

A comparative test of phylogenetic diversity indices

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Abstract Traditional measures of biodiversity, such as species richness, usually treat species as being equal. As this is obviously not the case, measuring diversity in terms of features accumulated over evolutionary history provides additional value to theoretical and applied ecology. Several phylogenetic diversity indices exist, but their behaviour has not yet been tested in a comparative framework. We provide a test of ten commonly used phylogenetic diversity indices based on 40 simulated phylogenies of varying topology. We restrict our analysis to a topological fully resolved tree without information on branch lengths and species lists with presence–absence data. A total of 38,000 artificial communities varying in species richness covering 5–95% of the phylogenies were created by random resampling. The indices were evaluated based on their ability to meet a priori defined requirements. No index meets all requirements, but three indices turned out to be more suitable than others under particular conditions. Average taxonomic distinctness (AvTD) and intensive quadratic entropy (J) are calculated by averaging and are, therefore, unbiased by species richness while reflecting phylogeny per se well. However, averaging leads to the violation of set monotonicity, which requires that species extinction cannot increase the index. Total taxonomic distinctness (TTD) sums up

distinctiveness values for particular species across the community. It is therefore strongly linked to species richness and reflects phylogeny per se weakly but satisfies set monotonicity. We suggest that AvTD and J are best applied to studies that compare spatially or temporally rather independent communities that potentially vary strongly in their phylogenetic composition—i.e. where set monotonicity is a more negligible issue, but independence of species richness is desired. In contrast, we suggest that TTD be used in studies that compare rather interdependent communities where changes occur more gradually by species extinction or introduction. Calculating AvTD or TTD, depending on the research question, in addition to species richness is strongly recommended.

Keywords Phylogenetic tree · Pure diversity · Quadratic entropy · Taxic weights · Taxonomic distinctness

Introduction

Many ecological studies, especially large-scale ones, rely on species richness as a measure of biodiversity because time and money constraints often impede efforts to obtain more detailed information. However, the use of species richness as the sole reflection of biodiversity may be of limited value since it treats all species as being equal and does not take into account phylogenetic relationships (Vane-Wright et al. 1991). The differences in the evolutionary history of community members result in a diversity of morphological, physiological, and behavioural characters (Williams and Humphries 1996) and of their features (Faith 1992), where a feature means a particular state of a character. Many of the characters may represent functional traits (e.g. Woodward and Cramer 1996; Lavorel et al. 1997;

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Diaz and Cabido 2001), and the feature richness of a community may be closely related to its functional diversity (e.g. Tilman et al. 1997; Petchey and Gaston 2002; Petchey et al. 2004).

Sechrest et al. (2002) showed that biodiversity hotspots across the globe harbour even greater amounts of evolutionary history than would be expected based on species richness. Heard and Mooers (2000) demonstrated that phylogenetic relationships are one of the most important factors determining species extinction, and Strauss et al. (2006) showed that the degree of phylogenetic distance may determine the invasion success of exotic taxa. Hence, phylogenetic information may be a better indicator of conservation value than species richness alone.

The application of information obtained by phylogenetic relationships therefore represents a promising approach (Webb et al. 2002). Several authors have proposed a variety of indices other than species richness which also take into account phylogenetic diversity; however, these differ greatly in their method of calculation (Vane-Wright et al. 1991; Faith 1992; Solow et al. 1993; Faith 1994; Warwick and Clarke 1998; Izsak and Papp 2000; Clarke and Warwick 2001a; Rodrigues and Gaston 2002). These indices can be separated in two categories: topology based and distance based (Krajewski 1994). Vane-Wright et al. (1991) were the first to propose the application of topology-based methods, which reflect the phylogenetic branching order within a monophyletic group. In this approach, each species of a community is weighted by the inverse number of nodes between that species and the root of the phylogenetic tree, in a way that the most distinctive (close-to-root) species have the highest weights. Community distinctness (as a measure of phylogenetic diversity) is then obtained simply by summing the weights of the species. In this paper, we use the terms “distinctiveness” and “distinctness” sensu Warwick and Clarke (2001). Following their definition, “distinctiveness” describes the relation of a particular species to the rest of the community, whereas “distinctness” represents a property of the community as a whole.

Distance-based methods use either a minimum spanning path or a pairwise distance approach. The minimum spanning path measures the phylogenetic diversity of a community by summing up the branch lengths of the subtree that includes the community’s species (PD in Faith 1992). Branch lengths indicate the expected number of molecular “features” accumulated over evolutionary history. Common branches reflect shared molecular information inherited from common ancestors, while the branch length of a single species not shared by others reflects exclusive information.

While the minimum spanning path approach measures overall phylogenetic information of a community, the pairwise distance approach is based on a distance matrix between all species of a community. Distances can be

based on morphological or functional differences (Izsak and Papp 1995), on Linnean taxonomy (Warwick and Clarke 1995), on branch lengths of phylogenies based on molecular data (Solow et al. 1993; Pavoine et al. 2005) or, if branch lengths are not known, on the number of nodes separating each pair of species (Faith 1992). The values within the distance matrix can be interpreted as the distinctiveness between each pair of species or each particular species and all other species (Rao 1982; Izsak and Papp 2000; Ricotta and Avena 2003). Several summary statistics have been proposed to obtain an index for the whole community. Rao (1982), for example, proposed a diversity index termed quadratic entropy (QE) that is based on both relative species abundances and a measure of the pairwise distances between community species. When information about any kind of distance measure is lacking, QE reduces to the Simpson index. When abundance data are lacking (or they are equal), QE will be a function of the species number (also called intensive quadratic entropy, J , in Izsak and Papp 2000). A similar index, average taxonomic distinctness (AvTD), was developed by Warwick and Clarke (1995), which measures the mean distance between two randomly chosen species.

