PART IV

Alternative measures of diversity

CHAPTER 14

Measuring phylogenetic biodiversity

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14.1 Introduction

14.1.1 Overview

Au: 1996 a or b?

Biodiversity has been described as the 'biology of numbers and difference' (Gaston 1996). Because species are different from one another, traditional metrics of biodiversity such as species richness or evenness increase when there are more species or when abundance is more equally apportioned among these species (see Chapters 4 and 5). Not only are species different from one another, the magnitude of these differences varies tremendously depending on the set of species in question. Consider two hypothetical islands, each with only two species of vertebrate animals in equal abundance: two birds in one case and a bird plus a mammal in the other. Both islands have species richness = 2 (for vertebrates) and the same maximal value of species evenness. However, our intuition tells us that a bird plus a mammal represents more biodiversity than does two birds (Purvis & Hector 2000). Metrics of phylogenetic diversity quantify the difference.

Differences among species can be characterized by measuring any number of traits, such as body size and shape, dietary requirements, physiological tolerance of various stressors, etc. (see Chapter 17). Particular traits may be of special interest to a researcher for various reasons, such as their hypothesized role in mediating species interactions (e.g. beak size in birds) or their importance in tolerating different environmental conditions (e.g. leaf thickness in plants). However, the degree of similarity or difference among species will depend strongly on the choice of traits measured, and many traits are only applicable to particular groups of organisms (e.g. photosynthetic rate in plants). A far more general method for quantifying diversity among species is an assessment of the species' evolutionary relationships, in the form of either taxonomy or a phylogeny. Modern phylogenies are derived from DNA-sequence data, which can be acquired for all organisms on the tree of life. The phylogenetic distance between two species is an estimate of the amount of time since the most recent common ancestor of both species, in other words the time that each has evolved independently of the other. While individual traits may show 'convergence', that is, similar values evolving in distantly related lineages, the phylogenetic distance represents a proxy for the magnitude of phenotypic differences (across a large number of traits) expected between any two species (Cavender-Bares et al. 2009).

Biologists have been interested in the phylogenetic component of biodiversity for two main reasons: (i) to explicitly incorporate species differences (via a common currency applicable to all taxa from bacteria to primates), rather than just species numbers, into conservation prioritization and (ii) to yield insights into the structure of ecological communities. In the first case, recognizing that difficult prioritization decisions need to be made concerning the investment of limited resources for conservation, it has been argued that the aim should not be just to protect the greatest number of species possible, but to protect sets of species that are most taxonomically distinct or that represent the greatest possible variety of biological features (Vane-Wright et al. 1991; Faith 1992; Mooers et al. 2005; Isaac et al. 2007). To this end, considerable effort has been aimed at quantifying the evolutionary distinctness (and therefore conservation value) of

individual species, or the 'phylogenetic diversity' of a group of species (Vane-Wright et al. 1991; Faith 1992; Altschul & Lipman 1990; Nixon & Wheeler
Au: 2005 a or b 1992; Pavoine et al. 2005; Redding and Mooers 2006).

In terms of analyses in community ecology, the incorporation of phylogenetic information has a relatively long history. Darwin (1859) first hypothesized that competition should be strongest between close relatives (e.g. congeners), leading subsequent researchers to explore ratios of species-to-genus numbers (or genus-to-family, etc.) as potentially indicative of the role of competition in structuring ecological communities (e.g, Elton 1946). More recently, the same conceptual question has been approached using modern phylogenies, which contain far more information on evolutionary relationships than taxonomic categories (reviewed in Webb et al. (2002), Vamosi et al. (2009), and Cavender-Bares et al. (2009)). If indeed close relatives compete most strongly, local communities should contain species that are relatively distantly related to one another. Alternatively, species membership in a local community might be most constrained by tolerance of abiotic environmental conditions, and if close relatives share similar tolerances, local communities should contain species that are relatively closely related to one another. To test these hypotheses, researchers have employed some of the phylogenetic diversity metrics from the conservation literature and also introduced some additional metrics of their own (Webb et al. 2008).

As applied to issues in both conservation biology and community ecology, phylogenetic diversity has been a topic of tremendous interest in the recent literature. As such, a large number of metrics to quantify phylogenetic diversity have been introduced, and for some subsets of these metrics analyses have been done to assess their redundancy or the degree to which they meet certain pre-set
Au: 2005 a or b? criteria (e.g. Pavoine et al. 2005; Kraft et al. 2007; Hardy 2008; Schweiger et al. 2008). In this chapter, we aim to provide guidance to researchers and practitioners for selecting particular metrics and for interpreting published results based on different metrics. After providing some important definitions (see Box 14.1) and a conceptual overview, we will first offer a categorization of metrics found in the literature, according to the functional form of the calculation and the nature of the input data (e.g. species presence–absence vs abundance data). Next we report results of simulation analyses, in which artificial communities were created under different assumptions about the processes by which phylogenies arise, and by which membership and abundance in local communities are determined. The goals here were to assess quantitative relationships among different metrics (e.g. which behave similarly?) and to assess the sensitivity of different metrics to underlying evolutionary and ecological processes. We will then discuss the qualitative and quantitative relationships among metrics and how researchers can go about choosing metrics for different purposes.

14.1.2 Approaching the study of phylogenetic diversity

The choice of metrics of phylogenetic diversity in empirical studies is entirely under the control of the researcher, but will be influenced by three key aspects of a particular system, which are typically not (or only partially) under a researcher's control: underlying processes, related patterns (other than phylogenetic diversity), and data constraints.

A variety of evolutionary and ecological processes influence the values of phylogenetic diversity metrics, either indirectly or directly. Macroevolutionary processes will create patterns that matter a great deal for phylogenetic community structure and the choice of metric. For example, the extent to which speciation is 'ecological' (i.e. driven by divergent selection) will affect the shape of the phylogeny and the phylogenetic conservatism of different traits. Both of these will in turn affect the extent to which species coexistence may be influenced by relatedness (Mooers & Heard 1997; Kembel & Hubbell 2006; Kraft et al. 2007; McPeek 2007, 2008). Ecological processes influencing community assembly, such as environmental constraints on fitness or competition for resources, will also influence phylogenetic diversity metrics (Webb et al. 2002).

