

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

Caroline M. Tucker^{1,*}, Marc W. Cadotte^{2,3}, Silvia B. Carvalho⁴, T. Jonathan Davies^{5,6}, Simon Ferrier⁷, Susanne A. Fritz^{8,9}, Rich Grenyer¹⁰, Matthew R. Helmus^{11,12}, Lanna S. Jin¹³, Arne O. Mooers¹⁴, Sandrine Pavoine^{15,16}, Oliver Purschke^{17,18,19}, David W. Redding²⁰, Dan F. Rosauer²¹, Marten Winter¹⁷ and Florent Mazel²²

¹Department of Ecology and Evolutionary Biology, University of Colorado, Box 334, Boulder, CO 80309-0334, U.S.A.

²Biological Sciences, University of Toronto-Scarborough, Scarborough M1C 1A4, Canada

³State Key Laboratory of Biocontrol, Key Laboratory of Biodiversity Dynamics and Conservation of Guangdong, Higher Education Institutes, College of Ecology and Evolution, Sun Yat-sen University, Guangzhou, PR China

⁴CIBIO/InBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos da Universidade do Porto, 4485-661 Vairão, Portugal

⁵Department of Biology, McGill University, Montréal, H3A 1B1, Canada

⁶African Centre for DNA Barcoding, University of Johannesburg, PO Box 524, Johannesburg 2006, South Africa

⁷CSIRO Ecosystem Sciences, Climate Adaptation Flagship, GPO BOX 1600, Canberra 2601, Australia

⁸Biodiversity & Climate Research Centre (BiK-F) and Senckenberg Gesellschaft für Naturforschung, 60325 Frankfurt am Main, Germany

⁹Institute of Ecology, Evolution and Diversity, Goethe University, 60438 Frankfurt, Germany

¹⁰School of Geography and the Environment, University of Oxford, Oxford OX1 3QY, U.K.

¹¹Department of Ecological Sciences - Animal Ecology, Vrije Universiteit, Amsterdam, Netherlands

¹²Center for Biodiversity, Department of Biology, Temple University, Suite 502, Philadelphia, PA 19122, U.S.A.

¹³Ecology & Evolutionary Biology, University of Toronto, Room 3055, Toronto, M5S 3B2, Canada

¹⁴Department of Biology, Simon Fraser University, Burnaby, V5A 1S6, Canada

¹⁵Centre of Ecology and Conservation Sciences (UMR 7204 CESCO), Museum National d'Histoire Naturelle, Paris, France

¹⁶Department of Zoology, University of Oxford, Oxford OX1 3QY, UK

¹⁷German Centre of Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, DE-04103 Leipzig, Germany

¹⁸Geobotany and Botanical Garden, Institute of Biology, Martin Luther University, Halle-Wittenberg, DE-06108 Halle (Saale), Germany

¹⁹Department of Computer Science, Martin-Luther-University, Halle-Wittenberg, DE-06120 Halle (Saale), Germany

²⁰Centre for Biodiversity and Environmental Research, Department of Genetics, Evolution and Environment, University College London, London, WC1E 6BT U.K.

²¹Research School of Biology, Australian National University, Acton 2601, Australia

²²Laboratoire d'Ecologie Alpine (LECA), CNRS - Université Grenoble Alpes (UMR 5553), BP 53, 38041 Grenoble Cedex 9, France

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.

* Address for correspondence (Tel: (303) 492-8961; E-mail: caroline.tucker@colorado.edu).

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	2
II. A unifying framework for phylo-diversity metrics	3
(1) Describing the framework	3
(2) Classifying phylo-diversity metrics using the dimensions framework	4
(a) Richness	4
(b) Divergence	4
(c) Regularity	7
(3) Analysing the dimensions framework through simulations	7
III. Additional complexities in metric formulation	9
(1) Abundances	9
(2) Parametric indices (Hill numbers and entropies)	10
(3) Metrics that depend on species richness	10
IV. Connecting ecological questions and hypotheses with phylo-diversity metrics	11
(1) Applying richness metrics	11
(2) Applying divergence metrics	12
(3) Applying regularity metrics	13
V. A guide to phylo-diversity metrics	13
(1) Metric selection for ecologists	13
(2) An example of metric selection	14
VI. Moving forward	15
VII. Conclusions	16
VIII. Acknowledgements	16
IX. References	16
X. Supporting Information	18

I. INTRODUCTION

Phylogenetic information is a critical component of modern ecology, particularly for the sub-disciplines of macroecology, community ecology, and conservation biology (Vane-Wright, Humphries & Williams, 1991; Crozier, 1992; Faith, 1992; Purvis *et al.*, 2000; Webb, 2000; Webb *et al.*, 2002; Winter *et al.*, 2009; Cadotte *et al.*, 2010; Davies & Cadotte, 2011; Beck *et al.*, 2012; Mouquet *et al.*, 2012). 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 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 (Wiens & Donoghue, 2004; Winter *et al.*, 2009; Fritz & Rahbek, 2012; Jetz *et al.*, 2012). 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) (Redding, 2003; Isaac, 2007) 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 (Vellend *et al.*, 2010; Mouquet *et al.*, 2012; Winter *et al.*, 2013; Chiu, Jost & Chao, 2014) have called for a unifying framework for phylo-diversity metrics, in order to clarify the conceptual relationships between existing metrics, to highlight their redundancies, and ultimately to encourage the correct usage and interpretation of metrics (Faith, 2008; Schweiger *et al.*, 2008; Pavoine, Love & Bonsall, 2009; Chao, Chiu & Jost, 2010, 2014; Pavoine & Bonsall, 2011; Swenson, 2011; Rosauer & Mooers, 2013; Tucker & Cadotte, 2013; Chiu *et al.*, 2014; Pearse *et al.*, 2014). 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 (i) comprehensive classification of metrics, since it included only a small subset of published phylo-diversity metrics, and (ii) 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, either: (i) the sum of accumulated phylogenetic differences among taxa ('richness'); (ii) the mean phylogenetic relatedness among taxa ('divergence'), representing the average phylogenetic difference between taxa in an assemblage; or (iii) 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 (i) provides an intuitive approach based on the mathematical formulations of the metrics, (ii) assesses both within- and between-assemblage diversity components, (iii) is analogous to the functional diversity framework, thus aiding comparisons between phylo- and functional diversity (Villéger, Mason & Mouillot, 2008) and (iv) 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,

