'disc' in the R-based package ade4 (Dray & Dufour 2007) as implemented in de Bello et al. (2010). We then applied a Mantel test to the plot-to-plot phylogenetic and functional dissimilarity matrices to quantify how much of the functional diversity within plots is predicted by the corresponding phylogenetic diversity. Since functional and phylogenetic diversity in this framework are both influenced by species richness and evenness (i.e. taxonomic diversity), a partial Mantel test was used to confirm the fit after partialling out the variation due to the corresponding pair-wise taxonomic distances J. Finally, as in Method 1, we checked for relationships between plot-to-plot phylogenetic/functional dissimilarity matrices and the main environmental gradient through Mantel correlation with matrix DE.

Results

At the species level, we found a significant Mantel correlation ($R = 0.169$, $P = 0.001$) between the pair-wise species functional distances and their phylogenetic relatedness, meaning that, overall, the traits used in this study showed significant phylogenetic signal.

At the community level, for Method 1, the correlation between functional and phylogenetic matrices (P and T) was higher than at the species pool level ($R = 0.219$), although this correlation was not significant when tested against a null model randomizing phylogenetic relationships ($P = 0.412$). Furthermore, there was a significant relationship between functional composition and the environmental gradient ($R = 0.349$, $P = 0.003$), but no relationship of phylogenetic composition with the environmental gradient ($R = 0.037$, $P = 0.5$). In contrast, Method 2 (Fig. 2a) showed a very high and significant fit between pair-wise differences in functional diversity and corresponding differences in phylogenetic diversity ($R = 0.81$, $P = 0.001$). Furthermore, this congruence remained highly significant, when controlling for the effect of the plot-to-plot taxonomic turnover through a partial Mantel test ($R = 0.37$, $P = 0.001$). Plot-to-plot variation in both functional and phylogenetic diversity was also significantly related to the sea–inland environmental gradient ($P = 0.001$ in both cases; Fig. 2b,c). These results suggest that at least the species functional diversity within plots is largely reflected by the underlying phylogenetic diversity, while phylogenetic composition seems to be only partially related to functional composition at the community level in our system.

Discussion

Community-weighted trait means (CWMs) and functional diversity (FD) indices are commonly used in plant ecology to describe different facets of functional turnover along gradients: one related to changes in the dominant ecological adaptations and the other to changes in the number of

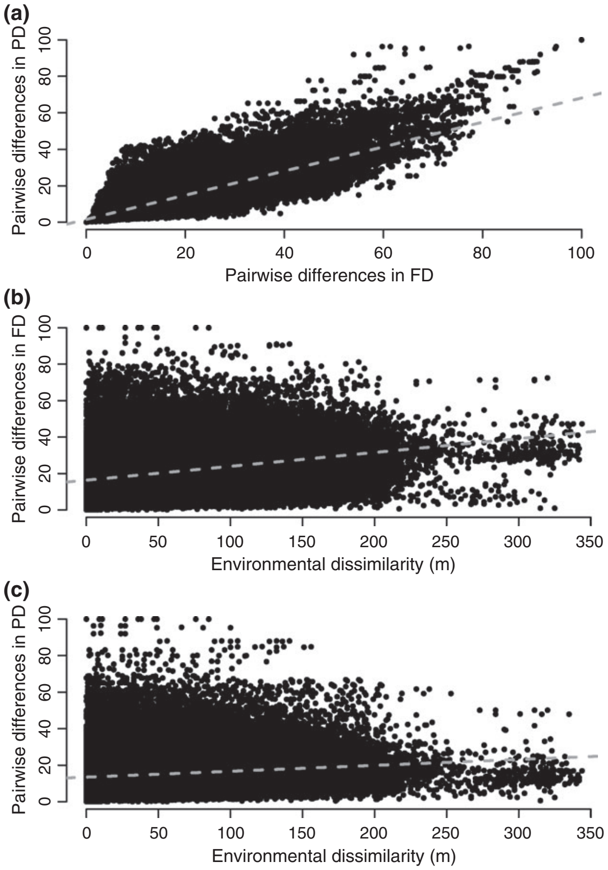

Fig. 2. Pair-wise dissimilarities among communities along the environmental gradient. (**a**) phylogenetic (PD) against functional (FD) pair-wise dissimilarities (Mantel-$R = 0.81$, $P = 0.001$); (**b–c**) PD and FD pair-wise dissimilarities against pair-wise environmental dissimilarities ($P = 0.001$). Environmental dissimilarities are the differences in plot distances to the sea (the main gradient). Simple linear regression lines are depicted on the graphs for a clearer visualization of the trends.