Some empirical patterns, including the distribution of species numbers and abundances among sites, and the degree of balance in a phylogenetic tree (see Box 14.1), may influence the range of

Box 14.1 Definitions of attributes of phylogenetic trees

A rooted phylogenetic tree summarizes hypothesized evolutionary relationships among species or other biological units such as lineages within species. Phylogenetic trees can be estimated using a variety of methods (see Felsenstein 2004), the details of which are beyond the scope of this chapter. For the purposes of this discussion we will assume that the **tips** (sometimes referred to as 'leaves') of the tree represent species (see Figure Box 14.1). A **node** represents the most recent common ancestor of all species descending from that point in the tree (i.e. where branches split) and the **root node** (often referred to simply as the root) is a single point from which it has been inferred that all species descend, thus giving the entire tree temporal directionality. The simplest type of phylogenetic tree represents only the topology, with no information on the lengths of branches connecting the nodes (e.g. taxonomies based on morphological data and some types of molecular data). We refer to such trees as **node-based trees**.

A branch in the phylogenetic tree (also referred to as an 'edge' in graph theory), and its associated **branch length**, may represent the accumulation of evolutionary change, in which case the tips may not line up because the rate of evolutionary change is not constant across all branches. Alternatively, branch lengths may be scaled to represent the passage of time, such that all tips line up in the same place. Each of these two types of phylogenetic trees are considered **additive**, and the latter type is additionally called **ultrametric** (all distances from root to tip are the same). We refer to trees with quantitative branch lengths as **distance-based trees**.

Nodes are usually bifurcating, such that lineages split into two. **Polytomies** are nodes where this is not the case, and the lineage splits into three or more. This arises most commonly due to data limitations. The **degree** of a node is the number of branches, both ancestral and descendant, connected to that node (three for a bifurcating node).

The shape of phylogenetic trees can be characterized by two key properties: their degree of balance and the degree to which divergence events happened predominantly early (divergence decelerating) or late (divergence accelerating) during the evolution of the group (the latter is characterized by the γ statistic). In a perfectly **balanced tree**, all tips are separated from the root by the same number of nodes, which is equivalent to saying that all lineages bifurcate the same number of times. In a perfectly **imbalanced tree**, one lineage descending from each node connects directly to a tip with no further bifurcations. In a tree with low γ divergence events are concentrated early during the evolution of the group, and vice versa.

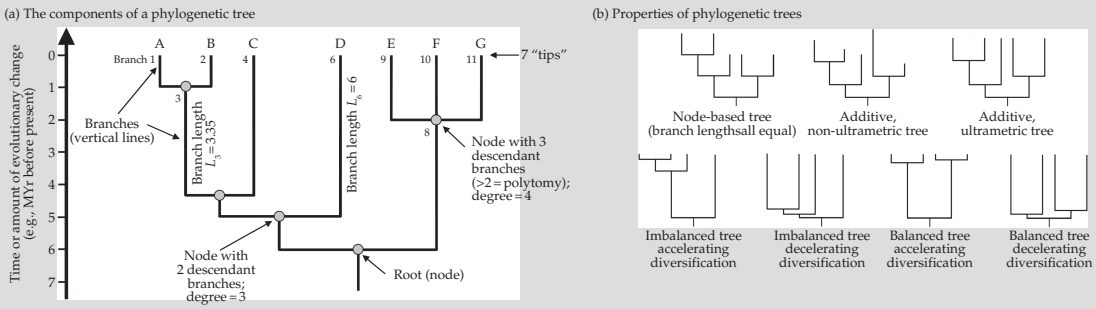

Figure Box 14.1 The components of a phylogenetic tree (a), and different representations and shapes of trees illustrating their properties (b).

possible values different metrics can take. The same factors may affect the degree to which particular metrics are distinct from others (e.g. Redding et al. 2008; Schweiger et al. 2008). These 'other' patterns may be influenced by some of the same processes as phylogenetic diversity, but they can be quantified independently and may on their own influence phylogenetic diversity metrics regardless of what processes created them.

Finally, there may be data constraints. Specifically, the nature of the phylogenetic information may only allow representation of the topology of a phylogenetic tree, or it may allow estimation of branch lengths connecting nodes in the tree (see

Box 14.1). In addition, data might be available only on the presence or absence of species in particular places without relative abundances. Unlike the processes and patterns mentioned under the first two considerations, these constraints are, in theory, under the control of the researcher, but, in practice, many studies are based on existing data, which may impose such constraints.

In this chapter we do not discuss the first consideration of the link between process and pattern (e.g. *why* do locally co-occurring species represent a non-random subset of a regional phylogeny?), which has been thoroughly reviewed elsewhere (Webb et al. 2002; McPeek 2008; Vamosi et al. 2009; Cavender-Bares et al. 2009). Instead we focus on the practical issue of what quantitative information is reflected in different metrics and on the latter considerations of how properties of the existing data may influence the choice or interpretation of different metrics. We restrict our attention to calculations of phylogenetic diversity within focal sets of species or local communities, rather than partitioning diversity among hierarchical levels (e.g. α, β, γ; Graham & Fine 2008).

14.2 State of the field

All empirical studies of phylogenetic diversity begin with an estimated phylogeny for the group of species of interest. The scope of this phylogeny varies—it may include all known species across some broader region (e.g. all birds of South America or of the world) or only those species present in particular surveyed areas (e.g. the birds found in a survey of five tropical forest plots). For convenience, we refer to these two options as a 'regional' phylogeny and a 'local' phylogeny, respectively. It is then typically of interest to quantify the relative magnitude of phylogenetic diversity among focal subsets of species, which may be defined as those co-occurring in a local area (e.g. the birds in one tropical forest plot) or a candidate set of species proposed for special conservation attention (e.g. the bird species listed as endangered in Brazil). We refer to the portion of the regional or local phylogeny that includes only the focal subset of species as the 'subset' phylogeny.

