A guide to phylogenetic metrics for conservation, community ecology and macroecology

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ABSTRACT

The use of phylogenies in ecology is increasingly common and has broadened our understanding of biological diversity. Ecological sub-disciplines, particularly conservation, community ecology and macroecology, all recognize the value of evolutionary relationships but the resulting development of phylogenetic approaches has led to a proliferation of phylogenetic diversity metrics. The use of many metrics across the sub-disciplines hampers potential meta-analyses, syntheses, and generalizations of existing results. Further, there is no guide for selecting the appropriate metric for a given question, and different metrics are frequently used to address similar questions. To improve the choice, application, and interpretation of phylo-diversity metrics, we organize existing metrics by expanding on a unifying framework for phylogenetic information.

Generally, questions about phylogenetic relationships within or between assemblages tend to ask three types of question: how much; how different; or how regular? We show that these questions reflect three dimensions of a phylogenetic tree: richness, divergence, and regularity. We classify 70 existing phylo-diversity metrics based on their mathematical form within these three dimensions and identify ‘anchor’ representatives: for α-diversity metrics these are PD (Faith’s phylogenetic diversity), MPD (mean pairwise distance), and VPD (variation of pairwise distances). By analysing mathematical formulae and using simulations, we use this framework to identify metrics that mix dimensions, and we provide a guide to choosing and using the most appropriate metrics. We show that metric choice requires connecting the research question with the correct dimension of the framework and that there are logical approaches to selecting and interpreting metrics. The guide outlined herein will help researchers navigate the current jungle of indices.

Key words: biodiversity hotspots, biogeography, community assembly, conservation, diversity metrics, evolutionary history, phylogenetic diversity, prioritization, range size.

CONTENTS

I. INTRODUCTION

Phylogenetic information is a critical component of modern ecology, particularly for the sub-disciplines of macroecology, community ecology, and conservation biology (Beck *et al.*, 2012; Cadotte *et al.*, 2010; Crozier, 1992; Davies & Cadotte, 2011; Faith, 1992; Mouquet *et al.*, 2012; Purvis *et al.*, 2000; Vane-Wright, Humphries & Williams, 1991; Webb, 2000; Webb *et al.*, 2002; Winter *et al.*, 2009). The growing use of phylogenies recognizes that the branching pattern on a phylogenetic tree reflects the accumulation of phenotypic, genetic, behavioural, and/or phenological differences between evolutionary lineages (Harvey & Pagel, 1991). These accumulated differences may in turn describe, explain, or predict biological and ecological processes. The potential usefulness of phylogenies to answer ecological questions, coupled with the exponentially growing availability of phylogenies for many taxonomic groups, has given rise to a proliferation of different phylogenetic metrics. Currently, there is an increasing “jungle of [phylogenetic] indices” (Winter, Devictor & Schweiger, 2013, p. 201) of at least 70 available metrics used to describe phylogenetic diversity (here ‘phylo-diversity’, see online supporting information, Appendix S1). This jungle reflects not only the increasing number of phylo-diversity metrics found in the literature, but also the confusion regarding how the different metrics relate to each other in both mathematical and ecological terms. Metric choice is often driven by historical precedence, individual experience, and sub-discipline tradition, rather than objective criteria. Phylo-diversity metrics first appeared in conservation biology in response to the perception that, in the face of widespread extinctions, minimizing loss of evolutionary diversity should be a priority (Vane-Wright *et al.*, 1991). Maximizing the evolutionary diversity of a group of species should maximize their feature (i.e. phenotypic, behavioural and/or ecological) diversity, and so phylogenetic measures should be more effective than species-based measures at preserving such diversity (Faith, 1992). Community ecology and macroecology more recently incorporated phylogenies into analyses, using evolutionary relationships to understand observed ecological and macroevolutionary patterns and processes, such as community assembly or biodiversity gradients. Community ecology tends to use phylogenetic relatedness between taxa or communities to infer local ecological processes (Webb *et al.*, 2002) or to predict ecosystem properties (Mouquet *et al.*, 2012), while macroecology uses phylogenetic information to help disentangle explanations for large-scale patterns of diversity (Fritz & Rahbek, 2012; Jetz *et al.*, 2012; Wiens & Donoghue, 2004; Winter *et al.*, 2009). Despite these different foci, there is considerable overlap in sub-discipline approaches and interests. Indeed, some metrics are commonly considered across all ecological sub-disciplines, such as Faith's PD (Faith, 1992), while others are restricted to particular sub-disciplines, e.g. evolutionary distinctiveness (ED) (Isaac, 2007; Redding, 2003) for conservation; MPD and mean nearest taxon distance (MNTD) for community ecology (Clarke & Warwick, 1998; but see Davies & Buckley, 2011; Webb *et al.*, 2002).

Choosing the most appropriate phylogenetic measure for a particular ecological question is complicated by the vast collection of phylo-diversity metrics available. Recent overviews (Chiu, Jost & Chao, 2014; Mouquet *et al.*, 2012; Vellend *et al.*, 2010; Winter *et al.*, 2013) have called for a unifying framework for phylo-diversity metrics, in order to clarify the conceptual relationships between existing metrics, to highlight their redundancies or complementarity, and ultimately to encourage the correct usage and interpretation of metrics (Chao, Chiu & Jost, 2010; Chao, Chiu & Jost, 2014; Chiu *et al.*, 2014; Faith, 2008; Pavoine & Bonsall, 2011; Pavoine, Love & Bonsall, 2009; Pearse *et al.*, 2014; Rosauer & Mooers, 2013; Schweiger *et al.*, 2008; Swenson, 2011; Tucker & Cadotte, 2013). A recent framework developed by Pavoine & Bonsall (2011) based on preliminary work by Mouillot *et al.* (2005) and Ricotta (2007), provides a broad clarification of the mathematical underpinnings of phylo-diversity metrics, allowing them to be grouped under three mathematical dimensions (richness, divergence, regularity). Although the Pavoine–Bonsall framework represents an important step forward in clarifying the conceptual relationships underlying metrics, it lacks (1) comprehensive classification of metrics, since it included only a small subset of published phylo-diversity metrics, and (2) guidance for the correct choice of metrics and connection of research questions with the appropriate dimension. The purpose of this review is to provide a comprehensive and practical guide to understanding and correctly applying phylo-diversity metrics to ecological questions. This should help in selecting from among the at least 70 metrics currently available, while emphasizing the value of distinguishing between and utilizing the three different dimensions of phylo-diversity metrics. We establish the connection between the types of ecological questions or hypotheses researchers test and the corresponding dimension identified by the Pavoine–Bonsall framework. Our goals are to incorporate existing phylo-diversity metrics into the framework and verify their fit, analyse redundancy and distinguish among metrics within dimensions, and provide examples to guide their use.