Krajewski (1994) investigated the behaviour of some phylogenetic diversity indices using the avian family Gruidae. Based on a comparison of the ability of these indices to rank species and contribute to phylogenetic diversity, he reported a serious disagreement between the indices, especially at intermediate levels of ranking, and concluded that “until some working consensus is reached [...], phylogenetic indices are unlikely to supersede more traditional measures of biodiversity”. Consequently, as long as the mathematical and ecological qualities of these indices are not sufficiently investigated in a comparative way, relying on species richness, for example, would be preferable since the selection of an index to account for phylogenetic relationships, and possibly the results and potential conservation recommendations, will be quite arbitrary.

While Krajewski (1994) investigated the ability of the indices to identify “phylogenetically unique” species, which was motivated by an individual species-focused conservation context, we focus on their ability to measure phylogenetic diversity at the community level. Community-wide phylogenetic diversity patterns can also be used for conservation concerns (e.g. the selection of priority areas; Posadas et al. 2001), but they are also highly suited for monitoring the effects of environmental change on overall community structure (e.g. Warwick and Clarke 1995; Knapp et al. 2008). By analogy with studies investigating the behaviour of evenness indices (Smith and Wilson 1996) or functional diversity indices (Mason et al. 2003), we provide a comparison of the following commonly used phylogenetic diversity indices.

Topology-based indices Two indices proposed by Vane-Wright et al. (1991) are used: the sum of basic taxic weights, Q , and the sum of standardised taxic weights, W (see Table 1 for calculations; for examples of applications, see Posadas et al. 2001 or Keith et al. 2005).

Distance-based indices using minimum spanning path based on Faith’s (1992) phylogenetic diversity Here we analyse three indices: the phylogenetic diversity, PD_{NODE} calculated as the sum of all nodes in the minimum sub-tree; the phylogenetic diversity using maximum spanning paths, PD_{ROOT} , following the argument of Rodrigues and Gaston (2002, pp. 104–105); the average phylogenetic diversity, AvPD (Clarke and Warwick 2001a, b; see Table 1 for calculations; for examples of applications see Parga et al. 1996; Williams and Humphries 1996 or Hacker et al. 1998).

Distance-based indices using pairwise distance We test five distance-based indices, calculated on distance matrices: the intensive quadratic entropy, J (Izsak and Papp 2000); the extensive quadratic entropy, F (Izsak and Papp 2000); the average taxonomic distinctness (Warwick and Clarke 1998); the total taxonomic distinctness, TTD (Clarke and Warwick 2001b); the pure diversity measure, D_{D} which is, in contrast to the other indices, based on the distance of a particular spe-

cies to its nearest neighbour (Weitzman 1992; also called p-median by Faith 1994; see Table 1 for calculations).

For comparison purposes, we calculated all indices on the basis of phylogenetic information obtained from a topological fully resolved (super-)tree with unit branch lengths. When branch length estimates are missing, they can be assigned unit length (Farris 1969; Gittleman and Kot 1990; Faith 1992), so that phylogenetic distance is then estimated by the number of nodes separating two taxa, thereby reflecting the topology of the tree. In spite of the vast development of phylogenetic trees based on molecular data, trees with unit branch length still represent the most common case, especially when studies are conducted at higher taxonomic levels and large spatial scales.

Warwick and Clarke’s AvTD and TTD were originally developed on the basis of taxonomic relationships, and they termed them accordingly. However, they can be easily adapted to phylogenetic information, and here we substitute taxonomic distance by phylogenetic distance. To avoid confusion by the introduction of new terms, we retain the original notations. There may be many different motivations for using phylogenetic diversity indices; consequently, there are accordingly different requirements for such an index. Based on experiences with other diversity indices and the mathematical construction of the tested

Table 1 Phylogenetic indices tested in this analysis

Index	Formula	Notes	Reference
Topology based			
Q	$Q = \sum Q_i, Q_i = III_i, I = \sum I_i$	Basic taxic weights. Sum of the contributions of each species to diversity	Vane-Wright et al. (1991)
W	$W = \sum W_i, W_i = Q_i/Q_{\text{min}}$	Standardised taxic weights	Vane-Wright et al. (1991)
Distance based—minimum spanning path			
PD_{NODE}	$PD_{\text{NODE}} = \sum n_i$	Phylogenetic diversity. Branch length substituted by number of nodes	Faith (1992)
PD_{ROOT}	$PD_{\text{ROOT}} = \sum n_{i \text{ ROOT}}$	Phylogenetic diversity including basal branches. Number of nodes within the rooted (maximum) spanning path	Rodrigues and Gaston (2002)
AvPD	$AvPD = PD_{\text{NODE}}/s$	Average phylogenetic diversity	Clarke and Warwick (2001a)
Distance based—pairwise distances			
J	$J = [\sum d_{i,j}]/s^2$	Intensive quadratic entropy. Mean distance between two randomly chosen species. Quadratic distance matrix	Izsak and Papp (2000)
F	$F = \sum d_{i,j}$	Extensive quadratic entropy. Sum of all pairwise distances	Izsak and Papp (2000)
AvTD	$AvTD = [\sum \sum_{i < j} d_{ij}]/[s(s-1)/2]$	Average taxonomic distinctness. Mean distance between two randomly chosen species. Triangular distance matrix	Warwick and Clarke (1998)
TTD	$TTD = \sum_i [(\sum_{j \neq i} d_{ij})/(s-1)]$	Total taxonomic distinctness. Average phylogenetic distinctiveness summed over all species	Clarke and Warwick (2001b)
D_{D}	$D_{\text{D}} = \sum d_{i \text{ min}}$	Pure diversity. Sum of nearest neighbour distances	Solow et al. (1993), Faith (1994)

AvTD Average taxonomic distinctness, TTD total taxonomic distinctness, PD phylogenetic diversity