Two qualitatively different types of metrics of phylogenetic diversity have been developed. We refer to type I metrics as those that begin by calculating a distinctness score for all species in a regional phylogeny and then calculating some function of these scores (typically the sum) for particular focal subsets of species to yield a metric of phylogenetic diversity. Type II metrics start with a local phylogeny (or possibly a regional phylogeny), and for a focal subset of species they depend only on properties of the subset phylogeny. Type I metrics have been used largely in conservation biology, while community ecologists have mostly employed type II metrics, but some have been used in both fields. For type I metrics, the motivation behind first calculating fixed individual species scores, rather than effectively allowing these to depend on the focal species set (as in type II metrics), is to permit individual species to be ranked in a way that does not depend on the status of other species (e.g. whether or not they are already protected).

Type I metrics of phylogenetic diversity are calculated in two stages. First, an index of distinctness is calculated for each species and second, these values are entered into a separate function to summarize the scores for a focal subset of species. In stage one, five different indices of species' distinctness have been used in the literature: taxonomic distinctness (TD), species originality (SO), pendant edge (PE), species evolutionary history (SEH), and originality of species within a set (OSS; see Table 14.1). The first two (TD, SO) are based only on node-based phylogenetic trees, and the other three (PE, SEH, OSS) are based on distance-based trees. In stage two, the most common function is simply the sum, which is obviously intended to incorporate species richness into the metric (all else being equal, more species represent more phylogenetic diversity). With species' abundance data it is also possible to apply a procedure similar to rarefaction (see Chapter 4) to yield an index that reflects the expected sum in a sample of x individuals chosen randomly from the community (Ricotta 2004), but this is seldom used in the literature. In theory it is also possible to calculate the mean of distinctness values, although this is also seldom done.

At first glance, the number of different type II metrics in the literature appears rather large, but the

Table 14.1 Indices of species distinctness for use in type I metrics of phylogenetic diversity.

Index	Description	Reference
Taxonomic distinctness (*TD*)	Reciprocal of number of nodes between species and root of tree (standardized by dividing by the sum of these scores across species and multiplying by 100)	Vane-Wright et al. (1991)
	Modification: To account for polytomies, count number of descendants at each node rather than number of nodes	May (1990)
Species originality (*SO*)	Assign each node in a tree a value of 1 if more species descend from that node than its sister node, and 0 otherwise; sum the values at the nodes between a species and the root; smaller values indicate greater distinctness	Nixon & Wheeler (1992)
	Modification: As above, but assign each node a value equal to the number of species that descend from that node Referred to as weighted species originality (*WSO*)	Nixon & Wheeler (1992)
Pendant edge (*PE*)	The length of the branch connecting a species to the rest of the regional tree	Altschul & Lipman (1990)
Species evolutionary history (*SEH*)	The portion of a phylogenetic tree attributable to a species; shared branches are apportioned equally among descendant lineages ('equal splits'), for example in a tree with no polytomies, the portion of a branch that is assigned to a species that is *n* nodes away from that branch is equal to $1/2^n$.	Redding & Mooers (2006)
	Modification: As above, but shared branches are apportioned equally among descendant species ('fair proportions', *SEH*_fair) Referred to as species evolutionary distinctiveness	Redding et al. (2008)
Originality of species within a set (*OSS*)	Values for each species that 'maximize the expected dissimilarity between two species randomly drawn from the set' There is no simpler way of describing this metric	Pavoine et al. (2005b)

Capitalized short forms are used in the text. Equations are not shown because in most cases either verbal descriptions are very simple (*TD*, *PE*) or it is not possible to write an equation that clarifies any further the meaning of the metric (*SO*, *OSS*). Original publications can be consulted for details.

distinction between many of these is based only on the nature of the input data rather than the equation into which the data enter. Two data characteristics in particular allow different sets of metrics to be aggregated. First is the nature of the phylogenetic tree (see Box 14.1). If only the tree topology has been estimated, 'distances' within the tree are quantified simply by counting the nodes along the path of interest (e.g. between two tips). Quantitative branch lengths allow distances to take a continuous range of values. Metrics based on counting nodes are effectively special cases of distance-based metrics in which all branch lengths are set equal to one. Second is the nature of species abundance data. There may be quantitative estimates of species' abundances, or only of species' presence or absence; metrics based on the latter are special cases of the former in which each species has the same abundance. Four distinct kinds of type II metric have been proposed (described in Table 14.2). Each of these can incorporate abundance data if available, and may also be expressed as deviations from expected values based on null models.

14.2.1 Null models

Any of the metrics we have described thus far can be expressed in their raw form or as deviations from an expectation derived from a null model. In practice, null models have not been employed in the conservation literature, but are commonplace in the community ecology literature. In addition, null models are almost always used only with presence–absence data at the smallest scale. The

Table 14.2 Type II metrics of phylogenetic diversity.

Metric	Presence–absence (PA) version	Abundance-weighted (AW) version	Equation	References
Phylogenetic diversity (*PD*)	Sum of all branch lengths in the portion of a phylogenetic tree connecting the focal set of species (*PD*, *PDn*)	For the subset tree, the number of branches multiplied by the weighted mean branch length, with weights equal to the average abundance of species sharing that branch* (*PDaw*, *PDnaw*)	$B \times \frac{\sum_{i}^{B} L_i A_i}{\sum_{i}^{B} A_i}$	PA: Faith (1992) AW: Barker (2002)
Mean phylogenetic distance (*MPD*)	Mean phylogenetic distance between each pair of species in the focal set (*MPD*, *MPDn*)	Mean phylogenetic distance between pairs of individuals (or other units of abundance), excluding same-species pairs (*MPDaw*, *MPDnaw*)	$\frac{\sum\sum_{m<n} d_{mn}a_m a_n}{\sum\sum_{m<n} a_m a_n}$	PA: Webb (2000) AW: Warwick & Clarke (1995)
		Modification: Mean phylogenetic distance between pairs of individuals (or other units of abundance), including same-species pairs	$\frac{\sum_m \sum_n d_{mn}a_m a_n}{\sum_m \sum_n a_m a_n}$	Rao (1982); Warwick & Clarke (1995)
Sum of phylogenetic distances (*SPD*)‡	Sum of phylogenetic distances between each pair of species Equivalent to *MPD* multiplied by the number of species pairs	Abundance-weighted *MPD* multiplied by the number of species pairs	$\left(\frac{S(S-1)}{2}\right) \frac{\sum\sum_{m<n} d_{mn}a_m a_n}{\sum\sum_{m<n} a_m a_n}$	PA: Crozier (1997); Helmus et al. (2007) AW: none
Mean nearest neighbour distance (*MNND*)	Mean phylogenetic distance from each species to its closest relative in the focal species set (MNND, *MNNDn*)	Weighted mean phylogenetic distance from each species to its closest relative, with weights equal to species' abundance (*MNNDaw*, *MNNDnaw*)	$\sum_{m}^{S} \min(d_{mn})a_m$	PA: Webb (2000) AW: none