II. A UNIFYING FRAMEWORK FOR PHYLO-DIVERSITY METRICS

(1) Describing the framework

Despite the vast array of phylo-diversity metrics, a simple set of mathematical underpinnings provides a natural scheme to group the metrics into three conceptual dimensions (Pavoine *et al.*, 2009): richness, divergence, and regularity. These dimensions capture the mathematical operation inherent to a metric, which includes: (*a*) the sum of accumulated phylogenetic differences among taxa (‘richness’); (*b*) the mean phylogenetic relatedness among taxa (‘divergence’), representing the average phylogenetic difference between taxa in an assemblage; or (*c*) the variance in differences among taxa, representing how regular the phylogenetic differences between taxa in an assemblage are (‘regularity’) (Fig. 1). We use regularity rather than the similar term ‘evenness’, because the latter has been used previously to describe how abundances are combined with measures of evolutionary distances (Pavoine & Bonsall, 2011; Pearse *et al.*, 2014).

A second axis of information in this framework reflects whether the metric uses information about a single set of tips of a phylogenetic tree within an assemblage (i.e. questions about a single community or regional species pool, hereafter referred to as α-diversity), or about several sets of tips (i.e. comparisons of assemblages over space or time, hereafter referred to as β-diversity). For the purposes of this paper, ‘assemblage’ simply denotes a group of taxa of interest: such taxa may, but need not, co-occur in space or time. Examples include taxa in a local community, regional species pool, or those selected in a particular conservation strategy. And similarly, although we may refer to species for simplicity, note that the metrics discussed are often applied to diversity below species level, or where species have not been described.

This framework (1) provides an intuitive approach based on the mathematical formulations of the metrics, (2) assesses both within- and between-assemblage diversity components, (3) is analogous to the functional diversity framework, thus aiding comparisons between phylo- and functional diversity (Villéger, Mason & Mouillot, 2008) and (4) is applicable to both abundance and presence/absence formulations.

Within each dimension, different phylogenetic metrics can be constructed using various types of phylogenetic components (referred to as ‘units’): these include branch lengths, pairwise phylogenetic distances between taxa, measures of phylogenetic or evolutionary isolation (e.g. species distinctiveness, fair proportion; Isaac, 2007; Redding, 2003), or other measures of tree topology. Thus within each dimension, we differentiate between metrics based on the phylogenetic unit used for their construction. We refer to groups of metrics in a particular dimension that are constructed using the same units as ‘families’. For example, richness metrics composed using branch lengths [e.g. PD, phylogenetic endemism (PE)] would be considered a family based on their shared dimension and unit of construction.

(2) Classifying phylo-diversity metrics using the dimensions framework

Here we use the dimensions framework introduced in Section II.1 to classify phylo-diversity metrics used to answer phylogeny-focused ecological questions. We searched the ecological literature and identified many common metrics not classified within the Pavoine–Bonsall framework, for a total of 70 metrics (we counted separately abundance and presence/absence versions of metrics, and identical metrics published with different names. Each set of parametric indices was counted a single unit). These metrics are diverse, but share many common properties (Pavoine & Bonsall, 2011; Pearse *et al.*, 2014; Vellend *et al.*, 2010). These metrics are included in Table 1, classified based on the mathematical dimension (richness, divergence, or regularity) and the diversity level (α-diversity or β-diversity). Formulae for all metrics and additional details can be found in Appendix S1 (metrics from Allen, Kon & Bar-Yam, 2009; Barker, 2002; Bryant *et al.*, 2008; Cadotte *et al.*, 2010; Chen *et al.*, 2012; Chiu *et al.*, 2014; Clarke & Warwick, 1998, 2001; Colless, 1982; Dehling *et al.*, 2014; Faith, 1992; Hardy & Jost, 2008; Hardy & Senterre, 2007; Helmus *et al.*, 2007; Isaac, 2007; Ives & Helmus, 2010; Izsák & Papp, 2000; Izsák & Szeidl, 2002; Jost, 2006; Jost, 2007; Kembel *et al.*, 2010; Leinster & Cobbold, 2012; Lozupone *et al.*, 2007; Lozupone & Knight, 2005; Miller, Zanne & Ricklefs, 2013; Mouchet & Mouillot, 2011; Nipperess, Faith & Barton, 2010; Pavoine *et al.*, 2009; Pavoine, Ollier & Pontier, 2005; Pavoine & Ricotta, 2014; Pybus & Harvey, 2000; Rao, 1982; Redding, 2003; Rosauer *et al.*, 2009; Safi *et al.*, 2013; Scheiner, 2012; Swenson, 2011; Vellend *et al.*, 2010; Villéger *et al.*, 2008; Webb, Ackerly & Kembel, 2008; Webb *et al.*, 2002; Weiher & Keddy, 1995). Table 1 also identifies the absence of published phylo-diversity metrics in some categories; for example, β-diversity in particular lacks metrics in a number of possible categories. However, particularly for α-diversity metrics, most categories in Table 1 include multiple phylo-diversity metrics. Further, while it is likely that additional metrics will be found in the literature that are missed here (or will be developed in the future), we believe that they can be easily placed within this framework.

