



## Correlations between phylogenetic and functional diversity: mathematical artefacts or true ecological and evolutionary processes?

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### Keywords

Assembly processes; Biodiversity; Diversity indices; Environmental filtering; Niche complementarity; Null model; Phylogenetic signal; Simpson index; Species richness; Surrogates

### Abbreviations

FD = Functional diversity; PD = Phylogenetic diversity

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### Abstract

**Questions:** Is phylogenetic diversity (PD) an accurate surrogate for functional diversity (FD)? How are FD:PD correlations affected by the diversity index used, covarying factors and/or the strength of the phylogenetic signal in ecological traits?

**Location:** Field study, coastal marsh plain Mekhada, Algeria, complemented by simulated data.

**Methods:** FD and PD indices might correlate simply because variation in species richness and evenness (referred to as co-factors) influences both FD and PD values. We partition FD and PD indices into components influenced by species richness, evenness and species' (functional and phylogenetic) characteristics. When a simple partition was not found, comparison to null models was used to remove the effects of co-factors. We examined correlations between ten FD and PD indices, among which several were shown to be connected using our mathematical partitioning approach and several were transformed by comparison with null models to control for effects of co-factors. In doing this, FD values were calculated using simulated trait values with varying phylogenetic signal. We then selected a subset of complementary FD and PD indices in exploring the influence of environmental variables on diversity across 75 plant assemblages in Mekhada.

**Results:** Altogether, mathematical partitioning and the comparison to null models successfully removed the effects of co-factors when comparing FD and PD. For all indices affected by species richness, FD:PD correlations approached 1, irrespective of the trait evolution model used. In contrast, simulations showed that FD:PD correlations measured with indices unaffected by co-factors decreased when the phylogenetic signal in traits decreased. Applied to plant assemblages in Mekhada, complementary diversity indices showed that, despite significant (but moderate) FD:PD correlation, FD but not PD was significantly correlated with the main stress gradient (salinity).

**Conclusions:** From both our simulations and analysis of plant community diversity, PD was a poor surrogate for FD. In Mekhada, PD was also less correlated with environmental variables than FD. Species richness was found to be a better surrogate for FD than PD in identifying the ecological processes that distribute species along the salinity gradient.

### Introduction

Phylogenetic diversity (PD) is increasingly used to understand community assembly processes, predict rates of

ecosystem function and prioritize areas for conservation. These studies generally assume that PD is a surrogate for functional diversity (FD), with closely related species being more similar in their functional traits than distantly related

ones (Webb et al. 2002; Blomberg et al. 2003). Disparities between FD and PD have also been used to infer that phylogeny captures more ecologically relevant functional variation than the limited number of traits used to estimate FD (Cadotte et al. 2009). However, there has been little critical assessment of whether PD can really act as a general surrogate for FD. Testing this requires appropriate indices for examining correlation and association between FD and PD. This study explores the relationships between FD and PD indices. Using real and simulated data, we test whether PD is likely to be a useful surrogate for FD in community ecological studies. In doing so we aim to identify which diversity indices have the power to discriminate relationships between FD and PD, and are not confounded by co-varying factors.

### IS PD likely to be a realistic surrogate for FD?

Our starting point, as with many studies, relies on the hypothesis that (unmeasured) traits are evolutionary conserved. As shown in Webb et al. (2002) and Kraft et al. (2007), patterns in PD depend on whether critical traits are conserved or convergent. For PD to be a generally useful surrogate of FD, the relationship between FD and PD thus needs to be robust against phylogenetically independent trait variation. Mismatch between FD and PD may be explained by lack of resolution in phylogenies but also by phenotypic plasticity in traits of distant species (Kluge & Kessler 2011). For many functional aspects of diversity, in a range of different phylogenies, phylogenetic distances are able to explain a significant amount of variation in trait values across taxa (Blomberg et al. 2003). However, variation in traits across species is the outcome of both environmental and historical factors (Freckleton & Jetz 2009), so that the strength of the phylogenetic signal in trait variation can differ markedly according to the specific traits and the phylogeny under investigation (Blomberg et al. 2003). Indeed, cases where phylogenetic and trait variation are very tightly linked may well be the exception rather than the rule (Blomberg et al. 2003). Both conserved and convergent traits have been found to be involved in ecological processes, such as environmental filtering and competition (Emerson & Gillepsie 2008). There are many biological reasons to expect no relationships between PD and FD, or even a negative relationship (Emerson & Gillepsie 2008). One obvious explanation is that species may evolve while persisting within an assemblage, thus decreasing the relationships between FD and PD (Kluge & Kessler 2011). Overall, trait divergence (Prinzing et al. 2008) and adaptive diversification (Fukami et al. 2007) can decrease the link between FD and PD.

As the ultimate objective for the use of PD is to elucidate the ecological mechanisms that structure communities,

simply correlating PD with FD is thus not sufficient; it is imperative to find an association between PD and some aspect of the ecological process (e.g. along an environmental gradient as in our case study) or processes affecting the community organization, similar to the association between FD and the same aspect of the ecological process (es). For example, several studies in meadow grassland communities have found that increased FD was associated with higher rates of productivity (Petchey et al. 2004). At a broader scale, the correlation between FD of forest tree assemblages and plant productivity was found to be higher in less productive, boreal environments (due to niche complementarity effects) compared to productive, temperate environments, where niche complementarity effects are weakened by highly productive species occurring in monospecific stands (Paquette & Messier 2011). As might be expected, the choice of which functional traits to include in an analysis is the most important aspect in measuring FD (Petchey & Gaston 2002). For example, PD has been found to be a better indicator of ecosystem function (e.g. primary productivity; Flynn et al. 2009) than FD, simply as a result of the difficulties associated with finding relevant traits with which to measure FD (Cadotte et al. 2009).