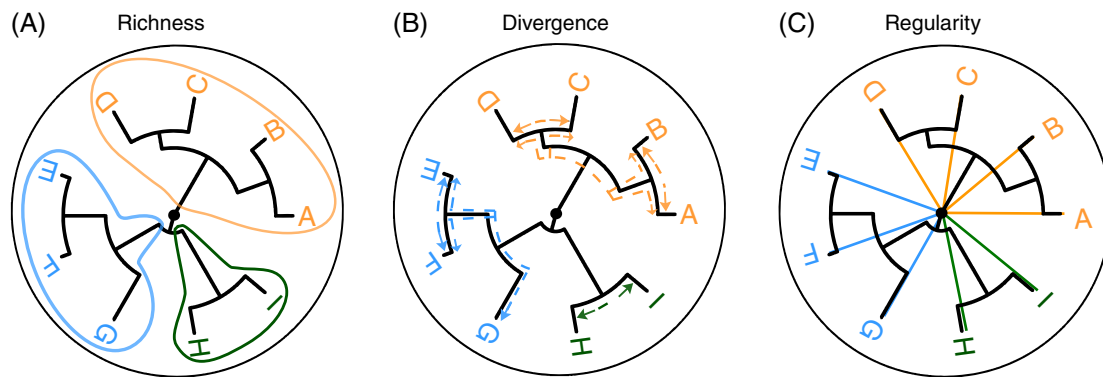


Fig. 1. Conceptual diagrams illustrating the calculation of each of the three dimensions of phylogenetic information: richness (A), divergence (B), and regularity (C). The branching diagram in each image is a phylogenetic tree representing the inferred evolutionary relationships among taxa A–I. Taxa A–I are grouped within three assemblages (A–D, orange; E–G, blue; and H–I, green). Tree branches represent accumulated differences 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 (Vellend *et al.*, 2010; Pavoine & Bonsall, 2011; Pearse *et al.*, 2014). 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 Colless, 1982; Rao, 1982; Faith, 1992; Weiher & Keddy, 1995; Clarke & Warwick, 1998, 2001; Izsák & Papp, 2000; Pybus & Harvey, 2000; Barker, 2002; Izsák & Szeidl, 2002; Webb *et al.*, 2002; Redding, 2003; Lozupone & Knight, 2005; Pavoine, Ollier & Pontier, 2005; Jost, 2006; Hardy & Senterre, 2007; Helmus *et al.*, 2007; Isaac, 2007; Jost, 2007; Lozupone *et al.*, 2007; Bryant *et al.*, 2008; Hardy & Jost, 2008; Villéger *et al.*, 2008; Webb, Ackerly & Kembel, 2008; Allen, Kon & Bar-Yam, 2009; Pavoine *et al.*, 2009; Rosauer *et al.*, 2009; Cadotte *et al.*, 2010; Ives & Helmus, 2010; Kembel *et al.*, 2010; Nipperess, Faith & Barton, 2010;

Vellend *et al.*, 2010; Mouchet & Mouillot, 2011; Swenson, 2011; Chen *et al.*, 2012; Leinster & Cobbold, 2012; Scheiner, 2012; Miller, Zanne & Ricklefs, 2013; Safi *et al.*, 2013; Chiu *et al.*, 2014; Dehling *et al.*, 2014; Pavoine & Ricotta, 2014). 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 to 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 lengths 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

α -diversity
(within sets)

Biological Reviews (2016) 000–000 © 2016 The Authors. *Biological Reviews* published by John Wiley & Sons Ltd on behalf of Cambridge Philosophical Society.

Table 1. Continued

1. Richness: how much? Sum of ...		2. Divergence: how different? Mean of ...		3. Regularity: how regular? Variance of ...					
Unit =>	1.1 Branch lengths	1.2 Pairwise distances	1.3 Phylogenetic isolation	2.1 Branch lengths	2.2 Pairwise distances / similarities	2.3 Phylogenetic isolation	3.1 Tree topology	3.2 Pairwise distances	3.3 Phylogenetic isolation
	1.1b Amount of (un)shared evolutionary history: Phylosor PhylosorAb Unifrac UnifracAb Faith's PD β	1.2b Sum of inter-set distances relative to intra-set distances: S_{Jaccard} S_{Sokal-Sneath} S_{Sorensen} S_{Ochial} Sβ (with absolute abundances)	NA	2.1b Effective number of sets: $qD_{\beta}(T)^*$ Amount of entropy gained on average by merging the sets: Hβ^* I$q\beta^*$	2.2.1b Average inter-set relative to intra-set distances: S_{Jaccard} S_{Sokal-Sneath} S_{Sorensen} S_{Ochial} Sβ (with relative abundances) Average inter-set distances conditionally to intra-set (dis)similarities: PCD Amount of average distances gained on average by merging the sets: Rao's DISC Proportion of average distances gained on average by merging the sets: F_{ST} P_{ST} Proportion of average inter-species distances gained on average by merging the sets: B_{ST} P_{ST} Average inter-set distances: COMDIST , Rao's D , Dpw COMDIST_{Ab} , Rao's D_{Ab} , Dpw_{Ab}	2.2.2b Average minimum distance between a species of a set and another set: COMDISTNT , Dnn COMDISTNT_{Ab} , Dnn_{Ab}	NA	NA	NA
β-diversity (between sets)									

For each category we provide verbal descriptions and corresponding published indices. For example, the indices belonging to the 'α-diversity/divergence indices' cell can be defined as the 'Mean shortest distance between a species and all others' with the corresponding published indices – MINTD and MINTDAb. Empty categories indicate that there are no corresponding published indices of which we are aware. Indices coloured in red can incorporate abundances. Indices separated by commas reflect indices that are mathematically interchangeable although referred to using different names (e.g. MPD, AvTD, PSV). Starred indices (*entropies and Hill numbers) are classified as 'parametric indices' in Appendix S1, for their shared reliance on a single 'scaling parameter', q , that determines the influence of rare taxa.

Table 2. Landscape types used for simulations of metrics: numbers indicate parameter values in the *scape* function of *pez*. For a trait, values of 1 reflect Brownian motion, and values less than 1 reflect rates of evolution that accelerate, values greater than 1 reflect rates of evolution that decelerate through time. See Appendix S2 for additional details

Landscape type	Phylogenetic signal, environmental optima	Environmental optima, signal type	Phylogenetic signal, range size	Range size, signal type	Spatial autocorrelation range
1	TRUE	Repulsion (0.2)	FALSE	N/A	TRUE
2	TRUE	Attraction (20)	FALSE	N/A	TRUE
3	TRUE	Repulsion (0.2)	TRUE	Repulsion (0.2)	TRUE
4	TRUE	Attraction (20)	TRUE	Attraction (20)	TRUE
5	FALSE	N/A	FALSE	N/A	TRUE
6	FALSE	N/A	FALSE	N/A	FALSE
7	FALSE	N/A	TRUE	N/A	TRUE
8	FALSE	N/A	TRUE	N/A	FALSE