I_i Number of nodes between species i and root of the tree, Q_{min} minimal basic taxic weight, n_i number of i nodes within the minimum spanning path, $n_{i \text{ ROOT}}$ number of i nodes within the rooted spanning path, $d_{i,j}$ distance matrix ($d_{i,j} = d_{j,i}; d_{i,i} = 0$), $d_{i \text{ min}}$ nearest neighbour distance of species i to all other species, s number of species

indices (Table 1), it is obvious that a “one-size-fits-all” index is unlikely to be obtainable and, therefore, appropriate, target-oriented indices have to be chosen. Here we provide guidelines for index selection by comparing the nature and behaviour of the selected indices according to the following requirements, which may well contradict each other:

- (1) To adequately reflect the breadth and topology of a communities’ phylogenetic tree, an index must increase with phylogenetic breadth and the relative frequencies of distantly related species.
- (2) To tease apart the effects of phylogeny and richness, an index must be totally independent of species richness (Clarke and Warwick 1998).
- (3) To allow the tracking of gradual changes in a community due to the fact that an addition (extinction) of a species increases (decreases) its diversity—regardless of the species’ distinctiveness—an index must reflect both species richness and phylogenetic relationships, but both in a balanced way. Therefore, such an index should satisfy set monotonicity, which requires that in the case of an extinction of a species from local communities the index cannot increase, while an addition of a species can not decrease the index. Consequently, the index of a subset has to be lower than the index of the whole phylogeny (set monotonicity sensu Solow et al. 1993 and Izsak and Papp 2000).
- (4) To provide information about potential deterministic assembly or extinction processes in the context of (3) an index must be able to unambiguously discriminate random extinction/assembly, extinction/assembly of closely related species, and extinction/assembly of distantly related species.
- (5) In general, an index should be independent of sampling effort (Clarke and Warwick 1998). For example, it would be an undesirable attribute if the index of a community consisting of only 10% of the species in the phylogeny reflects richness and phylogenetic diversity well, while it is solely a function of species richness when the community consists of 80% of the species.

Materials and methods

We tested whether the indices met the above-mentioned requirements using 40 artificial, simulated phylogenies, each consisting of 100 species. We let the topology of the trees vary from completely symmetric (bush-like) to random, to completely asymmetric (comb-like) in order to cover possible effects of different phylogenies (Fig. 1). From these phylogenies, we randomly sampled 5–95 species in steps of five. Random sampling was repeated 50

times for each richness class (5–95) and phylogeny, leading to a total of 38,000 artificial communities. The indices were calculated for all artificial communities, and their interrelationships were analysed using correspondence analysis (CA) based on scaled indices to 0 mean and unit variance (ter Braak 1986).

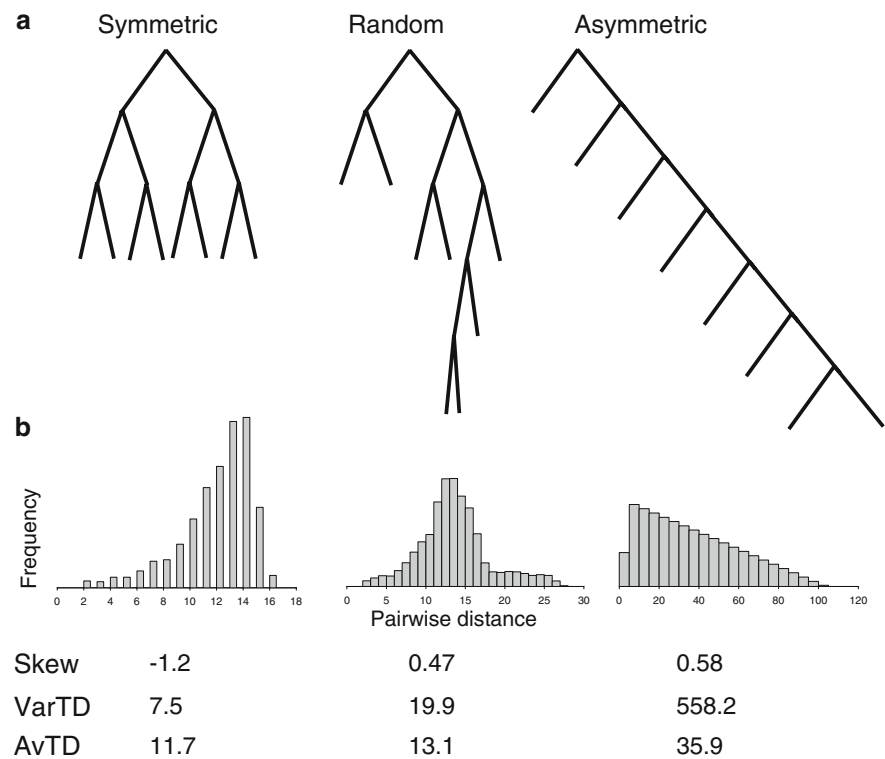
We compared the behaviour of the selected indices in relation to species richness and two measures that reflect phylogenetic breadth and topological structure of the tree (requirements 1 and 2). As a measure of phylogenetic breadth, we calculated the variance of pairwise distances given by the number of nodes separating each pair of species (variance within the distance matrix; VarTD sensu Clarke and Warwick 2001a), and the skewness of pairwise-distance distributions as a measure of subtree topology (hereafter simply referred to as “skewness”). Both measures are heuristic and do not uniquely identify a tree. However, together with species richness, they seem to capture fundamental aspects (Fig. 1) and serve as a basis for index comparisons.