### Identifying non-redundant indices for testing FD and PD correlations

In this study, we focus on the mathematical explanation that affects the relationships between PD and FD. Biodiversity is a multifaceted concept, which no single index can hope to quantify in an easily interpretable way (Pavoine & Bonsall 2011). Measures of both FD and PD are affected by how species are distributed in functional or phylogenetic space and also how abundances vary among species. When the objective of a study is to identify ecological mechanisms that explain species' occurrences and abundances, a guiding principle in selecting interpretable FD and PD indices is that each index should quantify a single, independent aspect of biodiversity (Mason et al. 2005). Interpreting correlations between FD and PD requires indices that uphold this principle.

The FD and PD indices depend on three metrics: (1) species' identities; (2) species' abundances; and (3) species' distribution in functional or phylogenetic space. In this study, our first aim is to provide a definitive means of assessing whether indices proposed to measure FD and PD are truly independent of diversity measures that depend only on species' identities and abundances, such as species richness and evenness. Our approach seeks to mathematically partition diversity indices into their basic components. This partitioning provides a more definitive approach to assessing whether an index is truly

independent from, or shares some redundancies with, other indices.

### Using null models to remove redundancy between indices

Recently, conceptual arguments have been made for using null models to explore (and hence remove) redundancy between FD or PD indices and existing diversity measures. We have explored this approach for those indices for which a simple mathematical partitioning has not been obtained. For example, for indices that are based only on species' characteristics, comparison of observed FD or PD values to those expected from null models that randomize species occurrences (Hardy 2008) have been used to control for the trivial effects of species richness. Also, indices that are based on species' characteristics and abundances can be compared with a null model that randomizes the abundances across species within each community (Hardy 2008) to control for the effect of the evenness of species' abundances.

### Aims and objectives

Our broad aim is to understand the association between FD and PD in communities. The ultimate objectives of this work are twofold. First, we aim to provide a test of whether (and under what conditions) PD is correlated with FD. Second, we aim to identify a set of appropriate indices for testing correlations between FD and PD in real plant communities, according to the following criteria:

1. Each index should quantify a single component of FD or PD that is independent of species richness and evenness.
2. Each index should provide good power to detect FD:PD correlations.
3. Correlation levels between FD and PD should not be dependent on any mathematical artefact.

We begin by decomposing FD and PD indices into simpler components to identify those that are truly independent from species richness and evenness. We then use null models to remove remaining redundancies between indices and analyse whether this affects the strength of FD:PD correlations. We simulate trait values to test whether the strength of the phylogenetic signal in trait variation affects FD:PD correlations. Finally, we examine FD:PD correlations across real plant assemblages in the Algerian coastal marsh plain using a subset of identified non-overlapping FD and PD indices. Doing this, we intend to examine the potential for FD:PD correlations to reveal underlying ecological processes that structure species communities rather than simply providing a robust test of a range of different processes. This especially relates to the use of diversity partitioning measures to identify indices where correlations

might arise simply due to some artefact (like variation in species richness), rather than a real ecological process.

### Methods

We have used real data to evaluate the relevance of statistical approaches that compare FD and PD. When necessary, this real data set was compared with simulated data (see FD and PD correlations in simulated data). The field study is located at La Mafragh, Mekhada, (15 000 ha, 36°48'N, 008°00'E), a coastal marsh plain of low elevation (from 1 to 4 m a.s.l. for most of the area) in the east of Annaba in Algeria. This region is located in a sub-humid bioclimate with warm winters (Emberger 1955). It is furrowed by rivers, and constitutes a basin filled by alluvial and colluvial deposits. The lowest parts are composed of large and small marshes. The study area was defined in de Bélair (1981). It constitutes 10 000 ha within the coastal plain where 102 sites were defined on a regular grid (average size of sites = 100 ha). Five of these sites, with very high heterogeneity, and 22 other sites (predominantly located in the central marsh) with three species or less, were excluded from our analyses, leaving 75 sites. The plant abundance data were collected in 1979 based on three relevés per site (separated by 200 m). Details on the sampling design can be found in de Bélair (1981) and Pavoine et al. (2011). A total of 56 plant species was observed. Nine biological traits are available for the recorded plant species: (1) life cycle (perennial, annual, biennial and/or seasonal), (2) pollination (autogamous, entomogamous and/or anemogamous), (3) median of the potential flowering period, (4) length of the flowering period, (5) maximum and (6) minimum height of adult individuals, (7) spikiness (absent, sometimes present, always present), (8) succulent leaves (absent, sometimes present, always present), (9) hairy leaves (absent, sometimes present, always present). Life cycle and flowering periods are important to determine how plants can cope with harsh (xeric) seasonal conditions. For instance, most dicots in La Mafragh were annual or biennial, completing their life cycle before the onset of the xeric season (Pavoine et al. 2011). Pollination mode may influence species occurrence along the main stress gradient if biotic pollen vectors are less abundant in high stress, low productivity sites. Spikiness, succulent leaves and hairy leaves are morphological adaptations that aid water conservation. Spikiness and hairy leaves also reflect solar radiation, which can be important for avoiding photoinhibition and photorespiration in high stress environments. Plant height is an indicator of light competition ability, and is usually associated with a K-selected (competitive) ecological strategy (Westoby et al. 2002).

A phylogenetic tree was established based on Webb & Donoghue (2005) for topology; further details are given in

Pavoine et al. (2011). As with any study in phylogenetic community ecology, our results might be affected by uncertainties associated with the phylogenetic tree (which is only an estimation of the unknown real tree). The phylogenetic tree we utilize has been widely used in studies on phylogenetic community analyses (179 citations for Webb & Donoghue 2005 according to the ISI Web of Knowledge, August 2012). Using this phylogenetic tree we integrated the most up-to-date estimates of branch lengths (Wikström et al. 2001; Hedges & Kumar 2009) (in contrast many previous studies on phylogenetic community diversity have just used Wikström et al. 2001; or simply counted nodes ignoring branch lengths, and hence lack comprehensive details on evolutionary history). The pedological data were also collected in 1979 from each site (de Bélaïr 1981). Eight soil variables were considered: Clay (%), silt (%), sand (%),  $K_2O$  (‰),  $Mg^{2+}$  (mEq 100 g<sup>-1</sup>),  $Na^+$  (mEq 100 g<sup>-1</sup>),  $K^+$  (mEq 100 g<sup>-1</sup>), elevation (m). The whole data set is described in detail and available as Supplementary Material in Pavoine et al. (2011).