Short forms correspond to labels in PCA plots (see Fig. 14.1); *n* = node-based metric. B, number of branches in tree; L_i, length of branch i; A_i, average abundance (measured in any units) of species that share branch i; d_{mn}, phylogenetic distance between species m and n; a_m, abundance of species m (with presence–absence data all species have the same abundance); S, number of species in the focal set; AW, abundance-weighted metric.

*This is our interpretation of how Barker's iterative method (for unrooted trees) would be applied most simply to a rooted tree.

For ultrametric trees, the presence–absence version of *MPD* is equivalent to twice the phylogenetic species variability (*PSV*) metric of Helmus et al. (2007), which was derived as the expected variance among species in a neutrally evolved trait. The phylogenetic species evenness (*PSE*) metric of Helmus et al. is a rescaled version of abundance-weighted *MPD* (both *PSV* and *PSE* are calculated using a phylogenetic tree with branch lengths scaled so that all root-to-tip distances are 1).

‡Helmus et al. (2007) calculate phylogenetic species richness (PSR) by multiplying *MPD* by the number of species, rather than the number of species pairs, although the two options scale monotonically with one another.

principle goal in constructing a null model is to ask what distribution of values is expected for focal sets of species in which there is no phylogenetic structure, but in which all other properties (e.g. species richness) are the same.

Two main classes of null models have been used. First, for a focal set of S species, one can take repeated draws of S species chosen randomly from the regional phylogenetic tree. In essence, this is like shuffling the species identities randomly among tips in the phylogenetic tree. Alternatively, with a species-by-site data matrix, one can repeatedly shuffle the species' presences among sites to essentially randomize which species co-occur while retaining each species' frequency across sites. It is also possible to place a variety of additional constraints on the shuffling procedure, such as retaining both the species richness of each site and the frequency of each species (Gotelli & Graves 1996).

Once a null model has been constructed, the metrics of interest are calculated for each simulated set

of species, and observed values can be expressed either as the number of standard deviations away from the expected mean (Webb et al. 2008) or the probability of obtaining a lower (or higher) value than that observed solely by chance. Since in many cases the distribution of values will depend on species richness, metrics expresses in this way are usually not monotonic transformations of the initial values. For example, phylogenetic diversity (PD) might be equivalent in two different communities with different numbers of species, but the one with fewer species will have a lower null expectation, and therefore the re-expressed value will be higher in the community with fewer species.

14.2.2 Simulation analyses

Different metrics can be compared and evaluated both qualitatively and quantitatively. In terms of qualitative comparisons, a researcher's choice of metric may depend on what information they want reflected in the metric (e.g. species' closest relatives or their full set of relationships), rather than any predetermined quantitative criteria (e.g. sensitivity to a non-random community assembly). Both qualitative and quantitative considerations are addressed in the Prospectus section, and to make quantitative comparisons we conducted a set of simulation analyses. The simulations were aimed at addressing the following three questions: (1) which metrics are redundant with one another, (2) how do metrics compare with respect to their sensitivity to different non-random community assembly processes, and (3) how does tree shape influence the answers to questions 1 and 2?

We simulated sets of species ('communities') under a number of scenarios that vary in the following respects: the degree of balance in the regional phylogenetic tree, the change or lack thereof in diversification rate through time in the regional phylogeny (decelerating or accelerating, according to the 'γ' parameter *sensu*; Pybus & Harvey 2000), the nature of (non)randomness in the community assembly process, and the number of species in the community. All regional phylogenetic trees were rooted, ultrametric, contained 100 species, and were created in five ways: (1) by a pure birth ('Yule') process (constant rate of diversification through time and across all lineages), (2) entirely imbalanced with decelerating diversification, (3) entirely imbalanced with accelerating diversification, (4) entirely balanced, decelerating diversification, and (5) entirely balanced, accelerating diversification. In order to span the range of empirical values of change in diversification rate, we rescaled the branch length of both the balanced and imbalanced trees to match the most extreme observations (measured via the γ statistic; see McPeek 2008). For each tree, we simulated local communities either by randomly selecting species or via algorithms that created phylogenetically clustered or over-dispersed sets of species, with each of the latter done in two ways. For phylogenetic over-dispersion, the first species was chosen randomly and each subsequent species was chosen with a probability proportional to the square root of its average phylogenetic distance to either species (method 1) or individuals (method 2) already in the community. Using the square root of phylogenetic distances approximates the expected trait difference based on a Brownian motion model of trait evolution (Felsenstein 1985). For method 2, the mean phylogenetic distances were calculated by weighting the distance to each already-chosen species by the abundance of that species. Phylogenetically clustered sets of species were created in an identical way, except that the mean phylogenetic distance to already-chosen species or individuals determined the probability of a species *not* being chosen. Abundances were either considered to be equivalent across species (presence–absence based metrics) or drawn from a log-normal distribution and assigned from highest to lowest in the sequence that species were chosen. Sets of species were selected with species richness of 10, 20, 30, or 40. For each of the five tree types, we simulated 500 sets of species for each of the four levels of species richness in each of the five community assembly processes, for a total of 20 000 sets of species.