(*a*) *Richness*

Richness metrics sum up the quantity of phylogenetic differences present in an assemblage, and we can further distinguish metrics according the type of basic units they sum across. Metrics may sum branch lengths (e.g. Faith's PD; Faith, 1992; PE, Rosauer *et al.*, 2009; 1.1a in Table 1); pairwise phylogenetic distances [e.g. phylogenetic species richness (PSR); Helmus *et al.*, 2007; 1.2a in Table 1]; or they may sum the phylogenetic isolation of the taxa in an assemblage (ED, Safi *et al.*, 2013). Richness metrics that compare diversity between sets (β-diversity) may calculate the proportion of shared branch length between two communities (e.g. Unifrac, Lozupone & Knight, 2005; 1.1b in Table 1) or a proportional measure of pairwise phylogenetic similarities among species (Pavoine & Ricotta, 2014; 1.2b in Table 1). These metrics capture the difference in phylogenetic composition between assemblages.

(*b*) *Divergence*

The divergence dimension contains metrics that average the distribution of units extracted from a phylogenetic tree. Divergence metrics that describe a single assemblage may be calculated using branch lengths (2.1a in Table 1), pairwise distances (2.2.1a and 2.2.2a in Table 1), or phylogenetic isolation (2.3a in Table 1). Distances may be measured using all pairwise distances for a group of taxa (e.g. MPD, Webb *et al.*, 2002; 2.2.1a in Table 1) or only a subset of the possible pairwise distances (2.2.2a in Table 1), in which case generally the shortest distances between taxa are considered (e.g. MNTD, Webb *et al.*, 2002). For metrics that compare divergence between assemblages (β-diversity), distances may be measured using branch lengths (e.g. H_β, which relies on additive decomposition, Mouchet *et al.*, 2011; 2.1b in Table 1), or else all (2.2.1b in Table 1) or the shortest pairwise distances (2.2.2b in Table 1).

(*c*) *Regularity*

The regularity dimension contains metrics that characterize how the phylogenetic tree differs from a star phylogeny (i.e. a phylogeny in which all species are equally unrelated). In other words these metrics quantify how regularly species are located along the phylogenetic tree and how evenly distant they are from each other species. They are grouped into three families based on the use of tree topology (3.1a in Table 1), pairwise distances (all or a subset of pairwise distances; 3.2.1a and 3.2.2a in Table 1), or phylogenetic isolation (3.3a in Table 1). We did not identify any published metrics comparing regularity between assemblages.

(3) Analysing the dimensions framework through simulations

Table 1 represents a consensus built on analysis of mathematical formulations as well as author opinions, yet metric behaviour may still vary within any particular subcategory (e.g. a cell in Table 1), since metrics that share general characteristics may still differ in behaviour. Additionally, some metrics may integrate components from more than one dimension of a phylogeny. Given the grouping of metrics into the three conceptual dimensions in Table 1, we predict that the similarity of metrics within a dimension should be higher (e.g. correlations between their values should be higher) than the similarity of metrics in different dimensions. We use simulations (described briefly below, and in detail in Appendix S2) to evaluate the coherence of metrics within their presumed dimension, and to identify any metrics that deviate notably from their dimension.

We simulated 100 phylogenetic trees with 64 taxa, with a wide distribution of branch lengths (δ statistic) and tree symmetry (I_C statistic) using the *sim.bdtree* function in the R package *geiger* (Harmon *et al.*, 2008). For each tree we created eight types of landscapes (each one a region containing 256 communities) that represented simplified outcomes of possible assembly processes, using the *scape* function in the R package *pez* (Pearse *et al.*, 2015). These landscapes varied in whether (1) there was a phylogenetic signal (*sensu* Blomberg, Garland & Ives, 2003) in species' environmental optima, and whether that signal reflected 'repulsion' (divergence of optima), 'attraction' (convergence of optima), or no phylogenetic correlation, (2) range size (repulsion, attraction, no signal), and (3) spatial autocorrelation in range distribution (Table 2). Thus, assemblages in these landscapes could vary from having spatially autocorrelated ranges and a strong phylogenetic signal for range size and environmental optima, to having random assembly with no phylogenetic structure in range size or environmental optima and no spatial autocorrelation. In total there were eight landscapes simulated for each tree, giving a total of 800 distinct landscapes. For the communities in each of these 800 landscapes, we calculated values for the α-diversity and β-diversity metrics listed in Table 1.

In addition to these analyses using the trees with 64 taxa, we generated 100 trees with 16 taxa and 100 trees with 256 taxa. For each tree size we similarly simulated 800 landscapes, thus constructing a total of 2400 landscapes. We calculated a subset of α-diversity metrics (omitting abundance-weighted and parametric metrics, for a total of 27 metrics) from Table 1 across each of these landscapes to consider briefly whether metric behaviour is sensitive to tree size.

We explored the underlying relationships between α-diversity metrics using principal components analysis (PCA) based on a pairwise Spearman correlation matrix between all α-diversity metrics for each landscape. We used Spearman correlation, as it is robust to nonlinear relationships and outliers. We included all metrics for α-diversity from Table 1 for the analysis: for visual clarity, Fig. 2A presents only presence/absence metrics and excludes abundance-weighted metrics, and parametric metrics and those that include multiple dimensions (these metrics are included in Fig. 2B and C, respectively). The total explained variance when all metrics were included for analysis was 41.8% for principal component 1, and 20.5% for principal component 2. The remaining axes explain much less variation (PC3 explained 6.9%), and so we display only the first two axes. Note that we use PCA here as a technique for visualizing the relationships between metrics: principle component axes are orthogonal and independent, and thus are not expected to be equivalent to the three dimensions we have identified. Although the dimensions capture different aspects of that phylogeny, ultimately all are dependent on the same underlying processes of evolution. Hence, fewer than three independent PCA axes should be necessary to capture variation related to these three dimensions.