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 & Mouillot, 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 details. Additionally, some metrics 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 there was a phylogenetic signal (*sensu* Blomberg, Garland & Ives, 2003) in (i) species' environmental optima, and whether that signal reflected 'repulsion' (divergence of optima), 'attraction' (convergence of optima), or no phylogenetic correlation, and (ii) range size (repulsion, attraction, no signal), and (iii) additionally whether there is 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

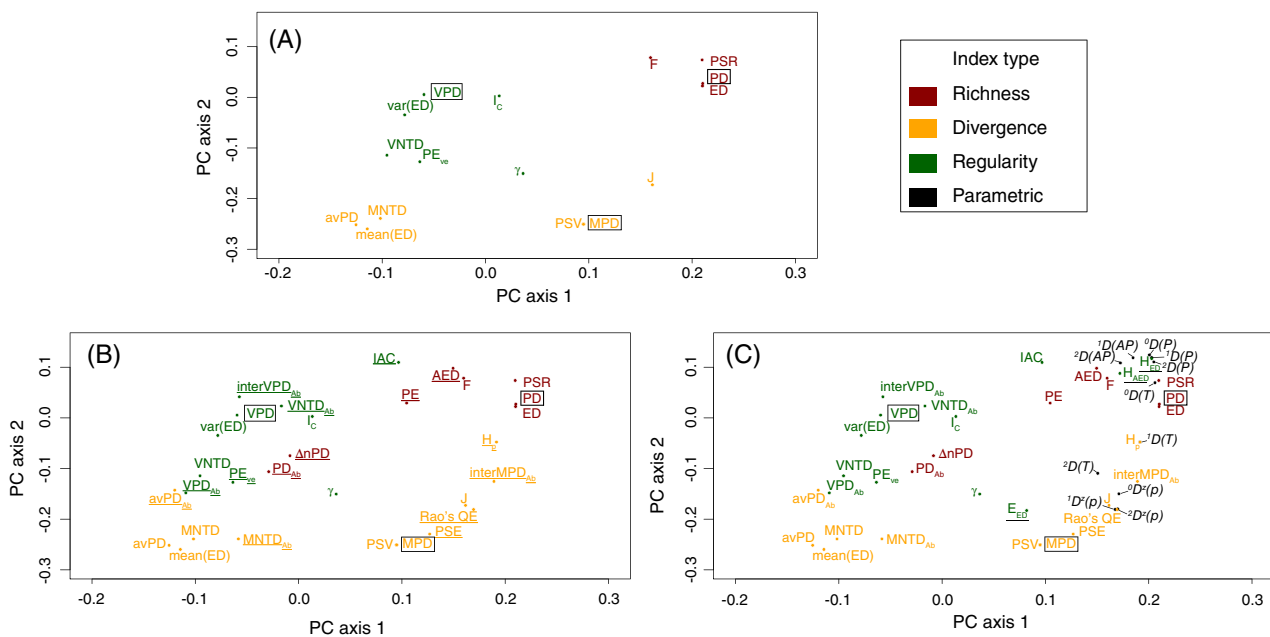


Fig. 2. Principal components analysis for Spearman's correlations between the α -diversity metrics shown in Table 1. Results represent measures taken from 800 simulated landscapes, based on 100 simulated phylogenetic trees and eight landscape types defined in Table 2 (see online Appendix S2 for detailed methods). (A) All metrics excluding abundance-weighted metrics and those classified as parametric indices. (B) As in A, but with abundance-weighted metrics included (underlined). (C) As in B, but with parametric indices (black), and indices that incorporate multiple dimensions (underlined) included (e.g. all α -diversity metrics). X and Y axes are scaled to reflect explained variance (PC1 = 41.8%; PC2 = 20.5% for the PCA performed with all metrics, shown in (C)). Boxed metrics reflect 'anchor' metrics (PD, MPD and VPD) that align most closely with the richness, divergence and regularity dimensions, respectively. Where metrics are identified in Table 1 as mathematically identical, we include only one (e.g. MPD is plotted, but not AvTD). See Appendix S1 for equalities among indices.

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, 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 that 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 (see online 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; $^qD_\beta(T)$] vary from being highly correlated with the richness dimension ($q = 0$, where q

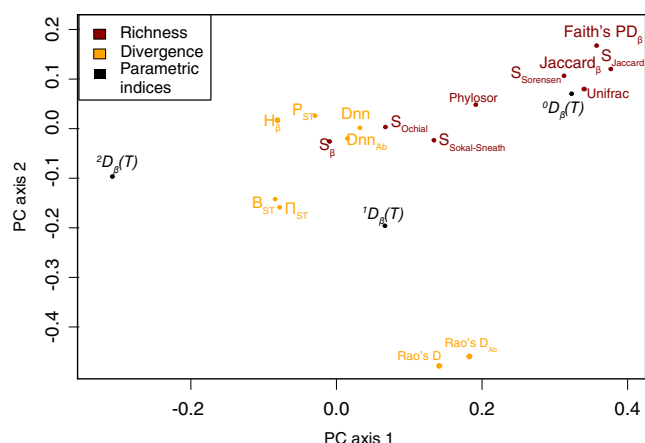


Fig. 3. Principal components analysis for Spearman's correlations between the β -diversity metrics shown in Table 1. Results represent measures taken from 800 simulated landscapes based on 100 simulated phylogenetic trees and eight landscape types defined in Table 2 (see online Appendix S2 for details). X and Y axes are scaled to reflect explained variance ($PC1 = 22.9\%$; $PC2 = 15.6\%$). Where metrics are identified in Table 1 as mathematically identical, we include only one (e.g. Rao's D is plotted, but not Dpw). See Appendix S1 for equalities among indices.

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 a MNTD-based measure 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 (Swenson, 2011; Jin, Cadotte & Fortin, 2015). 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: (i) 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* (ii) 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