We expect an index to increase with VarTD (Fig. 1). Given a constant mean, the variance can be used as a measure of the breadth of phylogenetic trees. Symmetric phylogenies, for example, exhibit low maximum distances and consequently low VarTD, while maximum distances and VarTD are high for asymmetric phylogenies, and intermediate for phylogenies with random topology (Fig. 1). In contrast, we expect an index to decrease with skewness (Fig. 1). Negatively skewed distance distributions occur when there are relatively more distant than closely related species, indicating high distinctness (e.g. symmetric trees), while positively skewed distributions occur in the opposite direction (for example, asymmetric trees; Fig. 1).

The relative impact of species richness, VarTD and skewness on the indices was investigated using hierarchical variance partitioning (Mac Nally 2000) for a data set obtained from a particular phylogeny, repeated over all 40 phylogenies.

We developed multiple linear mixed effects models using the calculated indices for all 38,000 artificial communities to investigate whether they meet our expectations regarding the response direction (positive or 0 to species richness, positive to VarTD and negative to skewness). A potential dependency of index behaviour on tree topology was accounted for by including the source phylogeny as a random variable in order to control for correlations in data arising from grouped observations. Thus, artificial communities were considered to be nested within source phylogenies. Species richness, VarTD and phylogenetic skewness were treated as fixed effects. Response and explanatory variables were standardised to 0 mean and unit variance to make the coefficient estimates comparable within and between the models (Quinn and Keough 2002). Initial mod-

Fig. 1 Schematic representation of phylogenies with symmetric, random and asymmetric topologies (a), and histograms of their frequency distributions of pairwise distances (b). The histograms represent artificial communities of 100 species. *Skew* Skewness, *VarTD* variance in taxonomic distinctness, *AvPD* average taxonomic distinctness



els were simplified by stepwise removing non-significant variables manually. Residual error distribution was approximately normal and showed no heteroscedasticity. Alternative models were compared by ANOVA.

Set monotonicity (requirement 3) was examined on 100 communities, each consisting of 50 randomly drawn species from a phylogeny with intermediate skewness and VarTD. Composition was manipulated community-wise by simulating species extinction in three ways: (1) random extinction, (2) extinction of the most distinctive species and (3) extinction of the least distinctive species. Distinctiveness was calculated as mean distance to all other species of the community. Response patterns were plotted as mean values per 100 communities against the number of extinct species. Standard error was obtained from the 100 repetitions.

We used this setup also to investigate the discriminative ability of indices to selective extinction events (requirement 4). While random extinction should result on average in an intermediate, linear response (under set monotonicity, we expect a decrease), the response of an index should be curvilinear when selective extinction applies. Extinction of the least distinctive species should result in continuously higher values compared to random extinction (under set monotonicity, we expect a convex shape), whereas extinction of the most distinctive species should cause the opposite—continuously lower values than those obtained by random extinction (under set monotonicity we expect a concave shape).

Index behaviour with respect to sampling effort (requirement 5) was investigated by creating five subsets for each particular source phylogeny. The subsets increased in species richness from 5–20%, 25–40%, 45–60%, 65–80% and 85–100% of source phylogeny richness by random species selection repeated 50 times per subset. Independent effects of species richness, VarTD and skewness relative to total explained variance were then calculated for each subset by hierarchical variance partitioning (Mac Nally 2000). The standard error was obtained by repetition over the 40 phylogenies.

All calculations were performed using the statistical software R 2.1.0 (R Development Core Team 2005) with the packages NLME (Pinheiro and Bates 2006), LME4 (Bates and Sarkar 2006), HIER.PART (Walsh and Mac Nally 2005) and VEGAN (Oksanen 2006).

Results

Influence of species richness, VarTD and skewness (requirements 1 and 2)

Correspondence analyses revealed that (1) AvPD was clearly distinct from the others, (2) AvTD and *J* were somewhat separated and (3) PD_{NODE} , PD_{BASE} and D_{D} ; TTD and *W*; *Q* and *F*, respectively, behaved similarly (Fig. 2). Since virtually no difference in the values of PD_{NODE} and PD_{BASE} was detectable across all artificial communities (Pearson corre-

lation coefficient $r > 0.999$), PD_{BASE} was excluded from further analysis. The similarity between the indices is reflected in their similar dependence on species richness, VarTD and skewness (Table 2). The indices AvTD and J were highly determined by phylogenetic relationships, whereas species richness was less important. While AvTD focused more on phylogeny (i.e. VarTD and skewness), the impact of richness, VarTD, and skewness was more evenly distributed in J . The comparably low total variance explained by both indices indicates that they also contain some considerable amount of additional phylogenetic information not accounted for by the three measures used. Although AvPD was more determined by richness, it also reflected VarTD and skewness. All other indices were predominantly determined by species richness, whereas grouping in the ordination diagram (Fig. 2) originated in different, but always high, levels of dependence on species richness.

In terms of effect direction, only AvTD and J behaved as expected (Table 3, Fig. 3a, b). They either showed an almost 0 (AvTD) or a positive (J) response to species richness, an increase with VarTD and a decrease with skewness

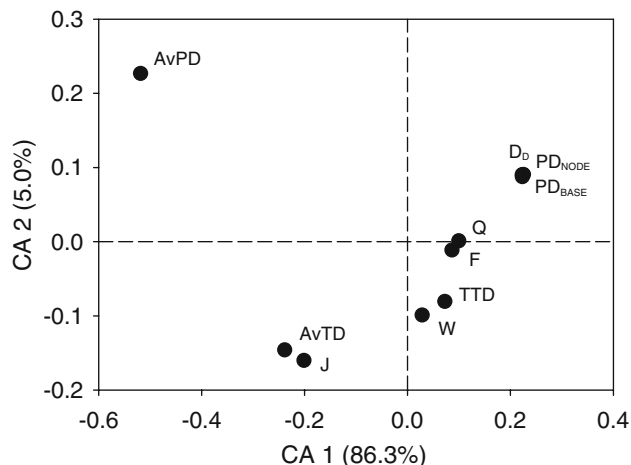


Fig. 2 Ordination diagram of phylogenetic diversity indices obtained from a correspondence analysis (CA). Explained variance of the first and second axis is given in *parenthesis*. For abbreviations, see Table 1