PCA results for the α-diversity metrics (Fig. 2A) suggest that the richness, divergence, and regularity dimensions are clearly divided within ordination space and to illustrate this we use the PD, MPD, and VPD metrics as anchors or guidelines for the expected position. The majority of the richness, divergence, and regularity metrics cluster with other metrics from the same dimension. In general, richness metrics load on positive values of PC1 and

2, divergence metrics load on negative values of PC2, while regularity metrics tend to load on negative values of the first axis. Divergence, as represented by the position of MPD, is also captured by phylogenetic species variability (PSV) and average taxonomic diversity (AvTD) because mathematically these metrics are identical (Appendix S1). It is notable however, that for the divergence dimension, metrics that rely on nearest neighbour distances (MNTD) or phylogenetic isolation [mean(ED)] do not cluster closely with MPD, which is composed using all pairwise phylogenetic distances. Regularity, as represented by the position of VPD, is closely correlated with a number of similar metrics, including variance in nearest taxonomic distance (VNTD) and the variance in evolutionary distinctiveness [var(ED)]. These results confirm that the similarity of metrics within a dimension is generally greater (e.g. correlations between their values are higher) than the similarity of metrics between different dimensions, although interesting divergences also occur (see Section III).

β-diversity metrics (Fig. 3) capture the dissimilarity between assemblages. The first PC axis explains 22.9% of variance and the second PC axis 15.6%. The first axis captures a gradient from the richness dimension (positive values) to the divergence dimension (negative values). The entropic metrics [Chiu *et al.*, 2014; ${}^{q}D_{\beta}(T)$] vary from being highly correlated with the richness dimension ($q = 0$, where q is a ‘scaling parameter’ that determines the influence of rare taxa), to being increasingly associated with the divergence metrics as the value of q increases. The second axis captures a separate source of information from the dimensions framework presented here: Swenson (2011) showed that β-diversity metrics can emphasize either differences among communities towards the base (‘basal’) or tips (‘terminal’) of a phylogenetic tree. In our simulations negative values along the second axis appear to capture basal metrics, such as Rao's D (equivalent to Dpw) which is a MPD-based measure of β-diversity, while known terminal metrics such as Dnn, which is MNTD-based measures of β-diversity, fall close to zero. This suggests that for β-diversity metrics, metric choice should additionally consider whether it is more of interest to capture internal *versus* terminal tree structure (Jin, Cadotte & Fortin, 2015; Swenson, 2011). Note that a few metrics were not included, for example, PCD (phylogenetic community dissimilarity), due to computing time requirements. Tree size of the source pool used to simulate communities influenced the similarity of metrics: the variation among α-diversity metrics increased when trees were small (16 taxa; Fig. 4). In general, the multidimensional space occupied by metrics measured on landscapes constructed with 64 and 256 taxa trees overlapped, while the metrics calculated for the trees with 16 taxa tended to occupy separate areas of the ordination. Further, some metrics (e.g. I_C; Fig. 4) behave similarly regardless of tree size. To understand completely the sensitivity or robustness of the different phylo-diversity metrics to changes in tree size, additional in-depth analyses are required. Nonetheless we feel our conclusions regarding metric behaviour within the dimensions framework will be general across a variety of tree sizes with the smallest trees accentuating small differences in metric calculations because the phylogenetic signal exhibited by small clades is inherently variable (Blomberg *et al.*, 2003).

III. ADDITIONAL COMPLEXITIES IN METRIC FORMULATION

Although the metrics generally group by dimension, we also consider a number of additional factors that can alter the usage and interpretation of phylo-diversity metrics.

Metric behaviour may be complicated by factors such as the inclusion of abundances, underlying correlations with species richness, and the emphasis on rare *versus* common species.

(1) Abundances

Species abundances are often an important source of information: for example, weighting schemes using abundances or range sizes have a long history for conservation prioritization (Vane-Wright *et al.*, 1991). All of the dimensions of phylogenetic information can be weighted using some measure of abundance or other weight that allows information about species' commonness or rarity to be incorporated (Table 1, metrics in red, and Fig. 2B).

Abundances may be incorporated in several ways. For metrics applied to a local assemblage, species' relative abundances may be incorporated. This is the ratio between species' absolute abundance (e.g. cover, number of individuals, or biomass) and total absolute abundance of the community (e.g. total cover, total number of individuals or total biomass). Relative abundances are then used to weight phylogenetic units such as pairwise distances [e.g. abundance-weighted MPD (MPD_{Ab}); Miller *et al.*, 2013] or branch lengths [e.g. abundance-weighted PD (PD_{Ab}); Vellend *et al.*, 2010)] There are two general weighting schemes: (1) those where locally abundant species are de-emphasized relative to locally rare species, which are weighted more highly because they may be important for conservation (Cadotte & Davies, 2010); *versus* (2) those that emphasize abundant species, such as when analysing species contributions to ecosystem function (Cadotte *et al.*, 2009). Such weighting schemes allow the impact of the number and relative abundance of rare and distinctive species in local communities to be considered explicitly. For questions that consider a larger spatial scale, range sizes or endemism may be alternative sources of abundance information (Isaac, 2007). For example the phylogenetic endemism metric (PE; Rosauer *et al.*, 2009) weights the length of a particular branch by its whole geographic extent (defined as the union of the distribution of species descending from it). Thus rarity is defined as species with small ranges, rather than low abundances.