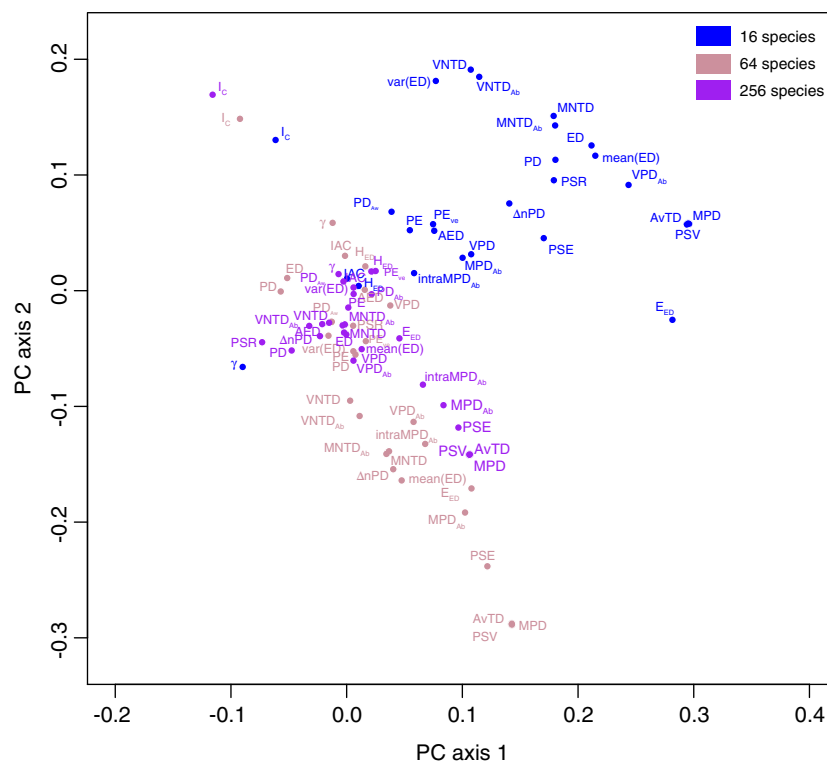


Fig. 4. Effect of tree size on relationships between a subset of α -diversity metrics. Principal components analysis for Spearman's correlations between 27 commonly used α -diversity metrics (Table 1). Abundance-weighted metrics and parametric indices are not included in this analysis. Results represent measures taken from 2400 simulated landscapes, based on 300 simulated phylogenetic trees with three different sizes (16, 64 and 256 taxa, 100 trees of each size) and eight landscape types defined in Table 2 (see online Appendix S2 for detailed methods). X and Y axes are scaled to reflect explained variance (PC1, 12.83%; PC2, 8.95%).

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; Leinster & Cobbold, 2012; Chiu *et al.*,

2014). 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; $^qD(T)$], $q = 0$ and $q = 2$ metrics correspond to a richness and a divergence metric, respectively. By contrast the Leinster framework [Leinster & Cobbold, 2012; $^qD^{\sim}(p)$] 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. $PSR = PSV \times \text{species richness}$) 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 (Rao, 1982; Clarke & Warwick, 1998) 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.

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 can be 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 (Mace, Gittleman & Purvis, 2003; Forest *et al.*, 2007) 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. Forest *et al.*, 2007; Isaac, 2007; Purvis, 2008; Rodrigues *et al.*, 2011; Bennett *et al.*, 2014; Jetz *et al.*, 2014). 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.

Dimension	Richness: <i>How much?</i>	Divergence: <i>How different?</i>	Regularity: <i>How regular?</i>
Definition	How much evolutionary history is associated with a set of tips?	How closely related (on average) are tips within a set?	How evenly is evolutionary history distributed between tips within a set?
Interpretation	<i>What is the total evolutionary history within (or between) assemblages?</i>	<i>How similar are species within (or between) assemblages?</i>	<i>How is similarity distributed within (or between) assemblages?</i>
Example Questions	(i) Evolutionary diversity as dependent variable		
	Is evolutionary history correlated with resource availability? How does compositional similarity decay with geographic distance? Do current protected areas adequately protect evolutionary history?	Is environmental filtering more important in high-elevation communities compared to low-elevation communities? Do geologically unstable regions have more recently diverged species? Where are concentrations of endemic evolutionary diversity?	Does biotic competition drive community structure? What is the relationship between evolutionary history and variation in function?
	(ii) Evolutionary diversity as independent variable		
	Are more diverse communities more productive? Does evolutionary diversity predict the spatial distribution of diversity? Do more diverse communities supply greater ecosystem services?	Are distinct species more invasive relative to community composition? Do island radiations influence bird co-occurrence patterns?	Do patterns of niche space occupancy affect community stability? Does a community with evenly distributed evolutionary history have greater potential to adapt to future habitats?

Fig. 5. Connecting the dimensions framework to ecological questions. Practical definition of each dimension and example questions for each from community ecology, macroecology, and conservation biology. Included are questions for which evolutionary history is considered as an (a) response or (b) predictor of the processes of interest. Column colours correspond to the three dimensions: richness (sum); divergence (mean distance); and regularity (variance).

(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. Weir & Schluter, 2007; Ackerly, 2009), to identify geographical centres of diversification (e.g. Jetz *et al.*, 2012), or the drivers of niche evolution or conservation (e.g. Wiens & Donoghue, 2004; Dormann *et al.*, 2009). 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* MPD_{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 $_{\beta}$ that captures the amount of shared evolutionary history. Figure 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.