Table 2 Relative independent effects of species richness, VarTD and phylogenetic skewness (\pm standard error) obtained from hierarchical variance partitioning, and their total explained variance (R^2)

Index	Richness	VarTD	Skewness	R^2
AvTD	13.1 (± 0.37)	52.8 (± 0.62)	34.1 (± 0.56)	0.62 (± 0.0071)
J	29.1 (± 0.47)	48.6 (± 0.59)	22.3 (± 0.42)	0.75 (± 0.0042)
AvPD	66.6 (± 0.36)	15.6 (± 0.27)	17.8 (± 0.32)	0.84 (± 0.0024)
PD_{NODE}	81.4 (± 0.21)	8.5 (± 0.16)	10.0 (± 0.18)	0.98 (± 0.0002)
D_d	82.5 (± 0.21)	7.8 (± 0.16)	9.7 (± 0.18)	0.96 (± 0.0006)
W	86.4 (± 0.17)	6.0 (± 0.12)	7.6 (± 0.15)	0.99 (± 0.0005)
TTD	87.2 (± 0.16)	6.0 (± 0.12)	6.8 (± 0.14)	0.99 (± 0.0000)
Q	90.9 (± 0.12)	4.0 (± 0.09)	5.1 (± 0.10)	0.95 (± 0.0003)
F	90.9 (± 0.12)	4.0 (± 0.09)	5.1 (± 0.10)	0.95 (± 0.0002)

(Table 2). However, AvPD exhibited an undesirable behaviour: it increased with VarTD and decreased with skewness as expected, but decreased with species richness (Table 3; Fig. 3c; see also Clarke and Warwick 2001a). All other indices failed the expectations since they increased with species richness, VarTD and skewness (Table 3). Moreover, the effect size of VarTD and skewness was very small (Table 2). Skewness was not even significant for Q and F (Table 3). It would appear that indices that are highly dependent on species richness are not able to reflect VarTD and skewness properly; instead they simply assign the highest values for communities having similar VarTD, and skewness as the source phylogeny and lowest values otherwise (such as e.g. PD_{NODE} ; Fig. 3d).

Set monotonicity and discriminative ability (requirements 3 and 4)

Some indices did not satisfy the criterion of set monotonicity (*sensu* Solow et al. 1993 and Izsak and Papp 2000). In fact, AvTD, J and AvPD, increased when the least distinctive species were deleted. However, they showed little non-monotonic response (increase or decrease) to random extinction, always decreasing when the most distinctive species became extinct (Fig. 4a–c). In contrast, D_d showed a general tendency to decrease with species extinction. However, its response to the three potential ways of extinction was nevertheless also non-monotonic (Fig. 4e). The other indices satisfied set monotonicity (Fig. 4d, f–i).

Discriminative abilities differed highly between the indices. Interestingly, the indices that did not satisfy set monotonicity performed best, especially AvTD (Fig. 4a–c). The only index of those satisfying set monotonicity that matched all expected response patterns was TTD: its response was convex shaped when the least distinctive species were deleted, it showed the opposite pattern when the most distinctive species were deleted and it decreased linearly when extinction was random (Fig. 4g). All other indices were not able to discriminate all ways of extinction as expected (Fig. 4d–f, h–i).

Table 3 Standardised partial regression slopes for the relation between phylogenetic diversity indices and species richness, VarTD and phylogenetic skewness (\pm standard error) obtained from linear mixed effects models

Index	Richness	VarTD	Skewness
AvTD	-0.008 (\pm 0.0006)	0.671 (\pm 0.003)	-0.077 (\pm 0.0021)
<i>J</i>	0.059 (\pm 0.0006)	0.677 (\pm 0.003)	-0.014 (\pm 0.0022)
AvPD	-0.703 (\pm 0.0033)	0.208 (\pm 0.015)	-0.386 (\pm 0.0121)
PD _{NODE}	0.962 (\pm 0.0011)	0.196 (\pm 0.005)	0.074 (\pm 0.0039)
<i>D_D</i>	0.957 (\pm 0.0012)	0.109 (\pm 0.005)	0.150 (\pm 0.0043)
<i>W</i>	0.597 (\pm 0.0020)	0.310 (\pm 0.009)	0.299 (\pm 0.0072)
TTD	0.719 (\pm 0.0017)	0.291 (\pm 0.007)	0.086 (\pm 0.0061)
<i>Q</i>	0.827 (\pm 0.0020)	0.134 (\pm 0.009)	n.s
<i>F</i>	0.798 (\pm 0.0021)	0.124 (\pm 0.010)	n.s

All *P* < 0.001

Impact of sampling effort (requirement 5)