available niches leading to convergence or divergence (Ricotta & Moretti 2011). Analogue phylogeny-based metrics are being increasingly used, assuming that variability in community functional composition and diversity along the gradient is reflected by phylogenetic variability. In this paper we provided a formal test of this assumption. We found that variation in community functional diversity at the plot level could be effectively summarized by applying analogue phylogenetic metrics when traits show phylogenetic signal at the species pool level, while little congruence exists for variation in community composition metrics. We discuss our results in relation to the underlying environmental gradient and in light of recent studies addressing similar questions. In conclusion, we caution against the use of phylogeny as a predictor of environmental selection for dominant traits (i.e. through CWMs), while providing some support for the use of PD patterns to reveal shifting assembly processes along the gradient (i.e. through FD shifts).

Coastal dune ecosystems have long been typical model systems for the study of community level changes along natural gradients (Oosting & Billings 1942; Hesp 1991; Stubbs & Wilson 2004; Forey et al. 2008; Feola et al. 2011). Previous studies in the same communities examined here highlighted the link between the complex gradient in water availability, wind intensity and soil complexity with vegetation turnover (Carboni et al. 2011). In this study, matrix correlation with plot-to-plot environmental dissimilarities showed that, parallel to this strong turnover in species composition and abundance, there is also a significant functional turnover along the sea–inland gradient in terms of average trait composition. Hence, dominant species with particular suites of traits (e.g. short annual species with succulent leaves on the beach) are gradually replaced by other dominant species with different traits (e.g. tall perennial rhizomatous species on the main dune ridge). These results support the existence of environmental sorting of species according to habitat preferences mediated by distinct suites of traits. Pavoine et al. (2011) using a different approach (RLQ ordination) also found highly significant functional and phylogenetic turnover along a salinity gradient in a coastal dune system in northeast Algeria. Nevertheless, in our case we found no evidence for a correlation between the variation in community functional composition and phylogenetic composition. The lack of significant congruence between the functional and phylogenetic composition metrics at the community level was reflected by the absence of a clear phylogenetic turnover in terms of community composition along the environmental gradient. This supports the hypothesis that phylogeny only partially captured the environmental selection for certain functional traits along the gradient in this system, even in the presence of significant phylogenetic signal at the species pool level.

With respect to diversity, we detected high plot-to-plot variability in the dispersion of trait values within communities (FD), as well as in the dispersion of phylogenetic lineages (PD) along the main sea–inland gradient. A previous study focusing on the same communities had already shown a clear pattern of variation in FD among the habitats of the coastal zonation through functional rarefaction (Ricotta et al. 2012b). Here, we confirmed a directional pattern in the dispersion of trait values, with a decreasing trend in FD along the sea–inland gradient (Fig. S1). Moreover, we detected greater FD differentiation between communities parallel to greater environmental dissimilarity between communities (i.e. significantly positive Mantel correlation; Fig. 2b). In addition, we found that not only functional but also phylogenetic dissimilarities among communities were related to environmental dissimilarities (although more moderately; Fig. 2c). Finally, functional and phylogenetic dissimilarities were highly congruent along the gradient, meaning that plots that were very different from each other in the dispersion of trait values were also phylogenetically very different. This was true even when accounting for variation in taxonomic diversity. Hence, we can conclude that variability in PD probably captured the same assembly processes that lead to functional turnover. Overall, these results suggest that analysing community phylogenetic patterns, rather than functional ones, by means of diversity measures to reveal the number of supported niches along this ecological gradient would lead to similar conclusions.