We focused our analyses on two groups of metrics, which correspond to those of interest to conservation biologists and those of interest to community ecologists. The 'conservation' group consisted of all type I metrics (sums of species distinctness values), plus Faith's (1992) phylogenetic diversity (PD) because type I metrics are often eval-

Table 14.3 Correlations among sums of type I metrics, as well as species richness (*SR*) and phylogenetic diversity (*PD*), for 10000 simulated species sets selected from a pure birth phylogenetic tree. Short forms correspond to those in Table 14.1.

TD	0.92							
SO	0.95	0.91						
WSO	0.94	0.92	0.98					
PE	0.93	0.83	0.91	0.87				
SEH	0.95	0.96	0.94	0.95	0.86			
SEH_fair	0.97	0.96	0.95	0.95	0.87	1.00		
OSS	0.73	0.91	0.76	0.79	0.62	0.88	0.87	
PD	0.87	0.90	0.85	0.86	0.78	0.94	0.94	0.87
	SR	TD	SO	WSO	PE	SEH	SHE_fair	OSS

uated with respect to their ability to capture PD (e.g. Redding et al. 2008). Because community ecologists are typically interested in assessing non-random phylogenetic structure in sets of species, rather than phylogenetic diversity per se, the 'community ecology' group of metrics included only the null-model corrected versions of each type II metric. These were calculated as the number of standard deviations from the mean across randomly assembled communities (described above). In addition, since the value of the summed phylogenetic distance (*SPD*) and the modified mean phylogenetic distance (*MPD*; see Table 14.2) differ from unmodified *MPD* only due to species richness or the species abundance distribution, both of which are accounted for in the null model, the null-model corrected versions of these are redundant. Thus, we focused on the four versions of *PD*, *MPD*, and *MNND*, depending on the combination of node- vs distance-based trees and presence–absence vs abundance data, for a total of 12 metrics in the community ecology group. To calculate these metrics, we drew on publicly available functions in the ape (v2.3), picante (v0.7), and ade4 (v1.4) libraries for R. New phylogenetic functions coded specifically for this analysis are available within the Picante library for R (http://picante.r-forge.r-project.org/).

14.2.3 Simulation results

Correlations among type I metrics, and between these metrics and phylogenetic diversity (*PD*), were typically very high. Principal component analyses for each tree type revealed that the variation among these metrics is essentially one dimensional, with >90% of the variance explained by the first principal component in all cases (figures not shown). Table 14.3 shows the correlation structure among these metrics (as well as species richness) for the pure birth tree, where $r > 0.7$ for all pairwise comparisons except one (for which $r > 0.6$). Correlations among metrics were even higher for all other tree types, with the one exception arising for balanced trees with accelerating diversification. In this case, all species receive highly similar distinctness scores (see example of this tree type in Box 14.1), such that type I sums give virtually identical results to each other and to species richness ($r > 0.99$). However, *PD* varies considerably depending on how many basal clades are included in a given sample of species, such that correlations between *PD* and the type I sums were relatively low ($r \approx 0.45$). For pure birth or balanced trees, correlations of these metrics with species richness were high (mean $r > 0.9$), whereas for imbalanced trees correlations with species richness were considerably lower (mean $r = 0.62$ for decelerating diversification, mean $r = 0.45$ for accelerating diversification).

Type II metrics also gave broadly similar results to one another for pure birth or balanced trees, but not for imbalanced trees (Table 14.4). For pure birth and imbalanced trees, correlations tended to be higher within distance-based or node-based groups of metrics than across these groups (Fig. 14.1). For imbalanced trees the correlations across the two groups were actually negative (Fig. 14.1), a result that can be explained as follows. Commu-

Table 14.4 Correlations of distance-based (*D*) vs. node-based (*N*), and presence-absence (PA) vs. abundance-weighted (AW) versions each of the three main type II metrics, in all cases expressed as deviations from a null model.

	Presence–absence version	Abundance-weighted version	Distances	Nodes	
	D vs. N	D vs. N	PA vs. AW	PA vs. AW	
Metric					
PD	0.79	0.68	0.89	0.85	Pure birth tree
MPD	0.69	0.80	0.91	0.79	
MNND	0.84	0.83	0.88	0.89	
PD	–0.75	–0.55	0.83	0.35	Imbalanced tree
MPD	–0.25	–0.15	0.95	0.84	Decelerating diversification
MNND	–0.10	0.02	0.96	0.53	
PD	–0.68	–0.45	0.86	0.40	Imbalanced tree
MPD	–0.71	–0.69	0.91	0.88	Accelerating diversification
MNND	–0.26	0.05	0.93	0.56	
PD	0.99	0.96	0.92	0.96	Balanced tree
MPD	0.98	0.98	0.95	0.97	Decelerating diversification
MNND	0.99	0.98	0.95	0.95	
PD	0.96	0.93	0.97	0.95	Balanced tree
MPD	0.96	0.97	0.91	0.95	Accelerating diversification
MNND	0.98	0.96	0.92	0.93	

nity assembly was based on a tree with quantitative distances along branches, such that over-dispersed sets of species contain many of the species that connect to the rest of the tree via long branches (early-divergent or 'basal' species). Although these species are relatively distantly related to most others, they are separated from one another by relatively few nodes, such that over-dispersed sets of species actually appear clustered on a node-based tree. For clustered community assembly, if the first species chosen (randomly) is relatively basal, then most other species will be equidistant from the first and therefore have similar probabilities of joining the community next. For the resulting set of species, the value of node-based metrics will actually be higher than when over-dispersed species were chosen during community assembly. This creates the observed negative correlations. Within the distance-based type II metrics (null-model corrected), variation among sets of species was largely one dimensional, with >85% of the variation in each PCA explained by the first axis (Fig. 14.1).