As we could not consider the myriad of diversity indices developed so far, we analysed the diversity of the 75 plant assemblages with the richness ( $S$  = number of species), the Gini–Simpson index ( $G = 1 - \sum_{i=1}^S p_i^2$ , where  $p_i$  is the relative abundance of a species) and ten distinct diversity indices that represented different aspects of PD and FD. These indices were originally developed to measure FD, PD or both. As shown in Pavoine & Bonsall (2011), all these indices of diversity can be adapted to describe either FD or PD.

### The indices

The ten diversity indices we studied include information on species richness, species' abundances and characteristics. Although the indices are based on similar assumptions, they differ in which aspect of FD and PD they describe. Basically, when applied to FD each of these indices is defined according to one of the following three criteria: functional distances among species (obtained through an extension of Gower distance; Gower 1971; Electronic Appendix S1); a functional space (obtained by principal coordinates analysis applied to functional distances; Gower 1966); a functional dendrogram (obtained by an unweighted pair group method based on the arithmetic mean, UPGMA, algorithm applied to functional distances; Petchey & Gaston 2002). Similarly, when applied to PD, each of the diversity indices is based on one of the following criteria: phylogenetic distances (sum of branch lengths on the shortest path that connects two species on the phylogenetic tree); a phylogenetic space (obtained by principal coordinates analysis applied to phylogenetic distances; Gower 1966); the phylogenetic tree. A complete description of the indices is given in Appendix S2.

Tree size (TS) is the sum of all branch lengths in a phylogeny (Faith 1992) or a functional dendrogram (Petchey & Gaston 2002). FEve (Villéger et al. 2008) is an abundance-weighted measure of functional regularity. If a single quantitative trait is considered, FEve would have its maximum value if all species' values were regularly spaced in the quantitative trait axis and if all species had similar abundances. We have also used this index when all species have equal abundances and named it FEvep. HED and EED (Cadotte et al. 2010) measure evenness in phylogenetic or functional distinctiveness (where distinctiveness is high for species that are distant to all others in a phylogeny or a functional dendrogram).  $B$  (Shimatani 2001) is a measure of the covariance between the abundances of pairs of species and the functional or phylogenetic distances between them. We also examined four indices that are very similar: FAD (Walker et al. 1999), which is the sum of pair-wise functional or phylogenetic distances between species; MFAD = FAD/( $S - 1$ ) (Schmera et al. 2009), where  $S$  is the number of species; meanD, which is the mean of pair-wise functional or phylogenetic distances between species (Weiher et al. 1998); and QE (Rao 1982), which is the mean of pair-wise functional or phylogenetic distances between species, where species are weighted by their relative abundances.

### Using mathematical partitioning to identify redundancy among diversity measures

Several of the ten diversity indices are known to depend on only a single aspect of diversity: meanD, which measures the functional/phylogenetic divergence among species;  $B$ , which measures the covariance between species' functional/phylogenetic distances and abundances; EED, which measures evenness in species' functional/phylogenetic distinctiveness. The other more integrative indices might depend on the effects of species number, evenness in the species abundance, species' functional and phylogenetic characteristics and the interaction between these components. We have partitioned these more integrative diversity indices into simple indices, i.e. into indices that depend on a single aspect of diversity. We did this by identifying, in the equations of these indices, terms that depend only on species richness (and not on species' abundances or characteristics), terms that depend only on species evenness, terms that depend only on species' characteristics and terms associated with an interaction between species' abundances and characteristics (if, for instance, some characteristics are common in more abundant species in a community while other characteristics are retained in rare species). Partitioning of indices reveals redundancy between indices.

### Using null models to provide complementary indices

We also evaluated the ability of null models (Gotelli & Graves 1996) to remove the confounding effects of species richness and evenness for estimating correlations of FD and PD. This approach, based on a transformation of each diversity index, was applied on both simulated and real data. A transformed index was defined as standardized effect size (SES) (Gotelli & McCabe 2002), such that  $SES = (obs_x - mean_x)/SD_x$  where the subscript ( $x$ ) denotes the original diversity index,  $obs_x$  is the observed value of the index in one of the 75 plant assemblages, and  $mean_x$  and  $SD_x$  are the mean and SD from an underlying null model.

We generate two different null models. A pool of species was defined by the 56 plant species observed in the study area. For the first null model, random assemblages were determined with the same number and abundance of species as that observed in the real assemblages. However, the identities of the species were replaced with the identity of species randomly drawn from the species pool (model 1p in Hardy 2008). This null model supposes that the presence and abundance of species within assemblages is independent of their traits and phylogeny. The second null model applies only to diversity indices that include species' abundances. It assumes that species have random abundances within an assemblage. Using each real assemblage, random assemblages were obtained by permuting abundances among present species (model 1s in Hardy 2008). SES1 will define the SES transformation associated with the first null model and SES2 the SES transformation associated with the second null model.

For all indices that do not include species' abundances, a transformation by SES1 is expected to provide new indices free from variations in species richness. For all other indices (QE, B, FEve), the new indices obtained by SES1 and SES2 transformations are expected to depend on interactions between abundances and species' characteristics only. All indices and the transformations used are summarized in Table 1.