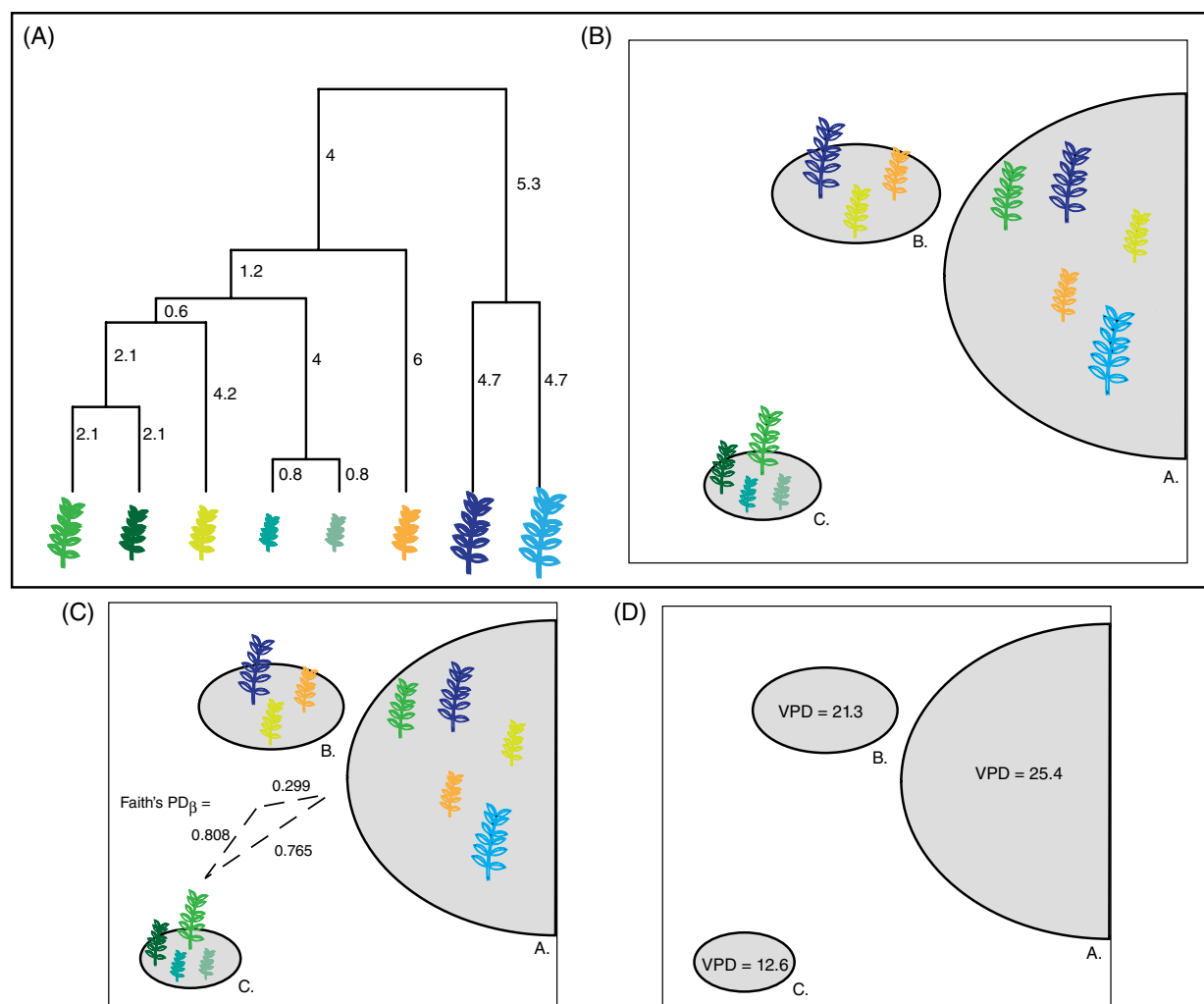


Fig. 6. Example involving the flora of an hypothetical island mainland system (top panel), for which a researcher wishes to choose appropriate phylo-diversity metrics to test how evolutionary diversity varies among the mainland and island sites. See Section V.2. Panel (A) and (B) shows the distribution of species among the sites, and their phylogenetic relatedness. Values on the phylogeny represent hypothetical distances between species (e.g. branch lengths, etc.). Panel (C) shows how evolutionary history is shared between sites (richness metric, β -diversity, Faith's PD_β). Panel (D) shows how evenly evolutionary history is distributed at each site (regularity metric, α -diversity VPD).

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 FORWARD

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.

VIII. ACKNOWLEDGEMENTS

This paper is a joint effort of the sPhy working group and an outcome of a workshop kindly supported by sDiv, the Synthesis Centre of the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig (DFG FZT 118). C.M.T., T.J.D., M.W.C. and A.O.M. acknowledge NSERC Canada; M.W.C. thanks the endowed TD Professor of Urban Forest Conservation and Biology chair. S.B.C. was funded by a postdoctoral grant from Fundação para a Ciência e a Tecnologia (FCT) (SFRH/BPD/74423/2010), and through the project PTDC/BIA-BIC/118624/2010-FCOMP-01-0124-FEDER-019676, supported by Fonds Européen de Développement Économique et Régional (FEDER) funds through the Operational Programme for Competitiveness Factors (COMPETE) and by National Funds through FCT. M.R.H. is supported by the Netherlands Organisation for Scientific Research (858.14.040). F.M. received funding from the European Research Council under the European Community's Seventh Framework Programme FP7/2007-2013 Grant Agreement no. 281422 (TEEMBIO). S.A.F. acknowledges funding by the LOEWE Zentrum AdRIA funding program, of Hesse's Ministry of Higher Education, Research, and the Arts.

IX. REFERENCES

- References marked with asterisk have been cited within the supporting information*
- ACKERLY, D. (2009). Conservatism and diversification of plant functional traits: evolutionary rates versus phylogenetic signal. *Proceedings of the National Academy of Sciences of the United States of America* **106**, 19699–19706.
- ALLEN, B. L., KON, M. & BAR-YAM, Y. (2009). A new phylogenetic diversity measure generalizing the shanno index and its application to phyllostomid bats. *American Naturalist* **174**, 236.
- BARKER, G. M. (2002). Phylogenetic diversity: a quantitative framework for measurement of priority and achievement in biodiversity conservation. *Biological Journal of the Linnean Society* **76**, 165–194.