Sensitivity to non-random community assembly processes varied considerably among metrics and among types of phylogenetic trees (Fig. 14.2), with several notable patterns. First, for imbalanced trees, node-based metrics are either insensitive to non-random community assembly or they actually deviate from the null model in the opposite direction than expected (Fig. 14.2b and 14.2c). In particular, over-dispersed communities had *lower* node-based metric values than expected, for the reasons explained above with respect to negative correlations between distance-based and node-based metrics on imbalanced trees.

The amount of variance among species in their phylogenetic distinctness mediated the effect of tree shape on the sensitivity of different metrics. We focus here only on distance-based metrics (the first and third panels from the left in Fig. 14.2). For balanced trees (Fig. 14.2d and 14.2e) there are relatively few basal clades, each with many species, such that overall, variance among species in their phylogenetic distinctness is small. In other words, on balanced trees most species in the phylogeny have very similar distribution of relatedness to other species on the tree and also very similar type I scores. In this evolutionary context, clustered assembly leads to sets of species that may be concentrated in only one of a few clades. In

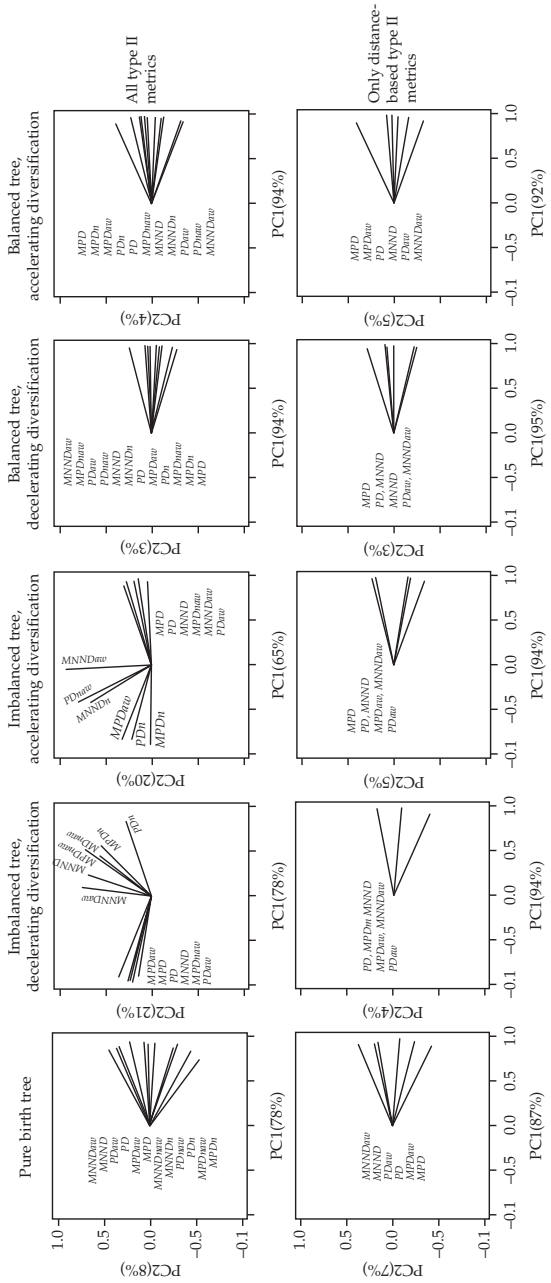

Figure 14.1 Principal component analyses for 12 type II null-model corrected metrics (top row) and for the six of these based on quantitative branch length information (distance-based metrics, bottom row). Labels correspond to those in Table 14.2 and the ordering in lists corresponds to the factor score for the relevant metric on PC2. The percentage variance accounted for by each axis is shown in the axis label.

contrast, randomly assembled communities (which contained at least 10 species) will probably have members from across many or all deep clades, leading to large deviations from random expectation in metrics for clustered communities. In contrast, over-dispersed communities have representatives from many clades just as randomly assembled communities often do, with the non-random selection of species within clades only capable of creating relatively small deviations from random expectation. In imbalanced trees with accelerating diversification (Fig. 14.2c), a relatively small proportion of species are far more phylogenetically distinct than most others, leading to large deviations of over-dispersed communities (which include these species) from random sets of species. With the first species in each simulation chosen randomly, even clustered communities will sometimes include basal species, and after the first species is chosen all more derived species are equally related and have an equal chance of being selected, such that clustered communities deviate from random to a lesser extent than over-dispersed communities despite symmetry in the ecological community assembly processes. In pure birth trees there is sufficiently little variation among species in distinctness that over-dispersion is easier to detect than clustering (Fig. 14.2a), and in imbalanced trees with decelerating diversification over-dispersed and clustered communities show approximately equal deviations from the null expectation.

The final point to make concerning Fig. 14.2 is that in some cases the sensitivity to non-random community assembly varies among metrics. Again focusing only on distance-based metrics, for pure birth or balanced trees, *MPD* was more sensitive than *PD* or *MNND*, while for imbalanced trees the differences among metrics were relatively small.

14.3 Prospectus

14.3.1 Phylogenetic diversity in conservation

To the extent that assigning individual species distinctness scores is itself of value in conservation biology, researchers and practitioners should continue to find type I metrics useful. The sums across