### The FD and PD correlations in simulated data

We analysed the impact of phylogenetic signal strength on the correlation between FD and PD. We assumed that the same index is used for measuring FD and PD (Appendix S3). The FD:PD correlation analyses were done for the ten raw diversity indices, the indices transformed by SES1 and the indices transformed by SES2.

For this analysis, we simulated traits with various phylogenetic signals. To do this, we applied the Brownian motion model (BM) and the accelerating (AC) model of trait evolution to the phylogenetic tree with different

accelerating rates of evolution (Blomberg et al. 2003). With the height of the phylogenetic tree standardized to equal one, and the variance-covariance matrix of species' trait values equal to  $\sigma^2 C(\theta, g)$ , where  $\theta$  is the value at the root node and  $g$  is the rate of trait change, we used the following parameter values for the AC model:  $\sigma^2 = 1$ ,  $\theta = 0$ ,  $g = \exp(-2)$ ,  $g = \exp(-10)$ ,  $g = \exp(-20)$ ; phylogenetic signal increases with  $g$ , when  $g$  tends towards 0 the model tends towards BM (see Blomberg et al. 2003 for details). We also used completely random traits drawn from a standard normal distribution with mean 0 and variance 1. We simulated species pools with nine quantitative traits based on one of the evolutionary models (we chose to simulate nine traits as our real data set contained nine traits). Species abundances for species pools were derived from the real abundances of plants within the 75 plant assemblages from Mekhada. The real phylogenetic tree associated with plant assemblages from Mekhada was used to describe evolutionary relationships between simulated species.

For diversity indices that required functional distances among species, we used the squared Euclidean metric because, by definition, it is expected to vary linearly with phylogenetic distances under the Brownian motion model (e.g. Harmon & Glor 2010). We simulated 1000 species pools per evolutionary model for the raw diversity indices, but only 50 species pools under the SES transformations (due to computational limits). Each SES transformation was based on 200 theoretical values per null model.

For each simulated data set, we applied all indices to evaluate PD and simulated FD within the 75 plant assemblages; we then computed Spearman rank correlation between FD and PD with each of the diversity indices. This non-parametric measure of correlation is more appropriate than Pearson product-moment correlation as the high number of simulations prevented us from analysing the effects of distribution shape and Pearson correlation is sensitive to extreme values.

### The FD and PD correlations in real data

We estimated the phylogenetic signal in functional trait variation with the Mantel test since it allows us to analyse the strength of the phylogenetic signal across all nine traits simultaneously. Based on our mathematical partitioning (see Using mathematical partitioning to identify redundancy among diversity measures) and simulations (see the FD and PD correlations in simulated data), we selected a subset of four diversity indices in addition to species richness and evenness. The SES transformation was applied with 1000 theoretical values per null model and assemblage. We analysed the impact of the choice of the diversity index on the FD:PD Spearman correlation. We then analysed the associations between FD, PD and environmental

**Table 1.** Summary of the indices used. Details on each index can be found in Appendix S2.

Short definitions	Abbreviations	References	Dependence on		
			Species richness	Species' abundances	Associated simpler indices <sup>1</sup>
Sum of differences among species	FAD	Walker et al. (1999)	Yes	No	meanD
Sum of differences among species divided by species richness	MFAD	Schmera et al. (2009)	Yes	No	meanD
Average difference between two species	meanD	Weiher et al. (1998)	No	No	
Covariance between species' characteristics and abundances	B	Shimatani (2001)	No	Yes	SES1B, SES2B
Average difference between two individuals	QE	Rao (1982)	Yes	Yes	meanD, B, SES1B, SES2B, SES1QE
Sum of branch lengths on a phylogenetic, functional tree	TS	Faith (1992); Petchey & Gaston (2002)	Yes	No	SES1TS <sup>2</sup>
Diversity in species distinctiveness	HED	Cadotte et al. (2010)	Yes	No	EED, SES1EED
Evenness in species distinctiveness	EED	Cadotte et al. (2010)	No	No	SES1EED
Evenness in differences among individuals	FEve	Villéger et al. (2008)	No <sup>3</sup>	Yes	SES1FEve <sup>2</sup> , SES2FEve <sup>2</sup>
Evenness in differences among species	FEvep	Villéger et al. (2008)	No <sup>3</sup>	No	SES1FEvep <sup>2</sup>

<sup>1</sup>By simple index we mean that unaffected by species richness and/or species' abundances.

<sup>2</sup>As in the main text, SES1 means standardized effect size (SES) transformation by the first null model, and SES2 means SES transformation by the second null model. These transformations are expected to remove the dependence on species richness and to control the dependence on species evenness.

<sup>3</sup>The ranges of these indices do not depend on species richness; however, the overall impact of species richness in the values of these indices has not been determined by our study. We thus relied on null models to remove any potential effects of species richness.

variables by linear additive regressions (nominal type I error  $\alpha = 5\%$ ) to evaluate whether PD can be used as a surrogate for FD. All calculations were completed in R (R Foundation for Statistical Computing, Vienna, AT, AU) with the packages listed in Appendix S4.

## Results

### Mathematical partitioning

*The FD:PD correlations for FAD, MFAD and HED can arise simply due to variation in species richness*

Mathematical analysis allows a better understanding of how species richness influences the correlation between FD:PD for MFAD and FAD. Because  $MFAD = (S - 1) \text{meanD}$ , and  $FAD = S(S - 1) \text{meanD}$ , where  $S$  is the species richness within an assemblage, the correlations between FD:PD for MFAD and FAD depends on (1) the mean and variance of species richness within assemblages, (2) the mean and variance of meanD for functional traits and phylogeny, (3) the pair-wise covariances (normed by means) between species richness, the phylogenetic meanD and the functional meanD (proof in Appendix S5-A). When comparing FD and PD with MFAD and FAD, it is thus difficult to unravel whether the observed correlation is due to species richness only or to similarities in the functional and phylogenetic characteristics of the species. To answer this question, MFAD and FAD have to be partitioned into species richness and meanD.