Simulation results (Fig. 2B) suggest that the incorporation of abundance into metrics in the divergence and regularity dimensions produced metrics that behaved similarly to other metrics in the same dimensions. Therefore, when abundances within an assemblage are of interest for questions about divergence and regularity, appropriate metric choices exist and can be clearly interpreted and reasonably compared to presence–absence metrics in those dimensions. For richness, the abundance-weighted metrics PE and abundance-weighted evolutionary distinctiveness (AED) clustered with other metrics in the richness dimension. However, several richness metrics that include weighting for abundance, such as PD_{Ab} or average abundance-weighted phylogenetic diversity (ΔnPD), did not cluster with the richness metrics. It may be that sensitivity of these indices to patterns in abundance evenness leads their behaviour to converge with that of indices from the other phylogenetic dimensions, and so the user should use caution when interpreting these particular metrics.

(2) Parametric indices (Hill numbers and entropies)

Hill numbers are a group of diversity measures that aim to quantify diversity in units of equivalent numbers of equally abundant species (Hill, 1973). Hill numbers incorporate information about abundances and variance in abundances, retain constant units (‘effective number of species’), and have recently been extended to include phylogenetic information (Chao *et al.*, 2010; Chiu *et al.*, 2014; Leinster & Cobbold, 2012). These frameworks rely on a unified formula of phylo-diversity that is adjusted using a single ‘scaling parameter’, *q*. The value of *q* should determine the influence of rare taxa. Within the richness/divergence/regularity framework, changes in the value of the *q* scaling parameter affect the dimension of the parametric index being measured, rather than simply altering the influence of rare species, as is the case for the taxonomic versions of these metrics (Fig. 2C). For example in the Chao framework [Chao *et al.*, 2010; ${}^{q}D(T)$], $q = 0$ and $q = 2$ metrics correspond to a richness and a divergence metric, respectively. By contrast the Leinster framework [Leinster & Cobbold, 2012; ${}^{q}D^{Z}(p)$] varied little in how it classified communities in our framework despite changes in *q*. Note that the Scheiner framework (Scheiner, 2012), although reliant on *q*, differs from the parametric indices in that it sums species-level ED instead of summing across edges in the phylogeny. Parametric indices require further theoretical treatment and applications to determine their properties fully, and so care must be taken in selecting and interpreting them.

(3) Metrics that depend on species richness

The original Pavoine–Bonsall framework was defined independently of species richness so that multiplying an index by species richness (e.g. PSR=PSV*species richness) would not change its classification (both PSR and PSV were considered in the Pavoine–Bonsall framework as divergence indices). Richness is here defined more broadly to include any counting of evolutionary units, be they branch lengths or other phylogenetic distances. As a result, some metrics are classified differently from in the original work, and our richness dimension is intrinsically more influenced by species richness than the other two dimensions.

Several indices that we classified *a priori* in other dimensions were found to be strongly correlated with the richness dimension, as a result of their underlying relationships with species richness. We suggest that this explains the behaviour of the parametric indices based on Hill numbers discussed above, as these are, by definition, dependent on species richness. Several entropic measures of evolutionary distinctiveness [Cadotte *et al.*, 2010; H_{ED}, H_{AED}], and metrics in the Scheiner framework combine phylogenetic regularity with species richness, which leads their behaviour to be strongly correlated with the richness dimension (PD), since PD and species richness are also often highly correlated. Rao's quadratic entropy (Rao's QE) is primarily an index of divergence (Clarke & Warwick, 1998; Rao, 1982) as most of its variation occurs along the divergence dimension – but it is also slightly correlated with the richness dimension since it includes the diagonal of the distance matrix. The equitability of H_{ED}, E_{ED} (Cadotte *et al.*, 2010), behaves differently from both its component dimensions because it quantifies the deviation of ED from a star phylogeny (all species equally related so they are maximally and equally distinct).

For some metrics, simple transformations can be applied to remove this dependence. For example, indices based on Hill numbers can be divided by species richness to remove its effect. The effects of species richness and abundance evenness can be removed by using appropriate null models (Pavoine *et al.*, 2013), which can also ease comparisons with functional diversity, since species richness and abundance evenness may artificially exaggerate correlations between phylogenetic diversity and functional diversity.

IV. CONNECTING ECOLOGICAL QUESTIONS AND HYPOTHESES WITH PHYLO-DIVERSITY METRICS

The dimensions classification framework unites metrics developed across ecological sub-disciplines and used for different purposes. However, the framework does not easily resolve the problem of choosing among metrics for a particular analysis. Ecological questions, whether from conservation, community ecology, or macroecology, all consider how accumulated differences between species (reflected by divergences along a phylogeny) may relate to biological processes or patterns. Evolutionary history is considered an outcome or predictor of processes of interest. We suggest that questions about these processes or patterns can be simplified and unified to recognize the three general themes of: how much total diversity is present in an assemblage (or among assemblages); how different, on average, are taxa in an assemblage (or among assemblages); and/or how regular or variable are the differences between taxa in an assemblage (or among assemblages) (Fig. 5). We review below the types of questions asked by ecologists using phylogenies, identify commonalities, and connect these questions with appropriate phylo-diversity metrics.