- BECK, J., BALLESTEROS-MEJIA, L., BUCHMANN, C. M., DENGLE, J., FRITZ, S. A., GRUBER, B., HOF, C., JANSSEN, F., KNAPP, S. & KREFT, H. (2012). What's on the horizon for macroecology? *Ecography* **35**, 673–683.
- BENNETT, J. R., ELLIOTT, G., MELLISH, B., JOSEPH, L. N., TULLOCH, A. I. T., PROBERT, W. J. M., DI FONZO, M. M. I., MONKS, J. M., POSSINGHAM, H. P. & MALONEY, R. (2014). Balancing phylogenetic diversity and species numbers in conservation prioritization, using a case study of threatened species in New Zealand. *Biological Conservation* **174**, 47–54.
- BLOMBERG, S. P., GARLAND, T. & IVES, A. R. (2003). Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* **57**, 717–745.
- BRYANT, J. A., LAMANNA, C., MORLON, H., KERKHOFF, A. J., ENQUIST, B. J. & GREEN, J. L. (2008). Microbes on mountainsides: contrasting elevational patterns of bacterial and plant diversity. *Proceedings of the National Academy of Sciences of the United States of America* **105**, 11505–11511.
- CADOTTE, M. W. (2013). Experimental evidence that evolutionarily diverse assemblages result in higher productivity. *Proceedings of the National Academy of Sciences of the United States of America* **110**, 8996–9000.
- CADOTTE, M. W., CAVENDER-BARES, J., TILMAN, D. & OAKLEY, T. H. (2009). Using phylogenetic, functional and trait diversity to understand patterns of plant community productivity. *PLoS One* **4**, e5695.
- CADOTTE, M. W. & DAVIES, T. J. (2010). Rarest of the rare: advances in combining evolutionary distinctiveness and scarcity to inform conservation at biogeographical scales. *Diversity and Distributions* **16**, 376–384.
- CADOTTE, M. W., DAVIES, T. J., REGETZ, J., KEMBEL, S. W., CLELAND, E. & OAKLEY, T. H. (2010). Phylogenetic diversity metrics for ecological communities: integrating species richness, abundance and evolutionary history. *Ecology Letters* **13**, 96–105.
- CAVENDER-BARES, J., KOZAK, K. H., FINE, P. V. A. & KEMBEL, S. W. (2009). The merging of community ecology and phylogenetic biology. *Ecology Letters* **12**, 693–715.
- CAVENDER-BARES, J. & WILCZEK, A. (2003). Integrating micro- and macroevolutionary processes in community ecology. *Ecology* **84**, 592–597.
- CHAO, A., CHIU, C.-H. & JOST, L. (2010). Phylogenetic diversity measures based on Hill numbers. *Philosophical Transactions of the Royal Society, B: Biological Sciences* **365**, 3599–3609.
- CHAO, A., CHIU, C.-H. & JOST, L. (2014). Unifying species diversity, phylogenetic diversity, functional diversity, and related similarity and differentiation measures through Hill numbers. *Annual Review of Ecology, Evolution, and Systematics* **45**, 297–324.
- CHEN, J., BITTINGER, K., CHARLSON, E. S., HOFFMANN, C., LEWIS, J., WU, G. D., COLLMAN, R. G., BUSHMAN, F. D. & LI, H. (2012). Associating microbiome composition with environmental covariates using generalized UniFrac distances. *Bioinformatics* **28**, 2106–2113.
- CHIU, C.-H., JOST, L. & CHAO, A. (2014). Phylogenetic beta diversity, similarity, and differentiation measures based on Hill numbers. *Ecological Monographs* **84**, 21–44.
- CLARKE, K. & WARWICK, R. (1998). Quantifying structural redundancy in ecological communities. *Oecologia* **113**, 278–289.
- CLARKE, K. & WARWICK, R. (2001). A further biodiversity index applicable to species lists: variation in taxonomic distinctness. *Marine Ecology Progress Series* **216**, 265–278.
- COLLESS, D. (1982). Review of phylogenetics: the theory and practice of phylogenetic systematics. *Systematic Zoology* **31**, 100–104.
- CONNOLLY, J., CADOTTE, M. W., BROPHY, C., DOOLEY, Á., FINN, J., KIRWAN, L., ROSCHER, C. & WEIGELT, A. (2011). Phylogenetically diverse grasslands are associated with pairwise interspecific processes that increase biomass. *Ecology* **92**, 1385–1392.
- CROZIER, R. H. (1992). Genetic diversity and the agony of choice. *Biological Conservation* **61**, 11–15.
- DAVIES, T. J. & BUCKLEY, L. B. (2011). Phylogenetic diversity as a window into the evolutionary and biogeographic histories of present-day richness gradients for mammals. *Philosophical Transactions of the Royal Society, B: Biological Sciences* **366**, 2414–2425.
- DAVIES, T. J. & CADOTTE, M. W. (2011). Quantifying biodiversity—does it matter what we measure?. In *Biodiversity Hotspots* (eds F. E. ZACHOS and J. C. HABEL), pp. 43–60. Springer, Heidelberg.
- DEHLING, D., FRITZ, S. A., TOPFER, T. & PACKERT, M. (2014). Functional and phylogenetic diversity and assemblage structure of frugivorous birds along an elevational gradient in the tropical Andes. *Ecography* **37**, 1047–1055.
- DORMANN, C. F., GRUBER, B., WINTER, M. & HERRMANN, D. (2009). Evolution of climate niches in European mammals? *Biological Letters* **6**, 229–232.
- FAITH, D. P. (1992). Conservation evaluation and phylogenetic diversity. *Biological Conservation* **61**, 1–10.
- FAITH, D. P. (2008). *Phylogenetic Diversity and Conservation*. Oxford University Press, New York.
- FOREST, F., GRENYER, R., ROUGET, M., DAVIES, T. J., COWLING, R. M., FAITH, D. P., BALMFORD, A., MANNING, J., PROCHES, S., VAN DER BANK, M., REEVES, G., HEDDERSON, T. A. J. & SAVOLAINEN, V. (2007). Preserving the evolutionary potential of floras in biodiversity hotspots. *Nature* **445**, 757–760.