Even if the pair-wise correlations between species richness, FD and PD (as measured by meanD) all equal zero,

the estimated FD:PD correlations for both MFAD and FAD can still approach 1 due to the effects of species richness in MFAD and FAD. In fact, FD:PD correlations are mostly driven by species richness if the coefficient of variation (CV) of species richness is much higher than the CV for functional and phylogenetic meanD (proof in Appendix S5-A). In this case, comparing functional and phylogenetic MFAD or FAD is like comparing species richness with itself, which, obviously, is rather meaningless.

The HED is also linked to EED by a function of species richness:  $HED = \ln(S) EED$ . Partitioning HED thus shows it is influenced by species richness, and as for FAD and MFAD, FD:PD correlations for HED approach 1 when variation in HED is mostly driven by variation in species richness.

*The TS: a complex function of species richness*

The last index based on species' presence/absence that we studied, TS, is known to be highly dependent on species richness (Petchey & Gaston 2002). Several studies have explored the link between TS and species richness by performing simulations with a regularly increasing number of species randomly drawn from a species pool. With these simulations, Petchey & Gaston (2002) found that TS increases roughly linearly with species richness for trees with many nodes close to the root; and that, in contrast, TS first increases drastically and then saturates with increasing species richness for trees with many nodes close to tips.

When species are randomly drawn from a pool, the connection between TS and species richness depends on tree shape. Consider a pool of  $S$  species, a tree (functional dendrogram or phylogeny) composed of  $K$  branches with lengths  $l_k$ ,  $k = 1, \dots, K$ . Let  $d_k$  be the number of tips that descend from branch  $k$ . On average, the expected value for TS in an assemblage of  $n$  species randomly drawn from the species pool is (proof in Appendix S5-B):

$$\overline{TS}(n) = \left[ \binom{S}{n} \sum_{k=1}^K l_k - \sum_{\substack{k \text{ such that} \\ d_k \geq n}} \binom{d_k}{n} l_k - \sum_{\substack{k \text{ such that} \\ S-d_k \geq n}} \binom{S-d_k}{n} l_k \right] / \binom{S}{n}$$

TS is thus a function of polygons of  $S$  and  $n$  of various degrees, which depends on the shape of the tree considered. We need a null model to remove trivial effects of species richness.

*The QE: a function of G, meanD and B indices*

For quadratic entropy (QE), Shimatani (2001) showed that  $QE = \text{meanD} \times G + B$ , where  $G$  is the Gini–Simpson index, which depends on species richness ( $S$ ) and species’ abundances ( $p_i$ ),  $G = 1 - \sum_{i=1}^S p_i^2$ ;  $B$  is the covariance-like measure between the abundances of pairs of species ( $p_i p_j$ ) and the distances between them ( $d_{ij}$ )  $B = 2 \sum_{i>j} (d_{ij} - \text{meanD}) (p_i p_j - \frac{G}{S(S-1)})$  and meanD is the average distance among species

$$\text{meanD} = \frac{1}{S(S-1)} \sum_{i=1}^S \sum_{j=1}^S d_{ij}$$

QE is thus dependent on the main effects of both species’ abundances ( $G$ ) and species characteristics (meanD), and on the interactions between species’ abundances and characteristics ( $B$ ).

The FD:PD correlation for QE depends on the pair-wise covariance between  $G$ , functional and phylogenetic meanD, and functional and phylogenetic  $B$  (Appendix S5-C). It can also be shown that, when there is no correlation between functional and phylogenetic distances between species, a FD:PD correlation for QE approaching 1 can only occur due to the effects of species abundances (Appendix S5-C). To extend this further,  $G$  can also be decomposed into the species richness (number of species,  $S$ ) and an index of species evenness independent of species richness:

$$E = \frac{S}{S-1} \left( 1 - \sum_{i=1}^S p_i^2 \right)$$

Given that the component of QE dependent on species richness is  $(S - 1)/S$ , the impact of species richness on its

values is expected only when species richness is low. To understand *how* and *why* each component of diversity drives the FD:PD correlation, one has to evaluate the effects of species richness, species evenness, meanD and  $B$  on the strength of the correlation.

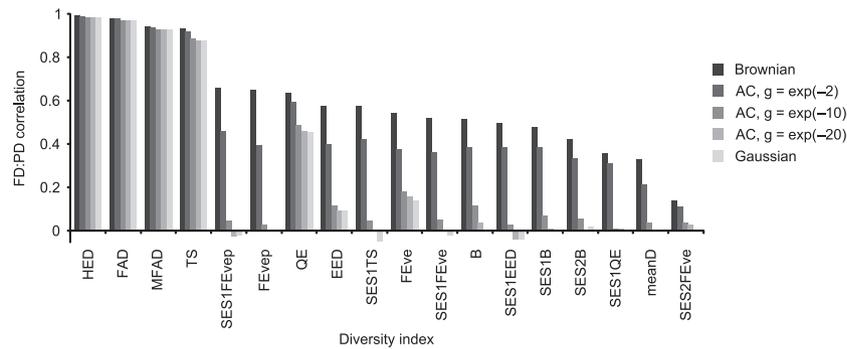
*Interpreting FEve and FEvep*

Null models are necessary to analyse FEve and FEvep as there is no simple way of extracting the contributions of species richness, species’ abundances and functional or phylogenetic characteristics from the mathematical expressions for these diversity indices. For FEve and FEvep a minimum spanning tree must be built but it is dependent on which species are in the assemblages. Although the range (0,1) of these indices is not dependent on species richness, we used the SES transformations to verify whether co-factors could affect their values.