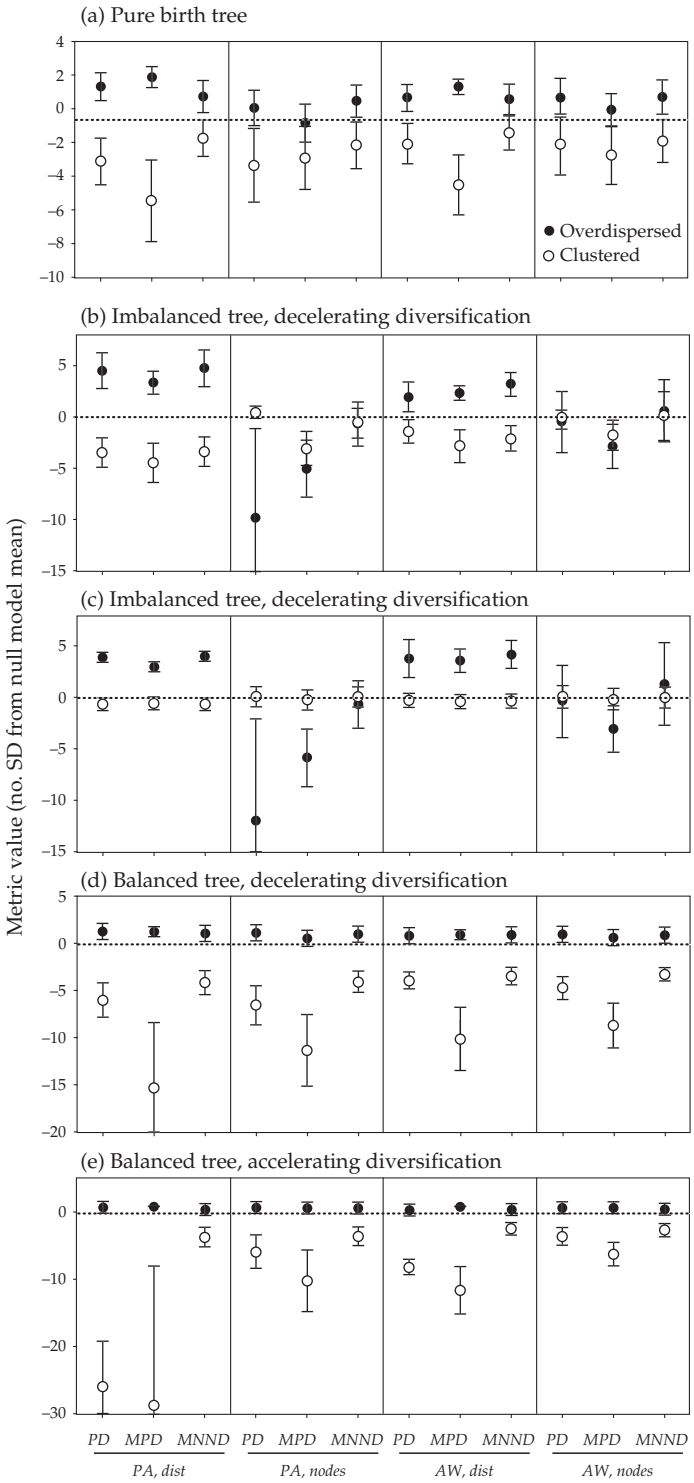

Figure 14.2 Sensitivity of each type II metric to over-dispersed or clustered phylogenetic community assembly processes. The *y*-axis shows the mean ±1 standard deviation for each type II metric, expressed as the number of standard deviations from a null-model mean, in 2000 focal species sets. Results are shown for community assembly processes in which species abundance was not part of the process (results were very similar for both versions of the community assembly process).

species for any of the type I metrics correlate fairly strongly with each other and with *PD*. Distance-based trees more completely represent evolutionary relationships than node-based trees, and since the use of node-based metrics appears to be motivated largely by logistical considerations (i.e. the lack of a distance-based tree), distance-based metrics seem clearly preferable. Within node-based and distance-based metrics, redundancy is quite high ($r > 0.9$ for most pairs of metrics across all tree types). As such, an appropriate criterion for choosing among metrics is their conceptual and mathematical simplicity. For node-based metrics, we recommend the taxonomic distinctness (*TD*) metric as it is more straightforward than either version of the species originality metrics (*OS*, *WOS*; see Table 14.1). For distance-based metrics, the originality-of-species-in-a-set (*OSS*) metric is conceptually less straightforward, requires an ultrametric tree, is mathematically much more complicated, and captures less *PD* than do the others (Redding et al. 2008), so we do not yet recommend its use, despite the fact that it shows relatively low correlations with *some* other metrics. The pendant-edge (*PE*) and species evolutionary history (*SEH*) metrics are both simple conceptually and mathematically (*PE* more so). Although *PE* and *SEH* are largely redundant on most tree shapes, *SEH* contains more information and will, for example, identify as evolutionarily distinct each species in a pair of close relatives when the species pair itself is evolutionarily distinct, whereas *PE* would be quite small in this case. It does not matter which method of apportioning shared branches is used in the calculation of *SEH* ($r \geq 0.98$ for all tree types).

In some cases a conservation biologist may not be interested in prioritizing species, but in prioritizing sites based on the species they contain (e.g. Forest et al. 2007) or in understanding how ecosystem processes depend on the phylogenetic diversity, rather than only the richness, of the species in a community (e.g. Cadotte et al. 2008). In such cases, there is no need to assign individual scores and it is more appropriate to use PD as a straightforward proxy for the quantity of evolutionary history and therefore trait variation in a community.

14.3.2 Phylogenetic diversity in community ecology

When community ecologists are interested in using phylogenetic information to assess the degree to which community assembly has been non-random with respect to species traits or relatedness, it is most appropriate to use null-model corrected versions of type II metrics. The mean value of some metrics (in their raw form) is correlated with species richness (e.g. *MNND* decreases as species are added to a community), and even for those that are not (e.g. *MPD*) the variance among randomly assembled communities may well be correlated with species richness. The range of possible *MPD* values, for example, declines as the number of species increases. As such, the extent to which the members of a community represent non-random selections from a phylogeny cannot generally be assessed using the raw values for type II metrics. In terms of null models, shuffling species among phylogeny tips seems most straightforward, as this most directly randomizes the key data attribute of interest—the phylogenetic positions of species in the community.

Perhaps the most striking result from our simulations was the faulty performance of node-based metrics on imbalanced phylogenetic trees. At best they are insensitive to non-random community assembly, and at worst they could lead to seriously flawed conclusions. For example, if community membership depends on a species being phylogenetically distinct from others, a node-based metric may actually suggest lower rather than higher phylogenetic diversity than expected based on a random selection of species (Fig. 14.2b, and 14.2c). Even for pure birth or balanced trees there is little to no power to detect over-dispersion using a node-based representation of a phylogenetic tree. As such, we recommend against the use of node-based trees in studies of phylogenetic community assembly and advocate great caution for researchers who nonetheless decide to proceed with studies of this kind.