(1) Applying richness metrics

Richness metrics can be used to measure or describe observed patterns of diversity; these values may also be compared to equivalent taxonomic and functional measures. As richness metrics sum the quantity of phylogenetic differences in an assemblage, they are often assumed to capture 'feature diversity' under some models of trait evolution (Kelly, Grenyer & Scotland, 2014). In this context, measures of phylogenetic richness may be used to answer questions about the quantity and distribution of extant biodiversity, arguably better than species-based metrics (Rosauer & Mooers, 2013). Phylogenetics offers metrics which are relatively insensitive to taxonomic inflation (Isaac, 2007), and which can easily incorporate taxa (or other evolutionary units) for which there is little information, other than their placement on the tree of life. Feature diversity may be considered a valuable indicator of either future utility or future evolutionary potential (Forest *et al.*, 2007; Mace, Gittleman & Purvis, 2003) and so conservation biologists have been interested in the protection of total feature diversity for questions of prioritization of taxa and/or areas (e.g. Bennett *et al.*, 2014; Forest *et al.*, 2007; Isaac, 2007; Jetz *et al.*, 2014; Purvis, 2008; Rodrigues *et al.*, 2011). For example, Tucker *et al*. (2012) asked how Proteaceae phylogenetic diversity was distributed spatially in the Cape Floristic Province. To capture the total evolutionary richness in a spatial unit, they considered two richness metrics – PD, and the sum of abundance-weighted ED (BED) – and compared the distributions of these metrics with Proteaceae species richness in the region.

Phylogenetic richness (either α- or β-diversity) has also been used as a predictor or response variable in numerous studies, across multiple spatial or temporal scales and for diverse natural systems. Variation in phylogenetic richness through space and time is often hypothesized to be an outcome of different ecological and evolutionary processes

(Cavender-Bares *et al.*, 2009; Mouquet *et al.*, 2012). For example, as invasive species represent a non-random combination of traits, and phylogenetic metrics can be used to capture such ‘feature diversity’, it may be hypothesized that invasion should lead to differential changes in phylogenetic richness (α- or β-diversity) compared to species richness. Winter *et al.* (2009) tested this by comparing taxonomic and phylogenetic richness metrics in invaded assemblages [ultimately showing that alien species led to a decrease in phylogenetic distinctness (i.e. divergence) rather than richness]. In a separate application Thuiller *et al.* (2011) found that species’ vulnerability to climate change clustered weakly along the phylogeny, and used this relationship to predict how the amount and distribution of phylogenetic richness will change in the future.

(2) Applying divergence metrics

Questions about ecological communities have frequently considered phylogenetic distance to be a proxy for differences in functional traits (Ackerly, 2009; reviewed in Freckleton, Harvey & Pagel, 2002; Mouquet *et al.*, 2012; Srivastava *et al.*, 2012), with the assumption that closely related species are more functionally similar, and thus overlap more in their ecological niche, than those that are more distantly related (Connolly *et al.*, 2011; Gerhold *et al.*, 2015; but see Narwani *et al.*, 2013; Purschke *et al.*, 2013; Violle *et al.*, 2011). Underlying this are additional assumptions that closely related species occur in sympatry and that trait evolution is divergent, so the most similar taxa are the most closely related (Gerhold *et al.*, 2015). When these assumptions hold, it is often hypothesized that if environmental filtering drives community assembly, taxa within an assemblage will be more related on average than expected in a random or null assemblage (Cavender-Bares & Wilczek, 2003; but see Mayfield & Levine, 2010; Webb *et al.*, 2002). Alternatively, if competitive interactions are important, it may be hypothesized that co-occurring taxa will be less related (i.e. more divergent) than expected on average. Divergence indices, particularly MPD and MNTD indices, have been used to test these types of hypotheses about the mean relatedness of taxa within an assemblage. For example, Helmus *et al*. (2010) considered whether disturbed communities tended to contain more closely related species, reflecting the role of environmental filtering in selecting disturbance-tolerant taxa. They hypothesized that more closely related species might have similar traits, and so be similarly adapted to disturbance conditions. To test this, the authors used the PSV metric, which is closely related to MPD, and compared the average relatedness of species in disturbed communities *versus* non-disturbed communities.

Note that although these are frequently expressed hypotheses in community ecology, there are many possible relationships between phylogenetic relatedness and co-occurrence that can be tested using divergence metrics. Gerhold *et al.* (2015) provide alternative scenarios that may preclude the interpretations described above – for example, trait similarity may actually facilitate coexistence (see also Mayfield & Levine, 2010), competitive exclusion may be incomplete in assemblages, and regional species pools and processes, rather than local processes, may determine local assembly. Thus, testing questions about evolutionary history requires both identifying the correct type of metric for a given question as well as considering the assumptions that might relate patterns to processes.

The phylogenetic topology of species' assemblages can further provide information about processes structuring regional species pools (Heard & Cox, 2007; Purvis *et al.*, 2011), and the likelihood that these will be invaded or altered (Gerhold *et al.*, 2011). Macroecological studies have incorporated information about divergences in phylogenies to compare phylogenetic distances separating sister lineages and capture variation in diversification rates (e.g. Ackerly, 2009; Weir & Schluter, 2007), to identify geographical centres of diversification (e.g. Jetz *et al.*, 2012), or the drivers of niche evolution or conservation (e.g. Dormann *et al.*, 2009; Wiens & Donoghue, 2004). Such macroecological approaches allow tests of whether diversification rates differ between biogeographical regions, across latitudes or at different times through history. In addition, patterns can be compared to null expectations generated from models that integrate the processes of speciation, extinction and colonization (Pigot & Etienne, 2015) providing more powerful tests of the mechanisms structuring regional species assemblages.

(3) Applying regularity metrics

The regularity metrics appear less frequently in the literature, and we identified no published examples for β-diversity. They are typically used for questions about how evenly evolutionary history is distributed between taxa in an assemblage, and as with divergence metrics, are often applied with the assumption that phylogenetic distance is a proxy for differences in functional traits. Under such a framework, one might hypothesize that greater evenness in the distribution of similarity among species should result in lower competition (Kraft, Valencia & Ackerly, 2008). Cadotte (2013) manipulated phylogenetic relatedness and species richness in plant communities, and tested whether the selection effect (the dominance of highly competitive or productive species, one putative mechanism underlying the diversity–ecosystem function correlation), might be related to the topology of the phylogenetic tree. In fact, the selection effect was correlated with a regularity metric, the imbalance in abundances among clades (IAC). As regularity metrics reflect evenness in the distribution of dissimilarity among species, this finding suggests that the selection effect is strongest when closely related species are present. In the field of macroecology, Davies & Buckley (2011) considered VPD to explore unevenness in the distribution of PD globally for terrestrial mammals, which provided insight into the historical processes behind global patterns of species richness.