**The FD and PD correlations in simulated data**

Although EED is, in theory, not expected to be affected by species richness, we found in our simulations unexpected moderate correlations between functional and phylogenetic EED even when traits were simulated independently of the phylogeny. We thus applied the SES1 transformation to EED. Under model 1, FD:PD correlations obtained with SES1HED and SES1EED are equal (Appendix S5-D). Henceforth, we considered only SES1EED. FD:PD correlations obtained with SES1FAD, SES1MFAD, SES1meanD and simply meanD are identical (Appendix S5-D). Henceforth, we only considered meanD. We applied the SES transformations to all indices that depended on species’ abundances because they could all potentially be affected by the shape of distribution of species’ abundances within the species pool and the communities. SES1 was thus applied to the following indices:  $B$ , EED, FEve, FEvep, QE and TS. Under null model 2, SES2QE = SES2B (Appendix S5-D), SES2 was thus applied to the following indices that depend on species’ abundances:  $B$ , FEve.

Indices confounded by species richness gave high correlations even when the phylogenetic signal in trait data was weak. Many of the indices (HED, FAD, MFAD, TS, QE and to a lesser extent EED and FEve) we have considered are confounded and were found to be influenced by co-factors (Fig. 1, Appendix S6). The indices  $B$ , FEvep and meanD seemed unaffected by co-factors. Given that when using null models, correlations are strongly influenced by the strength of the phylogenetic signal, null models correctly remove the influence of the co-factors on the FD:PD correlation. However, for many indices FD:PD correlations were moderate or low even when traits followed a Brownian model of evolution (i.e. when the phylogenetic signal was



**Fig. 1.** Bar plots of the average Spearman correlation between FD and PD obtained when simulating traits according to the Brownian model (Blomberg et al. 2003), AC model (with varying values for parameter  $g$ ), and random normal distribution. “SES1” is written before the name of indices transformed by method SES1 based on null model 1, and “SES2” before the name of indices transformed by method SES2 based on null model 2 (see Methods).

strong) and strongly decreased with increasing accelerating rate of evolution in the model AC (Fig. 1). All indices transformed by null model 2, where abundances are permuted among species within assemblages, were associated with low FD:PD correlations even when traits followed a Brownian model of evolution (Fig. 1). This might be due to a lack of abundance variability in our data set (phytosociological estimations).

Based on this analysis, we selected the following indices, which collectively quantify each of the primary components, richness, evenness and divergence, as identified by Mason et al. (2005), to analyse our real plant community diversity data set:

1. SES1TS and meanD, which both describe the size of functional or phylogenetic space occupied by the species of an assemblage (i.e. functional or phylogenetic richness), but SES1TS is more adapted to the tree-shape structure of phylogenetic data and meanD is more adapted to the analysis of a table of functional traits which does not have an intrinsic tree structure.
2. FEvep, which describes how regularly spaced species' traits or phylogenetic positions are in a multivariate space (i.e. a special case of functional or phylogenetic evenness where all species have the same abundance);
3.  $B$ , which determines whether the most functionally or phylogenetically distant species have the highest abundances (i.e. functional or phylogenetic divergence).

Species richness and evenness completed the list of diversity indices.

### The FD and PD correlations in real data

We found a significant phylogenetic signal in the functional distances among species (Mantel test,  $r = 0.310$ ,  $P = 0.001$ , 1000 permutations). FD:PD correlations depended on the index selected and varied from 0.149

(FEvep,  $df=73$ ,  $P = 0.202$ ), 0.398 ( $B$ ,  $P < 0.001$ ), 0.465 (SES1TS,  $P < 0.001$ ), to 0.526 (meanD,  $P < 0.001$ ). Despite these correlations, linear additive regression revealed that FD was more correlated with environmental variables than PD. For FD, we found that all indices except  $B$  were significantly correlated with the environmental variables: SES1TS ( $r^2=0.410$ ,  $P < 0.001$ ), FEvep ( $r^2=0.373$ ,  $P < 0.001$ ), meanD ( $r^2=0.250$ ,  $P = 0.011$ ),  $B$  ( $r^2=0.030$ ,  $P = 0.978$ ). In contrast, for PD, none of the indices were significantly correlated with the environmental variables: SES1TS ( $r^2=0.184$ ,  $P = 0.082$ ), meanD ( $r^2=0.169$ ,  $P = 0.122$ ),  $B$  ( $r^2=0.159$ ,  $P = 0.153$ ), FEvep ( $r^2=0.011$ ,  $P = 0.373$ ). Species richness (log-transformed,  $r^2=0.218$ ,  $P = 0.030$ ), but not species evenness ( $r^2=0.179$ ,  $P = 0.093$ ), was correlated with the environmental gradient. Overall, in our case study, PD was thus a poor surrogate for FD. Species richness was a better surrogate. Log-transformed species richness was correlated with FD (correlations,  $df = 73$ , FEvep,  $r = 0.314$ ,  $P = 0.006$ ; meanD,  $r = 0.413$ ,  $P < 0.001$ ; SES1TS,  $r = 0.437$ ,  $P < 0.001$ ), but not with PD (FEvep,  $r = -0.006$ ,  $P = 0.958$ ; meanD,  $r = 0.222$ ,  $P = 0.056$ ; SES1TS,  $r = 0.100$ ,  $P = 0.392$ ). A complementary analysis demonstrated that FD diversity indices SES1TS, FEvep and meanD increased with increasing elevation and with decreasing salinity (Appendix S7).

### Discussion

Throughout this paper we searched for interpretable FD and PD indices that could help tease apart the factors influencing the correlations between FD, PD and environmental gradients. All indices confounded by species richness provided high FD:PD correlation even for traits that evolved independently of the phylogeny. Mathematical partitioning and the comparison to null models led to a set of indices independent of species richness and where the effects of species' abundances are controlled. We selected

four of these indices and applied them to the plant community structure on the Mekhada coastal marsh plain. Below we discuss the results of our case study; highlight the problems our analyses exposed in comparing FD and PD; discuss the ability of our partitioning and null models to avoid these problems; and conclude by considering the implications of our results for the usefulness of PD as a surrogate for FD.