- FRECKLETON, R. P., HARVEY, P. H. & PAGEL, M. (2002). Phylogenetic analysis and comparative data: a test and review of evidence. *The American Naturalist* **160**, 712–726.
- FRITZ, S. A. & RAHBEK, C. (2012). Global patterns of amphibian phylogenetic diversity. *Journal of Biogeography* **39**, 1373–1382.
- GERHOLD, P., CAHILL, J. F. JR., WINTER, M., BARTISH, I. & PRINZING, A. (2015). Phylogenetic patterns are not proxies of community assembly mechanisms (they are far better). *Functional Ecology* **29**, 600–614.
- GERHOLD, P., PÄRTEL, M., TACKENBERG, O., HENNEKENS, S. M., BARTISH, I., SCHAMINÉE, J. H., FERGUS, A. J., OZINGA, W. A. & PRINZING, A. (2011). Phylogenetically poor plant communities receive more alien species, which more easily coexist with natives. *The American Naturalist* **177**, 668–680.
- HARDY, O. J. & JOST, L. (2008). Interpreting and estimating measures of community phylogenetic structuring. *Journal of Ecology* **96**, 849–852.
- HARDY, O. J. & SENTERRE, B. (2007). Characterizing the phylogenetic structure of communities by an additive partitioning of phylogenetic diversity. *Journal of Ecology* **95**, 493–506.
- HARMON, L. J., WEIR, J. T., BROCK, C., GLOR, R. E. & CHALLENGER, W. (2008). GEIGER: investigating evolutionary radiations. *Bioinformatics* **24**, 129–131.
- HARVEY, P. H. & PAGEL, M. (1991). *The Comparative Method in Evolutionary Biology*. Oxford University Press, Oxford.
- HEARD, S. B. & COX, G. H. (2007). The shapes of phylogenetic trees of clades, faunas, and local assemblages: exploring spatial pattern in differential diversification. *The American Naturalist* **169**, E107–E118.
- HELMUS, M. R., BLAND, T. J., WILLIAMS, C. K. & IVES, A. R. (2007). Phylogenetic measures of biodiversity. *The American Naturalist* **169**, E68–E83.
- HELMUS, M. R., KELLER, W., PATERSON, M. J., YAN, N. D., CANNON, C. H. & RUSAK, J. A. (2010). Communities contain closely related species during ecosystem disturbance. *Ecology Letters* **13**, 162–174.
- HILL, M. O. (1973). Diversity and evenness: a unifying notation and its consequences. *Ecology* **54**, 427–431.
- ISAAC, N. J. B. (2007). Mammals on the edge: conservation priorities based on threat and phylogeny. *PLoS One* **2**, e296.
- IVES, A. R. & HELMUS, M. R. (2010). Phylogenetic metrics of community similarity. *The American Naturalist* **176**, E128–E142.
- IZSÁK, J. & PAPP, L. (2000). A link between ecological diversity indices and measures of biodiversity. *Ecological Modelling* **130**, 151–156.
- IZSÁK, J. & SZEIDL, L. (2002). Quadratic diversity: its maximization can reduce the richness of species. *Environmental and Ecological Statistics* **9**, 423–430.
- JETZ, W., THOMAS, G., JOY, J., HARTMANN, K. & MOOERS, A. (2012). The global diversity of birds in space and time. *Nature* **491**, 444–448.
- JETZ, W., THOMAS, G., JOY, J., REDDING, D. W., HARTMANN, K. & MOOERS, A. O. (2014). Global distribution and conservation of evolutionary distinctness in birds. *Current Biology* **24**, 919–930.
- JIN, L. S., CADOTTE, M. W. & FORTIN, M.-J. (2015). Phylogenetic turnover implicates niche conservatism in montane plant species. *Journal of Ecology* **103**, 742–749.
- JOST, L. (2006). Entropy and diversity. *Oikos* **113**, 363–375.
- JOST, L. (2007). Partitioning diversity into independent alpha and beta components. *Ecology* **88**, 2427–2439.
- KELLY, S., GRENYER, R. & SCOTLAND, R. W. (2014). Phylogenetic trees do not reliably predict feature diversity. *Diversity and Distributions* **20**, 600–612.
- KEMBEL, S. W., COWAN, P. D., HELMUS, M. R., CORNWELL, W. K., MORLON, H., ACKERLY, D. D., BLOMBERG, S. P. & WEBB, C. O. (2010). Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* **26**, 1463–1464.
- KRAFT, N. J., VALENCIA, R. & ACKERLY, D. D. (2008). Functional traits and niche-based tree community assembly in an Amazonian forest. *Science* **322**, 580–582.
- LEINSTER, T. & COBBOLD, C. A. (2012). Measuring diversity: the importance of species similarity. *Ecology* **93**, 477–489.
- LOZUPONE, C. A., HAMADY, M., KELLEY, S. T. & KNIGHT, R. W. (2007). Quantitative and qualitative beta diversity measures lead to different insights into factors that structure microbial communities. *Applied and Environmental Microbiology* **73**, 1576–1578.
- LOZUPONE, C. A. & KNIGHT, R. W. (2005). UniFrac: a new phylogenetic method for comparing microbial communities. *Applied and Environmental Microbiology* **71**, 8228–8235.
- MACARTHUR, R. H. & WILSON, E. O. (1967). *The Theory of Island Biogeography*. Princeton University Press, Princeton.
- MACE, G. M., GITTLEMAN, J. L. & PURVIS, A. (2003). Preserving the tree of life. *Science* **300**, 1707–1709.
- MAYFIELD, M. M. & LEVINE, J. M. (2010). Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology Letters* **13**, 1085–1093.
- MILLER, E. T., ZANNE, A. E. & RICKLEFS, R. E. (2013). Niche conservatism constrains Australian honeyeater assemblages in stressful environments. *Ecology Letters* **16**, 1186–1194.
- MOUCHE, M. A. & MOUILLOT, D. (2011). Decomposing phylogenetic entropy into α , β and γ components. *Biological Letters* **7**, 205–209.
- MOUILLOT, D., MASON, N. W., DUMANY, O. & WILSON, J. B. (2005). Functional regularity: a neglected aspect of functional diversity. *Oecologia* **142**, 353–359.