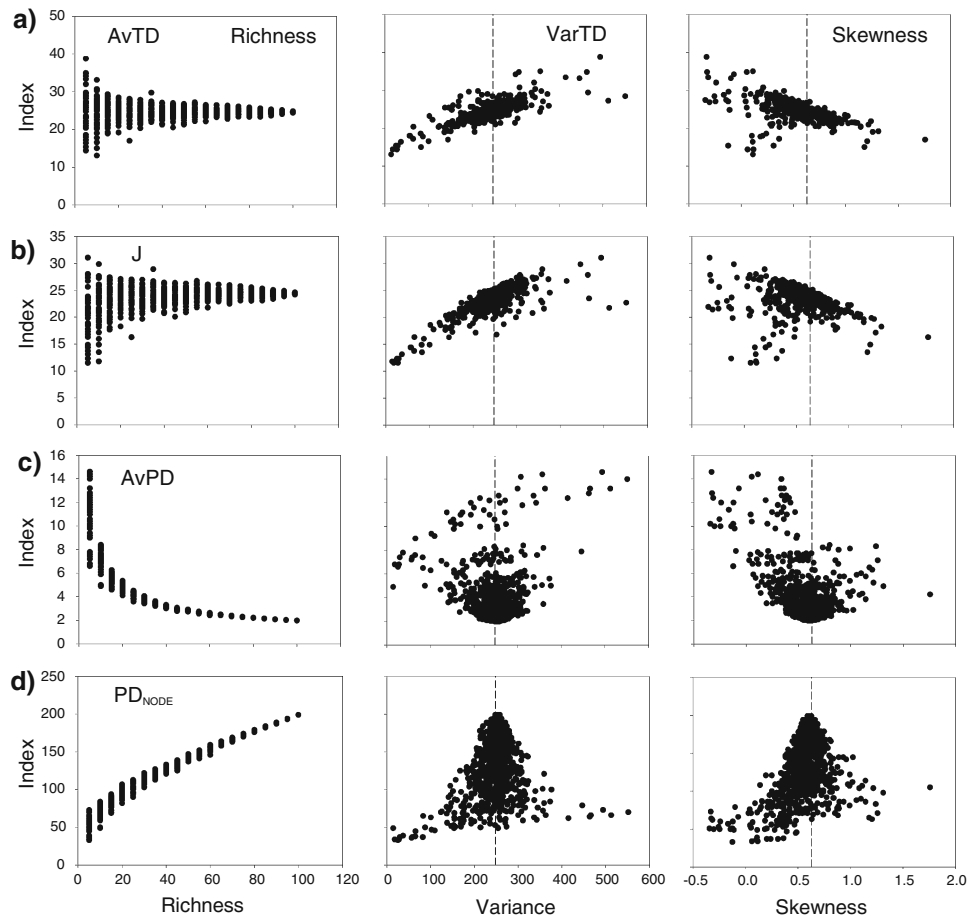
The proportion of species richness of a community relative to the total phylogeny had little effect on the behaviour of the indices. However, the indices reacted differently. For

AvTD and *J*, the independent effects of VarTD and skewness increased slightly with increasing proportional species richness, while they decreased (AvPD and PD_{NODE}) or showed an inverse hump-shaped relationship for all other indices (Fig. 5; for the ease of reading independent effects of VarTD and skewness are summed). The inverse hump-shaped relationship for *D_D*, *W*, TTD, *Q* and *F* indicated the highest dependencies on species richness at intermediate ranges of sampling effort. Dependence on sampling effort was most pronounced in *J*, AvPD and PD_{NODE}.

Discussion

There is general agreement that indices using branch lengths are preferable over measures relying solely on topology (Crozier 1997). However, in the majority of cases, proper branch lengths are not available, especially when studies are conducted at higher taxonomic levels and large spatial scales, but (super-)tree topologies mostly are. Under these circumstances, substituting branch lengths by the number of nodes (i.e. setting branch lengths to unity) can be a fruitful alternative. Incorporating even suboptimal phylo-

Fig. 3 Relation between phylogenetic diversity indices and species richness, VarTD and phylogenetic skewness. Artificial communities were resampled from an exemplary phylogeny with a variance of 248 and a skewness of 0.63 (indicated by dashed lines). PD_{NODE} serves as an example for all indices that are highly dependent on species richness (see Table 2); see Methods for further details. For abbreviations, see Table 1