### Salinity gradient in Mekhada marsh plain

In Mekhada, the main environmental gradient is a salinity gradient, with low elevation areas being on average more saline (Pavoine et al. 2011). We analysed whether environmental variables are similarly correlated with both FD and PD. Plant abundances were not influenced by functional traits or phylogeny. However, for indices based on species occurrences, FD significantly decreased with increasing salinity. This was found even though the functional traits available for this data set are expected to be less directly affected by the environmental gradient than unavailable physiological traits (Pavoine et al. 2011). We found moderate FD:PD correlations; and while relationships between PD and the primary stress gradient (salinity) in our study area were in the same direction as for FD, they were non-significant. Even species richness was a better surrogate for the connections between FD and the salinity gradient.

The correlation between FD and species richness is an ecological result rather than a mathematical artefact. Plots with low species richness in Mekhada are located in flooded, salty areas where only species with particular trait combinations can establish (low meanD and SESITS values, indicating reduced functional richness). In contrast, areas with higher species richness are located at higher elevations where silt and sand add to clay to provide greater heterogeneity of soil types and where more species with diverse traits can establish (high FE<sub>evp</sub> values, which may be associated with increased influence of niche complementarity). In the flooded, salty areas, all but the salt-tolerant and halophyte species are filtered out, which causes functional clustering in plant assemblages (where co-existing species have similar traits). In these locations, species were perennial, often with spiky structures and glabrous leaves, and they were mostly anemogamous. Indeed the most salty areas are likely to be unfavourable habitats for pollinators due to the high level of disturbance through regular flooding (Pavoine et al. 2011). More generally, on a stress gradient, functional diversity and species richness can be correlated if only a few species with similar traits can establish in the harshest areas (following the “physiological tolerance” hypothesis of Mason et al. 2008).

Patterns of PD were found to be less clear, which can be explained by the moderate, instead of strong, phylogenetic

signal. Further, phylogenetically distant species often co-occurred in the most stressful conditions, with salt-tolerant monocots (i.e. *Juncaceae* and *Cyperaceae*) and halophyte dicots (i.e. *Amaranthaceae*) both common in highly saline environments (Pavoine et al. 2011). The fact that PD is a poor surrogate of FD, when unbiased measures or null models are used, is not due to a lack of quality of the phylogenetic tree. It is due to a convergence in traits between dicots (*Amaranthaceae*) and monocots (*Juncaceae*, *Cyperaceae*). The separation between these two clades is acknowledged in all current phylogenies. The lack of association between PD and the salinity gradient is thus, at least partly, due to similarities in the traits of distant clades with different biogeographic origins. Both the salinity gradient and the phylogeny are associated with trait values but are independent of one another.

### Issues raised when comparing FD and PD

A simple error when comparing FD and PD would be to think that there is only a single way to measure diversity. In our simulations, we obtained very different FD:PD correlations according to the diversity index used. This was partly due to co-factors affecting diversity values and also partly due to the infinite possible ways of measuring diversity even with the same data and the same objective.

Over the last 30 years, a huge range of diversity indices has been developed (Schweiger et al. 2008; Pavoine & Bonsall 2011). When analysing their data, ecologists are thus often confronted with the difficult choice of which indices are best for their circumstances (data, objective etc.; Ricotta 2005). A typical reaction is to apply the most widely used index. However, different disciplines seem to be biased towards using different indices. One can thus be tempted to measure FD with the most widely used index in functional community ecology, and to measure PD with the most widely used index in phylogenetic community ecology. However, there should be good biological arguments for doing this, since results produced using two different indices to measure FD and PD are hardly interpretable (Appendix S3). The first basic rule when comparing FD and PD is thus to use the same index of diversity for the two aspects. We followed this rule throughout our study.

In this choice for an index of diversity, it should be kept in mind that interpreting diversity indices is difficult when different aspects influence diversity. Simple mathematical partitioning of diversity indices allowed us to separate the effects of species richness, species' abundances and functional or phylogenetic characteristics. Knowing these relative effects is important as, for instance, we showed that multiplying meanD by the species richness (MFAD) or the squared species richness (FAD) considerably increases FD:

PD correlations. A common error when measuring FD and PD is to assume that we are only measuring the functional and phylogenetic characteristics of the species. However, the relative influence of species richness and/or species' abundances on FD and PD in comparison with species' functional and phylogenetic characteristics depends on the index used. Choosing an index of FD and PD is thus adopting a very particular view of biodiversity.

### Removing co-factors to disentangle ecological mechanisms

The FD:PD correlations should reflect the degree to which phylogenetic relatedness corresponds with functional similarity. The fact that indices confounded by species richness give high FD:PD correlations even when the phylogenetic signal in trait data is weak is undesirable when the aim is to reveal assembly mechanisms. Consequently, we require methods to remove these co-factors when analysing the correlations between FD and PD and when analysing the correlations between either FD or PD and environmental factors (e.g. Moullot et al. 2011).

An often-reported strategy to remove the influence of co-factors consists of regressing FD (and/or PD) on the co-factors and working on functional (or phylogenetic) residuals. However, our results (especially for index TS) highlight that we need to know how FD and PD are linked via co-factors before deciding how to remove these co-factors. To analyse variation in TS relative to species richness, some studies have, for instance, used species richness and/or its quadratic term as an explanatory variable in a linear regression and have analysed the residuals of the regression. The equation that links TS with species richness showed that TS does not have a linear relationship with species richness or its quadratic term.

We found that at least one index is, by definition of its mathematical formula, unaffected by co-factors: meanD. We can be confident that any observed correlation between this index and a co-factor in field or experimental studies would be due to ecological mechanisms rather than to a mathematical artefact. In contrast, measures of diversity based on indices such as MFAD, FAD, HED, TS and QE confound several components of diversity. Mathematical partitioning is sufficient to decompose MFAD, FAD, HED and QE into simpler indices, necessary to decipher the mechanisms that lead to observed diversity patterns. However, for other indices such as TS, null models are required. In addition, any index using species' abundances might be affected by the shape of the distribution of abundance (skewed vs. even). Null models can also help to control for these sorts of issue.