For distance-based metrics, *MPD* showed greater power than *PD* or *NMMD* to detect non-random community assembly. However, the probability of

species being added to communities in our simulations was a function of their mean phylogenetic distance to already-chosen species, so this result is unlikely to generalize across different kinds of non-random community assembly processes. In theory, the relative magnitudes of different metrics' deviation from a null model might itself reveal something about underlying processes (e.g. does community membership depend on having few very close relatives or on average relatedness?), but more work is needed to determine whether such differences might also arise as artefacts of the nature of underlying data.

A more pronounced concern than which distance-based metric to select is how the shape of the phylogenetic tree itself influences the likelihood of detecting non-random community assembly. Balanced trees make it easy to detect phylogenetic clustering but quite difficult to detect phylogenetic over-dispersion, whereas the opposite is true for imbalanced trees with accelerating diversification (Fig. 14.2). Fortunately, many phylogenetic trees are more imbalanced than a pure birth tree with decelerating diversification (Mooers and Heard 1997; McPeek 2008), in which case clustering and over-dispersion have similar chances of being detected (Fig. 14.2b). Statistics exist for quantifying both balance (Heard 1992) and trends in diversification (Pybus & Harvey 2000); these statistics should be calculated by researchers interested in phylogenetic community structure, used to interpret the statistical power of the analysis, and reported with empirical results. Our most general recommendation is for researchers to think carefully about this issue when drawing conclusions, especially when making the explicit or implicit assumption that phylogenetic similarity is a proxy for trait similarity. For example, even a small degree of convergent evolution in a balanced tree (e.g. one or two species in one clade evolve similar phenotypes as a different clade) could lead to phylogenetic over-dispersion when really the species in a set are highly clustered in trait space (see also Kraft et al. (2007)). Exploring some simulation results using the empirical phylogeny of interest seems warranted in this case, despite the non-trivial burden this places on the researcher.

14.3.3 Abundance vs presence–absence data

The vast majority of empirical studies on phylogenetic diversity have not incorporated data on species' abundances. In conservation, some effort has been made to combine phylogenetic distinctness and extinction risk in prioritizing species (Redding & Mooers, 2006; Isaac et al. 2007), which effectively assigns greater weight to species with *lower* abundance. Given the many criteria, in addition to phylogenetic distinctness, that might enter into the equation for conservation prioritization we did not explore the explicit incorporation of abundance data into type I measures of phylogenetic diversity.

One of the underlying premises of many studies in phylogenetic community ecology is that the fitness of individual organisms depends on their similarity to other organisms in the community, in which case species' abundances should be an important consideration. To an individual organism, if several species in the community are close relatives, it should matter far more if those species are abundant than if they are rare. In our simulations, non-randomly assembled communities were created either with abundance taken into consideration or not, but this had virtually no influence on the values of different null-corrected type II metrics or their dependence on tree shape (comparison not shown; Fig. 14.2 shows only the case in which abundances were not incorporated into community assembly). This was counter to our expectation that abundance-weighted metrics would be more sensitive to abundance-weighted community assembly.

The reason appears to be that the particular nature of the phylogeny obscures the abundance-weighted metrics' ability to recover the pattern. Consider the clustering assembly process: in our assembly algorithm, the first and most abundant species was chosen randomly from the phylogeny of potential species, and that species' lineage may or may not have close relatives. If that most abundant species does have close relatives, those closely related species are very likely to be chosen and the abundance-weighted metrics will detect a closely related community. However, in many trials the

most abundant species will not have close relatives and so weighting the selection process by this species abundance will have little effect. The second most abundant species may be the most abundant species' closest relative, but in the context of the broader phylogeny those species could be relatively distantly related. In this case, despite the abundance-weighted assembly process, the abundance-weighted metrics perform poorly. Thus, the particular location on the phylogeny of the most abundant species adds considerably random variation to the performance of the abundance-weighted metrics, making them generally less sensitive to non-random assembly (Fig. 14.2). There was one exception to the general pattern: abundance-weighted MNND was more sensitive to abundance-weighted over-dispersion compared to the non-abundance-weighted measure.

For different kinds of non-random community assembly, for example if abundance is the outcome of competitive interactions rather than determined based on assembly order, we might expect abundance data to reveal more than presence–absence data. Another case in which abundance seems likely to be important is when ecosystem function depends on phylogenetic diversity (as a proxy for trait variation; see, for example, Cadotte et al. (2008)), as these ecosystem functions are performed by individual organisms rather than species per se. Comparison of abundance-weighted metrics with their presence–absence counterparts appears to be a potentially fruitful avenue of future research.

14.4 Key pointS

1. Metrics of phylogenetic diversity are used in conservation biology, where it is desirable to first assign individual species distinctness scores, and in community ecology, where it is of interest to assess the degree to which the species in a community represent a non-random subset of the species in a reference phylogenetic tree.
2. The metrics used in conservation biology show a high degree of redundancy (i.e. strong correlations) with one another and with total phylogenetic diversity (the sum of branch lengths connecting the species in a focal set). For a node-based phylogenetic tree (i.e. no information on branch lengths), the taxonomic diversity (*TD*) measure is conceptually the most straightforward, and for a distance-based tree, the pendant-edge (*PE*) and species evolutionary history (*SEH*) metrics are both conceptually straightforward and mathematically simple.
3. In tests of non-random community assembly, metrics need to be standardized based on null models to remove inherent dependence on species richness. For such null-corrected metrics, those calculated from node-based trees can be seriously misleading. Redundancy is fairly high among those calculated from distance-based trees. We recommend against the use of node-based trees in phylogenetic community ecology.
4. The sensitivity of phylogenetic diversity metrics depends strongly on the shape of the phylogenetic tree, with phylogenetic clustering far more detectable in some cases (balanced trees) and phylogenetic over-dispersion far more detectable in others (e.g. imbalanced trees with accelerating diversification). It is important for empirical researchers to take the effect of their particular tree shape on statistical power into account.