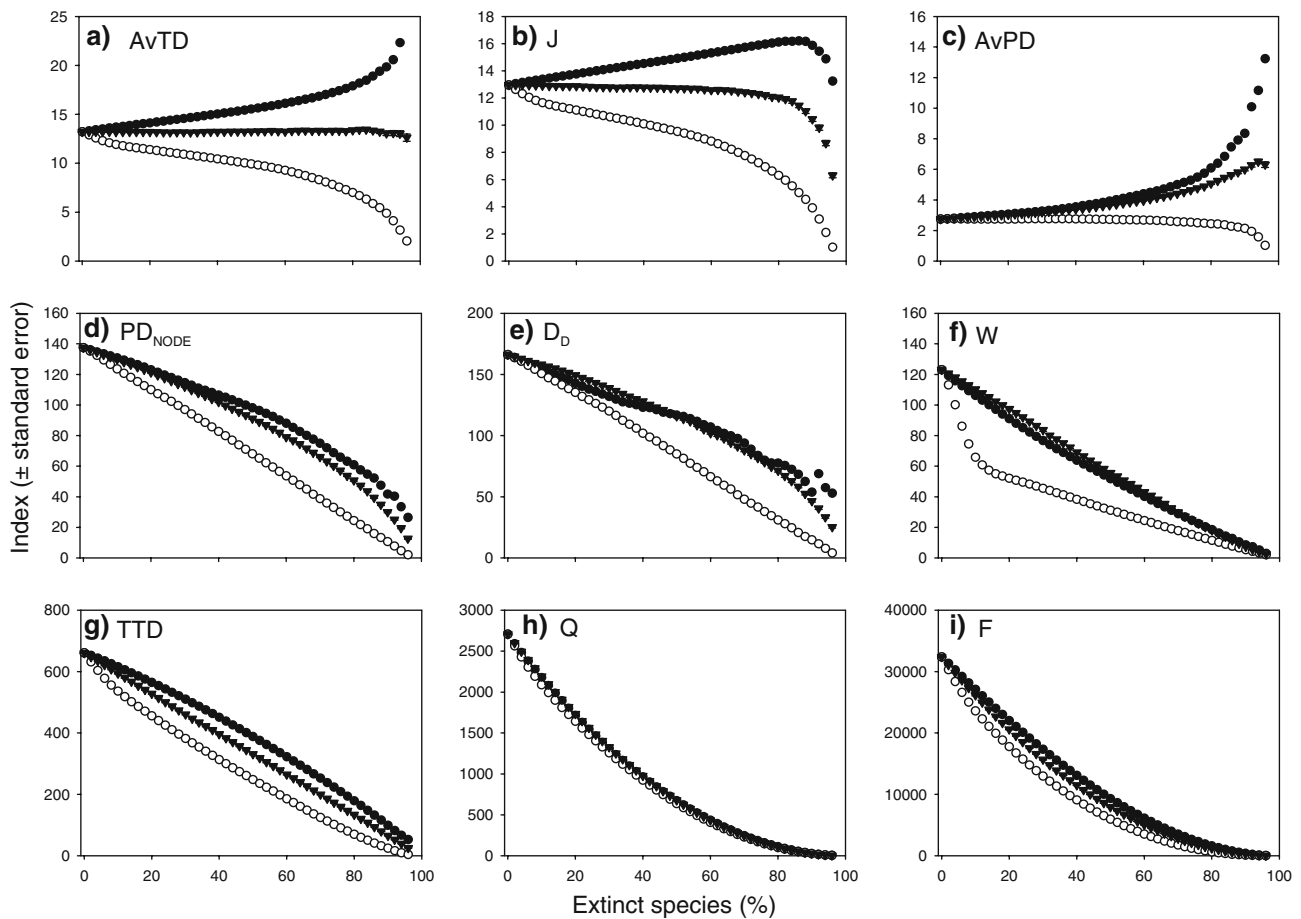


Fig. 4 Index behaviour on set monotonicity under three hypothetical ways of extinction within a particular community: extinction of least distinctive species (*shaded circles*), extinction of most distinctive spe-

cies (*empty circles*) and random extinction (*triangles*). Standard error was obtained by random resampling 100 times. For abbreviations, see Table 1

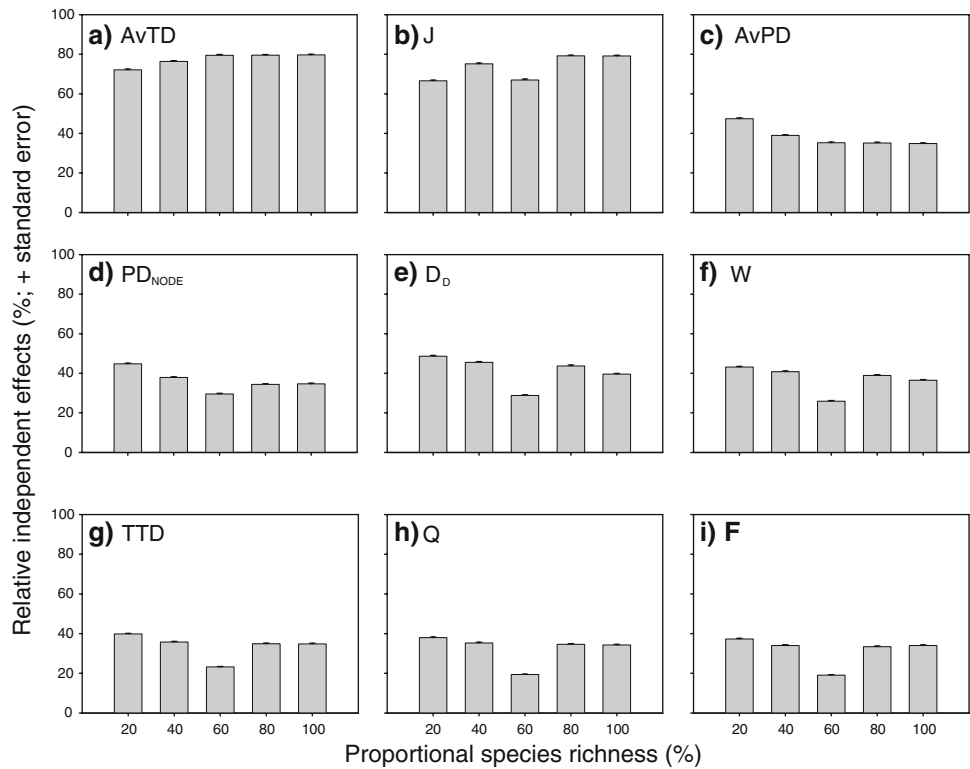
genetic information (also including polytomies) obviously provides a better insight into ecological and evolutionary processes and potential mechanisms of species assembly than relying simply on species richness. We restricted our analysis to cases where branch lengths are substituted by node counts. When available branch lengths would be incorporated into the calculation of phylogenetic diversity indices where possible, this would of course lead to greater precision. However, we believe that the general results and conclusions of our study will remain valid since the imminent mathematical properties and thus the behaviour of the indices will persist.

As expected there was no index that matches all predefined requirements. However, some are more suited than others depending on the focus of the study. A clear discrimination in index behaviour is apparent for two groups of indices resulting from different ways of calculation: (1) “averaged indices”; and (2) “total indices”.