In our empirical study, we considered a comprehensive set of traits summarizing relevant aspects of the plant strategies and adaptations in the coastal environment (e.g. overcoming the summer drought period by 'escaping' in the seed bank or preventing dehydration through specialized leaf anatomy and structure). In good agreement with recent works (Kraft & Ackerly 2010; Pillar & Duarte 2010; Uriarte et al. 2010), here at the species pool level we observed a moderate although significant overall phylogenetic signal. We found that in this coastal system the existence of phylogenetic signal in traits was a good indicator of the correlation between functional and phylogenetic diversity. A possible explanation (confirmed by preliminary analyses) is that, at least in our study system, functional traits exhibit on average higher levels of phylogenetic signal for the most dominant species than for the more subordinate ones. Given that dominant species tend to be strongly sorted along the coastal zonation, this is likely to lead to a significant relationship between phylogeny and functional diversity, since the Rao index is sensitive to species relative abundances in its formulation. However, it is not obvious how well phylogenetic history can predict functional diversity variability in other systems. For example, both Mason & Pavoine (2013) and Pavoine et al. (2013) suggest that PD is a poor surrogate of FD. Pavoine et al. (2013) point out that PD and FD indices are often found to correlate simply because variation in species richness and evenness influences both FD and PD values. However, in our case the relationship between pair-wise dissimilarities in PD and FD remained significant even when accounting for the effect of taxonomic diversity (TD). Nevertheless, in a recent study in a Mediterranean rangeland, Bernard-Verdier et al. (2013) found that phylogenetic diversity was generally a poor predictor of multivariate functional diversity along the main environmental gradient even after partialling out the effect of TD. However, they did find significant correlations for some traits when considering plot-to-plot variability in diversity measures, as in our study, which is partially in accordance with our results. Kraft & Ackerly (2010) also showed that phylogenetic community tests captured much of the same filtering patterns detected by trait-based methods. Taken together, their conclusions and our results provide some support for methods based on phylogenetic relatedness to investigate community assembly along environmental gradients. The presence of many other contrasting results, however, suggests that more studies analysing specifically the turnover in functional and phylogenetic diversity are needed along a variety of environmental gradients.

While the Rao coefficient is broadly applied in community phylogenetics, together with a multitude of other indices for summarizing phylogenetic diversity (Crozier 1992; Faith 1992; Pavoine et al. 2009a; Chao et al. 2010; Bernard-Verdier et al. 2013), the combined evaluation of the congruence between phylogenetic and functional composition is rare. Here, we showed that congruence in shifts of functional and phylogenetic diversity by no means implies the same fit at the level of community composition, even in the presence of significant phylogenetic signal overall at the species pool level. This is because shifts in composition and in trait dispersion capture signals of different ecological mechanisms, which may be more or less adequately reflected by phylogenetic variation. For instance, if traits related to habitat filtering were more labile than traits related to competition/facilitation, phylogeny should reflect shifting divergence/convergence patterns better than environmental sorting along the gradient. Competitive exclusion (through niche overlap) can lead to divergence of relevant traits, with the consequence that competition-related traits will contribute best to the diversity of communities, while traits associated to environmental preferences will determine the dominant trait composition of communities. Hence, if habitat-filtering traits are less well conserved, we would expect less congruence for functional and phylogenetic composition metrics, in accordance with our results. However, in contrast with this hypothesis, some authors have suggested that traits related to habitat preferences should rather be more phylogenetically conserved within lineages than traits determining convergence or divergence (i.e. functional diversity) within communities (Silvertown et al. 2001). There may also be other reasons why congruence of functional metrics with phylogeny could be more strongly dependent on phylogenetic signal for composition than for diversity metrics. For instance, phylogenetic signal at the species level could be generally poorly maintained at the meta-community level in terms of differences in species composition. Mason & Pavoine (2013), this issue), in a simulation study, consistently found poor congruence of functional and phylogenetic composition at the meta-community level (measured as in our study) along a hypothetical stress gradient, even when traits were strongly phylogenetically conserved in the species pool. As in our study, even when the functionally determined species composition of communities was significantly correlated with their position along the stress gradient, there was no such correlation for phylogenetic composition. However, the causes of this mismatch at the meta-community level are not yet clear, and this remains an open question that merits further investigation.

In conclusion, on the one hand our results suggest that community-level phylogenetic variability among plots can in some cases be used as proxy of overall functional variability, calculated based on a high number of measured and collected traits. On the other hand, we also found that phylogenetic methods may at the same time fail to reveal functional patterns when examining shifts in average composition, pointing to environmental sorting along a gradient. Overall, these results show that even when there is evidence of phylogenetic trait conservatism at the species pool level, phylogeny may be unable to capture all aspects of functional community structure. This emphasizes the need for caution when interpreting measures of phylogenetic community structure as proxies of functional community structure and the need to carefully weigh the choice of approach depending on the question asked.

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Supporting Information

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

Figure S1. FD (a) and PD (b) in the plots along the environmental gradient (distance to the sea – meters).