- MOUQUET, N., DEVICTOR, V., MEYNARD, C. N., MUNOZ, F., BERSIER, L. F., CHAVE, J., COUTERON, P., DALECKY, A., FONTAINE, C. & GRAVEL, D. (2012). Ecophylogenetics: advances and perspectives. *Biological Reviews* **87**, 769–785.
- NARWANI, A., ALEXANDROU, M. A., OAKLEY, T. H., CARROLL, I. T. & CARDINALE, B. J. (2013). Experimental evidence that evolutionary relatedness does not affect the ecological mechanisms of coexistence in freshwater green algae. *Ecology Letters* **16**, 1373–1381.
- NIPPERESS, D. A., FAITH, D. P. & BARTON, K. (2010). Resemblance in phylogenetic diversity among ecological assemblages. *Journal of Vegetation Science* **21**, 809–820.
- *PARADIS, E., CLAUDE, J. & STRIMMER, K. (2004). APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* **20**, 289–290.
- PAVOINE, S. & BONSAI, M. (2011). Measuring biodiversity to explain community assembly: a unified approach. *Biological Reviews* **86**, 792–812.
- PAVOINE, S., GASC, A., BONSAI, M. & MASON, N. W. (2013). Correlations between phylogenetic and functional diversity: mathematical artefacts or true ecological and evolutionary processes. *Journal of Vegetation Science* **24**, 781–793.
- *PAVOINE, S. & IZSÁK, J. (2014). New biodiversity measure that includes consistent interspecific and intraspecific components. *Methods in Ecology and Evolution* **5**, 165–172.
- PAVOINE, S., LOVE, M. S. & BONSAI, M. B. (2009). Hierarchical partitioning of evolutionary and ecological patterns in the organization of phylogenetically-structured species assemblages: application to rockfish (genus: *Sebastes*) in the Southern California Bight. *Ecology Letters* **12**, 898–908.
- PAVOINE, S., OLLIER, S. & PONTIER, D. (2005). Measuring diversity from dissimilarities with Rao's quadratic entropy: are any dissimilarities suitable? *Theoretical Population Biology* **67**, 231–239.
- PAVOINE, S. & RICOTTA, C. (2014). Functional and phylogenetic similarity among communities. *Methods in Ecology and Evolution* **5**, 666–675.
- PEARSE, W. D., CADOTTE, M. W., CAVENDER-BARES, J., IVES, A. R., TUCKER, C. M., WALKER, S. & HELMUS, M. R. (2015). pez: phylogenetics for the environmental sciences. *Bioinformatics*, btv277.
- PEARSE, W. D., CAVENDER-BARES, J., PURVIS, A. & HELMUS, M. R. (2014). Metrics and models of community phylogenetics. In *Modern Phylogenetic Comparative Methods and Their Application in Evolutionary Biology* (ed L. Z. GARAMSZEGI), pp. 451–454. Springer-Verlag, Berlin.
- PIGOT, A. L. & ETIENNE, R. S. (2015). A dynamic null model for phylogenetic community structure. *Ecology Letters* **18**, 153–163.
- PURSCHE, O., SCHMID, B., SYKES, M. T., POSCHLOD, P., MICHALSKI, S. G., DURKA, W., KUHN, I., WINTER, M. & PRENTICE, H. C. (2013). Contrasting changes in taxonomic, phylogenetic and functional diversity during a long-term succession: insights into assembly processes. *Journal of Ecology* **101**, 857–866.
- PURVIS, A. (2008). Phylogenetic approaches to the study of extinction. *Annual Review of Ecology, Evolution, and Systematics* **39**, 301–319.
- PURVIS, A., AGAPOW, P. M., GITTLEMAN, J. L. & MACE, G. M. (2000). Nonrandom extinction and the loss of evolutionary history. *Science* **288**, 328–330.
- PURVIS, A., FRITZ, S. A., RODRIGUEZ, J., HARVEY, P. H. & GRENYER, R. (2011). The shape of mammalian phylogeny: patterns, processes and scales. *Philosophical Transactions of the Royal Society, B: Biological Sciences* **366**, 2462–2477.
- PYBUS, O. & HARVEY, P. H. (2000). Testing macro-evolutionary models using incomplete molecular phylogenies. *Proceedings of the Royal Society B: Biological Sciences* **267**, 2267–2272.
- RAO, R. C. (1982). Diversity and dissimilarity coefficients: a unified approach. *Theoretical Population Biology* **21**, 24–43.
- REDDING, D. W. (2003). *Incorporating genetic distinctness and reserve occupancy into a conservation prioritisation approach*. Masters Thesis: University of East Anglia, Norwich.
- RICOTTA, C. (2007). A semantic taxonomy for diversity measures. *Acta Biotheoretica* **55**, 23–33.
- RODRIGUES, A. S. L., BROOKS, T. M. & GASTON, K. J. (2005). Integrating phylogenetic diversity in the selection of priority areas for conservation: does it make a difference?. In *Phylogeny and Conservation* (eds A. PURVIS, J. L. GITTLEMAN and T. M. BROOKS), pp. 101–199. Cambridge University Press, Cambridge.
- RODRIGUES, A. S. L., GRENYER, R., BAILLIE, J. E. M., BININDA-EMONDS, O. R. P., GITTLEMAN, J. L., HOFFMANN, M., SAFI, K., SCHIPPER, J., STUART, S. N. & BROOKS, T. M. (2011). Complete, accurate, mammalian phylogenies aid conservation planning, but not much. *Philosophical Transactions of the Royal Society of London B* **1579**, 2652–2660.
- ROSAUER, D., LAFFAN, S. W., CRISP, M. D., DONNELLAN, S. C. & COOK, L. G. (2009). Phylogenetic endemism: a new approach for identifying geographical concentrations of evolutionary history. *Molecular Ecology* **18**, 4061–4072.
- ROSAUER, D. F. & MOOERS, A. O. (2013). Nurturing the use of evolutionary diversity in nature conservation. *Trends in Ecology & Evolution* **28**, 322–323.
- SAFI, K., ARMOUR-MARSHALL, K., BAILLIE, J. E. M. & ISAAC, N. J. B. (2013). Global patterns of evolutionary distinct and globally endangered amphibians and mammals. *PLoS One* **8**, e63582.
- SCHNEIDER, S. M. (2012). A metric of biodiversity that integrates abundance, phylogeny, and function. *Oikos* **121**, 1191–1202.
- SCHWEIGER, O., KLOTZ, S., DURKA, W. & KUHN, I. (2008). A comparative test of phylogenetic diversity indices. *Oecologia* **157**, 485–495.
- SRIVASTAVA, D. S., CADOTTE, M. W., MACDONALD, A. A. M., MARUSHIA, R. G. & MIROTCHEV, N. (2012). Phylogenetic diversity and the functioning of ecosystems. *Ecology Letters* **15**, 637–648.
- SWENSON, N. G. (2011). Phylogenetic beta diversity metrics, trait evolution and inferring the functional beta diversity of communities. *PLoS One* **6**, e21264.
- THUILLER, W., LAVERGNE, S., ROQUET, C., BOULANGEAT, I., LAFOURCADE, B. & ARAUJO, M. B. (2011). Consequences of climate change on the tree of life in Europe. *Nature* **470**, 531–534.
- TUCKER, C. M. & CADOTTE, M. W. (2013). Unifying measures of biodiversity: understanding when richness and phylogenetic diversity should be congruent. *Diversity and Distributions* **19**, 845–854.
- TUCKER, C. M., CADOTTE, M. W., DAVIES, T. J. & REBELO, A. G. (2012). The distribution of biodiversity: linking richness to geographical and evolutionary rarity in a biodiversity hotspot. *Conservation Biology* **25**, 593–601.
- UNDERWOOD, A. J. (1997). *Experiments in Ecology*. Cambridge University Press, Cambridge.
- VANE-WRIGHT, R. I., HUMPHRIES, C. J. & WILLIAMS, P. H. (1991). What to protect?—Systematics and the agony of choice. *Biological Conservation* **55**, 235–254.
- VELLEND, M., CORNWELL, W. K., MAGNUSON-FORD, K. & MOOERS, A. O. (2010). Measuring phylogenetic biodiversity. In *Biological Diversity: Frontiers in Measurement and Assessment* (eds A. E. MAGURRAN and B. J. MCGILL), pp. 194–207. Oxford University Press, Oxford.
- VILLÉGER, S., MASON, N. W. & MOUILLOT, D. (2008). New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* **89**, 2290–2301.
- VIOLLE, C., NEMERGUT, D. R., PU, Z. & JIANG, L. (2011). Phylogenetic limiting similarity and competitive exclusion. *Ecology Letters* **14**, 782–787.
- WEBB, C. O. (2000). Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. *The American Naturalist* **156**, 145–155.
- WEBB, C. O., ACKERLY, D. D. & KEMBEL, S. W. (2008). Phylocom: software for the analysis of phylogenetic community structure and trait evolution. *Bioinformatics* **24**, 2098–2100.
- WEBB, C. O., ACKERLY, D. D., MCPEEK, M. A. & DONOGHUE, M. J. (2002). Phylogenies and community ecology. *Annual Review of Ecology, Evolution, and Systematics* **33**, 475–505.
- WEIHER, E. & KEDDY, P. A. (1995). Assembly rules, null models, and trait dispersion: new questions from old patterns. *Oikos* **74**, 159–164.
- WEIR, J. T. & SCHLUTER, D. (2007). The latitudinal gradient in recent speciation and extinction rates of birds and mammals. *Science* **315**, 1574–1576.
- WIENS, J. J. & DONOGHUE, M. J. (2004). Historical biogeography, ecology and species richness. *Trends in Ecology & Evolution* **19**, 639–644.
- WINTER, M., DEVICTOR, V. & SCHWEIGER, O. (2013). Phylogenetic diversity and nature conservation: where are we? *Trends in Ecology & Evolution* **28**, 199–204.
- WINTER, M., SCHWEIGER, O., KLOTZ, S., NENTWIG, W., ANDRIOPOULOS, P., ARIANOUTSOU, M., BASNOU, C., DELIPELIDOU, P., DIDZIULIS, V., HEJDA, M., HULME, P. E., LAMBON, P. W., PERGL, J., PYSEK, P., ROY, D. P. & KUHN, I. (2009). Plant extinctions and introductions lead to phylogenetic and taxonomic homogenization of the European flora. *Proceedings of the National Academy of Sciences of the United States of America* **106**, 21721–21725.

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*.

(Received 18 May 2015; revised 1 December 2015; accepted 14 December 2015)