V. A GUIDE TO PHYLO-DIVERSITY METRICS

Here we provide a robust and intuitive framework to guide researchers and practitioners on the selection and matching of phylo-diversity metrics to their research questions. We have shown that the different metrics align with three dimensions of phylo-diversity: richness, divergence, and regularity; dimensions that themselves align naturally with common research questions (Fig. 5). In highlighting this natural linkage between research questions and associated hypotheses, phylogenetic dimensions, and appropriate metrics, we hope to facilitate the growing usage of phylogenies in ecology. Further, we hope that this work will encourage researchers to choose amongst existing metrics rather than formulate new metrics that have properties similar to those already in existence.

(1) Metric selection for ecologists

Importantly, our classification framework predicts metric behaviour based on their mathematical properties. Although particular metrics have become entrenched in particular fields, we show that there is mathematical redundancy among them and that alternative metrics may be equally able to address similar questions. This suggests that the choice of metric could be simplified. Researchers must first specify whether they are most interested in describing properties within a set or between sets, and then determine whether their research question(s) necessitate the use of ‘how much’, ‘how different’ or ‘how regular’ dimensions. By placing their questions within these dimensions, the researcher can then identify the set of most appropriate metrics to choose from (Fig. 5). The choice of metric need not depend on discipline, or whether the taxa of interest represent those found in an experimental sample, ecological community, biogeographical region, or clade of conservation interest.

It is sometimes suggested that the choice of statistical analyses should be made *a priori*, during experimental design and before performing actual experiments (Underwood, 1997). Although this is frequently unfeasible, especially for studies using observational data, this is meant to prevent issues related to multiple comparisons or bias in variable selection. Similar issues occur when multiple phylo-diversity metrics are used interchangeably in analyses. Although simply comparing models for all possible metrics and selecting the one with the best explanatory power has been employed in the past (see, e.g. Cadotte, 2013), it results in poorly justified analyses and potentially confusing inference and we do not recommend it. The general ‘phylogeny should be important’ hypothesis that accompanies multi-metric analyses obscures interpretation. As we have shown throughout this review, metrics from different dimensions should not be treated interchangeably as they represent different types of information and effectively test different hypotheses.

A recommended strategy is to find the most appropriate metric through *a priori* identification of the key components of the research hypothesis. If our question is about the total evolutionary diversity contained within a reserve (richness), or say, the average species distinctiveness (divergence) within assemblages across an environmental gradient, then the correct dimension should be straightforward to identify (Fig. 5). Once the dimension associated with the question is identified, researchers can restrict their choices to those the associated column in Table 1. They can also reduce the possible metric choices to those for either α-diversity or β-diversity, depending on which they are asking questions about.

There can be validity in comparing multiple metrics within a dimension, particularly if the metrics have different properties (e.g. units, formulation) of interest to the researcher, and they are all appropriate to the particular question or conclusion. In addition, high redundancy amongst metrics within a dimension can make selection among them somewhat arbitrary. As a result it is usually easier to select the ‘anchor’ metric that represents a dimension (for α-diversity, PD for richness, MPD or perhaps MNTD for divergence, and VPD for regularity), given their ease of interpretation and precedence in the literature. One might use MPD when questions relate to branching occurring deep within a tree *versus* MNTD for questions related to terminal branching. Users may consider alternatives to the anchor metrics if these provide better fit to a specific question and analysis. For example, parametric indices (i.e. Hill numbers across a range of values of q) allow users to fully consider the impact of rare and common species on evolutionary diversity. In addition, they may be used for comparative analysis of parametric indices across phylogenetic, taxonomic, and functional diversity. Alternatively, users may want to account for abundances in some form (range sizes, rarity, etc.), or compare results for presence–absence and abundance-weighted versions of metrics (e.g. MPD *versus* $\mathrm{MPD}_{\mathrm{Ab}}$). In other cases, it may be reasonable to select a metric if direct comparison with previously published values is desired. Even in these cases, we stress that our simulation results can be used to guide interpretation of alternative metrics, including through comparison of their behaviour with that of anchor metrics.

The choice of phylogenetic units merits additional discussion. Metrics may be constructed using different countable units, including using branch lengths, pairwise phylogenetic distances between taxa, or evolutionary isolation. Each of these components can be measured similarly (i.e. time of evolution in millions of years), and should rather be understood as differing in their ‘targets’ or objectives. If one wants to conserve as many evolutionary units as possible, branch lengths should be the target of interest. If users wish to consider competition among species, pairwise distances may be an appropriate choice of unit. Phylogenetic isolation should be the target if users want to conserve unique species or relate conservation prioritization or ecological processes to differences in the rate of diversification across the tree. However, it is important to note that metric behaviour often did not differ significantly between metrics within the same dimension but constructed using different units (Fig. 2).

There could also be cases in which a researcher wishes to consider the effect of multiple dimensions on a process or variable (for example, how does primary productivity in a site relate to richness and divergence in its plant community?). It is possible to use an approach that matches questions and inference to the metric, while also assessing how the different dimensions influence the variable of interest. For this approach the analysis would consist of creating a statistical model that includes metrics from multiple dimensions. The logical way to do this would be to select a metric within each dimension following the recommendations in the previous section and then investigate nested models with subsets of the metrics. In the example above, if model selection suggests that a model containing both richness and divergence metrics is best, a researcher might conclude that both the total amount of history and the relative spacing of species are important predictors of productivity.