The “averaged indices” AvTD, J and AvPD are calculated by weighting phylogenetic distance by number of species. They provide a measure of mean distance between two

randomly chosen species (AvTD, J), or the mean contribution of a randomly chosen species to overall diversity (AvPD). AvTD is exactly, and J relatively unbiased by species richness, and both reflect phylogenetic conditions well (see also Clarke and Warwick 1998). The low total explained variance by the three measures used (species richness, VarTD and skewness) indicates that they even include additional phylogenetic information that was not covered by the three measures. Differences in the independent effects of species richness between both indices allow the impact of species richness to be regarded differently. When no impact of species richness is desired, AvTD should be used; when more weight on species richness is wanted, J is the index of choice. Both indices are calculated in a similar way, but by including zeroes in the diagonal of the distance matrix and thus adding species counts but not distance values to the index, J becomes rather determined by species richness compared to AvTD. Both indices behave as desired since they increase with VarTD and decrease with its skewness. This does not contradict findings that in real data sets the relationship between AvTD

Fig. 5 Relative independent effects of variance in taxonomic distinctness (VarTD) + phylogenetic skewness for different proportions of community species richness relative to species richness in the phylogeny. Values are obtained from hierarchical variance partitioning. Remaining variance (difference to 100%) is explained by species richness. **a–i** Analysed indices. For abbreviations, see Table 1



and VarTD can also be negative or even zero (Clark and Warwick 2001a). The observed behaviour is based on random species aggregation from phylogenies with any potential possible topology and thus reflects the principle ability of this index to capture phylogenetic breadth. Any deviation from that in real nature should be no surprise because of obviously acting selective environmental filters. Additionally, the independency and low dependency on species richness, respectively, together with rather weak effects of sampling effort confirm both indices to be highly suited to compare species lists of different studies with different sampling intensities (see also Warwick and Clarke 1998).

The third tested “averaged index”, AvPD, is not recommended since index behaviour is not consistent across species richness and phylogenetic structure (negative effect of richness, while the effect of VarTD was positive).

Although the averaging procedure makes AvTD exactly, and J quite unbiased by species richness (for detailed discussion see Clarke and Warwick 1998), it also causes a violation of set monotonicity, which is not the case for “total indices”. “Total indices” are calculated by summing up values for particular species, such as individual species weights for Q and W , number of nodes for PD_{NODE} and PD_{ROOT} , pairwise distances of one species to all others for F , average distances of one species to all others for TTD or nearest neighbour distances for D_D . This calculation approach makes “total indices” heavily biased by species richness, which has already been demonstrated for PD with

simulated and observational data (Clarke and Warwick 2001a, b; Torres and Diniz-Filho 2004; Diniz-Filho 2004; Soutullo et al. 2005), even though index calculation was based on branch lengths. Therefore, “total indices” reflect phylogenetic conditions weakly; in contrast, the method of calculation causes them to satisfy set monotonicity. However, set monotonicity and independency from species richness obviously contradict each other. No index can, due to inherent mathematical properties, meet both conditions. Consequently, there is no universally applicable phylogenetic diversity index but, rather, different indices are suggested under different conditions.

When temporally or spatially rather independent communities are to be compared, “averaged indices” seem to qualify. Highly independent communities can potentially vary strongly in their phylogenetic composition, or even differ totally. Under such circumstances, set monotonicity should be a minor issue because the expectation is not of gradual changes but rather pronounced ones. Therefore, the index should be able to capture phylogenetic conditions per se, unbiased by species richness, and it should be able to assign higher values to few but very distinct species compared to many but closely related species. The index should also have the potential to discriminate communities with the same number of species but differing in composition and relatedness otherwise. This would hardly be the case when highly species-richness biased “total indices” are used but can be provided by “averaged indices”.

Set monotonicity might be a minor issue in the case of independent communities, but its violation nevertheless exists for “averaged indices”. Therefore, we suggest always providing phylogenetic diversity together with species richness data. In doing so, the effects of explanatory variables on species richness and phylogenetic diversity can be disentangled, and potentially mechanistic insights will be gained (e.g. Rogers et al. 1999; von Euler and Svensson 2001; Poulin and Mouillot 2004; Ellingsen et al. 2005; Heino et al. 2005; La Sorte and Boecklen 2005).

In contrast to “averaged indices”, “total indices” may be applied to studies that monitor the same communities or compare spatially rather interdependent ones, although they do not resolve problems arising from temporal or spatial autocorrelation. When the communities are interdependent over time or space, their composition may be very similar. In such cases, variation in phylogenetic composition between the communities is still important, but it is not the major issue. Moreover, the index should be capable of detecting more gradual changes in community composition due to species extinction or introduction—i.e., it should satisfy set monotonicity. A bias by species richness should be outweighed by the satisfaction of set monotonicity. Additionally, an index should be sensitive to different ways of community change and its potential causes. In this sense, TTD performs best. As in the other “total indices”, extinction of species results in a strictly monotone decrease of the index. However, in contrast to PD_{NODE} , PD_{ROOT} , D_D , W , Q and F , only TTD is a “total index” that clearly discriminates random extinction, the extinction of the most distinctive species and the extinction of the least distinctive species, and where the shapes of these relationships meet the expectations.

Clarke and Warwick (1998) showed that a randomised resampling procedure can be used to test departures in AvTD of observed communities from expected values based on a master list or inventory of a species pool. Observed values higher than random indicate higher community distinctness than that expected by general phylogenetic relationships in the species pool (for detailed calculations see Clarke and Warwick 1998), while observed values lower than random indicate a lower community distinctness than expected. Our study shows that this approach is also applicable to J and the “total index” TTD. Thus, TTD, AvTD and J can provide valuable information on the potential deterministic community assembly processes. Simulations of selective extinctions show that observed values above the confidence limits for a model of random extinction may indicate extinction of the least distinctive species, while observed values below random extinction may indicate extinction of the most distinctive species. This approach may contribute to the understanding of recently reported positive, negative or non-significant

relationships between AvTD and species richness (Bates et al. 2005; Heino et al. 2005; La Sorte and Boecklen 2005).

Conclusions

Average taxonomic distinctness and, to a lesser extent, J are the methods of choice for comparing communities which are more or less independent—i.e. where set monotonicity is a more negligible issue but independence from species richness is desired. In time series (monitoring) or spatially autocorrelated analyses, however, TTD is the index of choice, since it exhibits set monotonicity and is able to discriminate in the desired way between random extinction, extinction of the least distinctive species and extinction of the most distinctive species. Consequently, calculating AvTD or TTD, depending on the research question, in addition to species richness is strongly recommended to gain more detailed insights.

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