The use of null models (SES approach), however, adds a critical methodological decision – which null model to

choose (Hardy 2008). To avoid unnecessary complications, the SES approach should thus be used exclusively when mathematical partitioning is not possible. For instance, mathematical partitioning revealed that the complementary index meanD could be extracted from both FAD and QE. It also showed that the SES1 approach is useless with FAD, MFAD and meanD, since it provides similar results to those observed using meanD.

We have seen that disentangling effects of species' characteristics, species' abundances and species richness, through partitioning or using null models, is essential when correlating FD and PD to avoid misleading and exaggerated correlations due to co-factors (species richness and evenness) that are independent of species' characteristics. Even if only FD or only PD is considered, this approach to disentangling multiple contributions to assessment of diversity might be also very informative. For example, Walker et al. (1999) analysed graminoid species in a lightly grazed site and in a heavily grazed site in an Australian rangeland. They found that within the lightly grazed grassland, dominant species were functionally more dissimilar to one another, and functionally similar species more separated in abundance rank, than expected on the basis of average ecological distances in the community (index meanD). They found that this functional redundancy between minor and dominant species led to increased resilience in biomass production, with minor species increasing in abundance when abundance of the dominant species was reduced by intense grazing. This study shows that removing the influence of covarying factors from measures of FD or PD can aid in revealing ecological processes. More generally, Table 2 in Pavoine & Bonsall (2011) demonstrated how comparing patterns in FD/PD and patterns in species richness or evenness can help to tease apart mechanisms of community assembly.

### The PD is a poor surrogate for FD

A critical ecological question when comparing FD with PD is whether similarities between phylogenetic distances and functional distances among species translate into similarities between the FD and PD of species assemblages. Using simulations, we found that FD:PD correlations are moderate or low, depending on the diversity index used, even with the Brownian model of trait evolution. The Brownian model assumes a correlation close to 1 between the squared Euclidean functional distances and time-scaled phylogenetic distances used here among species. A significant phylogenetic signal in functions is thus not sufficient for ensuring high FD:PD correlation. Recent simulation studies corroborate this and have shown that this can affect conclusions about ecological processes. Mason et al. (2013) found that FD indices gave high power to detect

changes in assembly processes along a hypothetical stress gradient, while PD indices gave only weak power for the same assembly model (Mason & Pavoine 2013). Kraft et al. (2007) found that the power of PD to detect community patterns is higher with environmental filtering, larger species pool sizes and higher number of traits considered, and lower with competition. When communities were structured by competition, the power to detect phylogenetic community structure was found to be high only if traits were more conserved than expected according to a Brownian model. Kraft et al. (2007) also found that this power depends on the index of PD used. The power of detection of phylogenetic community structure thus definitely depends on the evolution of traits, the diversity index used and the ecological processes underpinning community composition.

A phylogenetic signal in traits at the species pool level is not sufficient to ensure a FD:PD correlation, as illustrated by our case study and simulations. Concrete examples are also given elsewhere, e.g. in Pillar & Duarte (2010). They measure a phylogenetic signal at the species pool level and a phylogenetic signal at the metacommunity level. The phylogenetic signal at the species pool level corresponds simply to the degree of evolutionary conservatism of trait differentiation in the species pool. The phylogenetic signal at the metacommunity level consists in comparing the phylogenetic structure of a community with its trait-based structure. Contrary to the phylogenetic signal at the species pool level, the phylogenetic signal at the metacommunity level includes information on occurrence or abundance of species within a metacommunity. Applying their approach to grassland communities in Brazil, Pillar & Duarte (2010) found that, among seven traits examined individually, four of them had a significant phylogenetic signal at species pool level but only two had significant phylogenetic signal at the metacommunity level. Pillar & Duarte (2010) provided two models of how phylogeny affects trait values: model 1 =  $T \rightarrow P \rightarrow E$ , where the correlation between traits and environment is mediated by the phylogeny; and model 2 =  $P \rightarrow T \leftarrow E$ , where both the environment and the phylogeny are associated with trait values but independent of one another. The latter model necessarily involves moderate phylogenetic signal. Only under the former model, can we expect the relationship between PD and environment to act as a surrogate for the relationship between FD and environment.

### Conclusions and directions for future research

Comparing two aspects of biodiversity (i.e. functional and phylogenetic diversity), which share common components (species richness and species' abundances), raise new

questions that were not solved by previous analyses that focused on a single aspect of biodiversity.

Analysing the relative contributions and pair-wise correlations of species richness, species' abundances and characteristics allows identification of the mechanisms controlling species occurrences and abundances. This approach that details FD and PD patterns can be usefully applied at local scales to analyse community and ecosystem processes, and also at broader scales, to explore, for example, variation in FD and PD along altitudinal and latitudinal gradients (Tallents et al. 2005). Finally, simple calculation of correlation between FD and PD can be complemented by methods that analyse the detailed functional and phylogenetic compositions of assemblages in a more descriptive way (Pavoine et al. 2011). These analyses can identify which traits and which clades are responsible for the levels of FD and PD and further our understanding of how ecological communities are structured and function.

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## Supporting Information

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

**Appendix S1.** Calculation of functional distances among species.

**Appendix S2.** Complete description of the diversity indices.

**Appendix S3.** Using different indices for measuring FD and PD increases the risk of misinterpretation.

**Appendix S4.** List of R packages used.

**Appendix S5.** Mathematical details.

**Appendix S6.** Average Spearman correlation between FD and PD obtained with trait simulations.

**Appendix S7.** Correlations between environmental variables and diversity indices on the marsh plain Mekhada.