(2) An example of metric selection

To illustrate the process of metric selection with a more realistic scenario, we provide the following example. Consider an island mainland system with a number of plant species (Fig. 6) for which a researcher is interested in how evolutionary diversity varies between the mainland and islands (here, sites and islands are referred to interchangeably). The researcher first asks whether there are different amounts of evolutionary history represented by the plant communities at each site. As this is a question about the amount or sum of units of evolutionary history, metric choice should focus on the richness dimension (see Fig. 5). They may hypothesize that the most distant site (Island C) will share the least amount of evolutionary history with the remaining sites, since its distance should decrease the probability that species arrive from the mainland or potentially encourage diversification *in situ* (MacArthur & Wilson, 1967; Wiens & Donoghue, 2004). To compare the evolutionary history between the three sites, the researcher chooses a β-diversity richness metric (Table 1, red metrics in Fig. 3), perhaps a branch-length-based metric such as Faith's PD_{β} that captures the amount of shared evolutionary history. Fig. 3 shows that a number of metrics cluster closely and appear to capture the richness dimension, and a choice between these (Unifrac, $S_{Jaccard}$, $S_{Sorensen}$) should yield very similar results.

Using the same system and phylogeny, the researcher asks additional questions regarding whether there are differences in how evenly evolutionary history is distributed within the plant assemblages on each of sites A–C. Given that they found that Island C shares the least amount of total evolutionary history with the other sites (Fig. 6, lower left panel), and Island C contains a number of endemic species, the researchers may now be interested in whether diversification rates differ between sites and if the endemic species on Island C reflect a recent radiation. The researchers recognize that this relates to the evenness or regularity of the distribution of evolutionary history, and so they choose a metric from the α-diversity regularity dimension (Table 1). They hypothesize that assemblages should be least even on Island C because the biota might derive from independent colonization events by evolutionarily distinct lineages (i.e. lineages separated by large phylogenetic distances) which subsequently radiated *in situ*, giving rise to clusters of species separated by short evolutionary distances. The researchers calculate VPD for each site, and can then compare these with the VPD expected if the island biota was randomly assembled. This hypothetical example illustrates how a researcher's various questions can be connected simply with phylo-diversity metrics and how careful choice leads to clear interpretation of results.

VI. MOVING FORWARDS

One result of our categorization of metrics is that researchers may be encouraged to look beyond a single frequently used metric and dimension and compare different dimensions, as is already done with the analogous framework for functional diversity (Villéger *et al.*, 2008). For example, PD and, less often, abundance-weighted versions such as PE, have been the dominant measure of phylogenetic information in conservation biology research. Although we question whether the multiplicity of phylogenetic metrics in the literature has in general advanced research, conservation biology, more than for the other fields, has limited its perspective to the richness dimension alone. Metrics from the divergence or regularity dimensions might provide complementary information about the distribution of biodiversity across taxa in a site, for example.

We hope that this review stimulates broader thinking and discussion about the use of phylogenies in ecology, conservation and macroecology. However, it represents a starting point for deciding which metrics to apply to data; more analyses and work is still required to advance our understanding of these metrics.

In our analyses we simulated a large number of landscape types and randomly generated trees in order to capture typical or average metric behaviour. However, parameter space is vast and future simulations should consider additional phylogeny and landscape attributes that may also influence metric behaviour. For example, it is understood that PD is strongly correlated with species richness, although less so when trees are unbalanced or distinct species are also spatially restricted (Rodrigues, Brooks & Gaston, 2005; Tucker & Cadotte, 2013). Thus, more complete consideration of parameter space is required to assess metric behaviour fully across a range of phylogenetic topologies and branch-length distributions, as well as the phylogenetic signal strength in niche position and range size. Repeating tests with real, rather than simulated trees would also provide important information on expected values for metrics in natural systems. In addition, we still must determine whether metric correlations are robust to all types of phylogenies and landscapes, or whether certain types of perturbations inflate the importance of subtle metric differences.

We believe that our framework supplies guidance to researchers and practitioners on how to use and interpret results from phylogenetic analyses. As noted previously, the three dimensions we employ are simplifications, although their use in both functional and phylogenetic approaches suggests they have utility. In addition, simulation results largely support the classification of metrics and so we suggest that this framework should serve as a starting point for choosing metrics, applying questions and interpreting results.

VII. CONCLUSIONS

(1) The use of phylogenies in community ecology, macroecology, and conservation biology reflects the shared recognition that accumulated evolutionary differences may explain or predict biological and ecological processes. Phylogenetic approaches have revolutionized these disciplines.

(2) The rapid growth of new phylogenetic metrics has limited the development of phylogenetic methods in ecology and conservation, and prevents meta-analysis and clear interpretation of metrics.

(3) We suggest that the intuitive, unifying framework of the phylogenetic dimensions – richness, divergence, and regularity – is very useful, since it applies to biological

questions at multiple ecological scales, for single or multiple groups of species, and across fields.

(4) We encourage appropriate metric selection by highlighting links between research questions and metrics falling in the appropriate phylogenetic dimensions; interpretation is made simple by understanding the relationship between a metric's dimension and the mathematical basis of that dimension.

(5) Informed metric selection and interpretation will allow the use of published results across subfields and applications and encourage future work.

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X. SUPPORTING INFORMATION

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

Appendix S1. Definition, equations and references for the indices.

Appendix S2. Description of simulations run using *scape* – a phylogenetically informed community assembly simulation platform in the R package *pez*.

Table S1. Parameter values used for the eight types of communities simulated using *scape*.

Fig. S1. *scape* workflow showing the necessary input information and the path by which these are used to produce output from the assembly model.