Forum

Oikos 121: 1191–1202, 2012
doi: 10.1111/j.1600-0706.2012.20607.x

Subject Editor: Tom J. Webb. Accepted 22 March 2012

A metric of biodiversity that integrates abundance, phylogeny, and function

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A metric of biodiversity is proposed that combines three of its key components: abundance, phylogeny, and ecological function. This metric is an expansion of the current abundance-based metric that uses Hill numbers, the effective number of types in a sample if all types had the same mean proportional abundance. I define analogous proportional measures of phylogenetic divergence and functional distinctiveness. Phylogenetic divergence is measured as the sum of the proportional share of each species of a given branch of a phylogeny. Functional distinctiveness can be measured in two ways, as the proportional share of each species of a specified ecological function, or as the relative distance of each species based on functional trait values. Because all three aspects of biodiversity are measured in the same fashion (relative proportions) in similar units (effective numbers of species), an integrated metric can be defined. The combined metric provides understanding of covariation among the components and how management for one component may trade off against others. The metric can be partitioned into components of richness and evenness, and into subsets and variation among subsets, all of which can be related through a simple multiplicative framework. This metric is a complement to, rather than a replacement of, current metrics of phylogenetic and functional diversity. More work is needed to link this new metric to ecological theory, determine its error structure, and devise methods for its effective assessment.

The concept of biodiversity is central to ecology and evolutionary biology, especially with regard to concerns over management and sustainability in the face of global change. Yet, there is much debate over what this concept encompasses. The term 'biodiversity' first came to prominence with the 'National Forum on BioDiversity', held in Washington, D.C. in September 1986 (Wilson and Peter 1988), although concepts of diversity go back to the Greek roots of Western science. In its broadest sense 'biodiversity' has been used to include variation in biological components from genes to ecosystems and beyond, as well as interactions among those components.

My purpose is twofold. My first goal is to provide a metric for the concept of biodiversity that encompasses some, but not all, of those components. My metric focuses on three core components: the abundance of organisms, the phylogenetic relationships among those organisms, and the ecological functions that they perform and ecosystem functions that they affect. This metric is organism focused. Variation at other levels (e.g. genetic, ecosystem) and interactions among components may contribute to that organismal variation or vary as a consequence, but are not directly part of the measure. That is not to say that these other aspects of biodiversity are not worthy of concern. Rather, my purpose is to create a metric that has a coherent set of units and can be used in comparisons among sets of organisms. The concept of biodiversity remains broad, beyond the aspects captured within this particular metric.

I focus on abundance, phylogeny, and function because these components are seen as crucial in our attempts to preserve biological diversity (Mace and Baillie 2007, Baillie et al. 2008, Butchart et al. 2010, Cianciaruso 2011). In recent years there has been a flurry of activity concerning abundance-based measures (Jost 2006, 2007, 2010, Tuomisto 2010a, b, Tuomisto and Ruokolainen 2006) that has succeeded in tying together several aspects of diversity (e.g. evenness and scale) into a single unified framework that I review in the next section. This unification sets the stage for my effort to further integrate phylogeny and function into an overall diversity metric that can also be related to aspects of evenness and scale. There is a growing literature addressing phylogenetic diversity (reviewed by Vellend et al. 2010, 2011) and a recent paper (Chao et al. 2010) attempts to integrate among metrics and to include measures of abundance. Similarly, metrics of functional diversity have had increased attention in the past decade (reviewed by Petchey and Gaston 2006, Weiher 2011), including efforts to integrate function and abundance (Villéger et al. 2008).

My second goal is to clear up conceptual and linguistic confusion that has arisen within this literature. The efforts at unification of abundance-based metrics has highlighted

that often concepts given the same name measure different properties with different units (Scheiner 2011, Tuomisto 2010b). Because diversity values are nearly always presented without units, such differences are often not obvious. It is only by being explicit about units can we be sure that we are making meaningful comparisons (Houle et al. 2011). There is a growing number of studies (Cianciaruso 2011) attempting to compare abundance-based, phylogeny-based and function-based measures of diversity (Devictor et al. 2010, Stegen and Hurlbert 2011, Swenson et al. 2011). Interpreting these results requires conceptual clarity. For example, if those measures are in different units or are measuring different types of properties, direct comparisons may not be warranted (Tuomisto 2011).

I take a different approach to phylogenetic and functional diversity from those proposed so far. In doing so, I add clarity about the aspects of phylogenetic and functional diversity that need to be measured. The result is a single, flexible metric that can be used for any of the three aspects of biodiversity – abundance, phylogeny and function – either independently or in all possible combinations. By doing so we will now have the ability to understand how the various components of diversity covary with each other and how management to maximize one component may trade off against another. These diversity components represent both current ecological processes (functional diversity) and future evolutionary potential (phylogenetic diversity). Managing both aspects is critical for long-term sustainability of the biosphere.

Abundance-based measures

I first summarize recent efforts to consolidate abundance-based measures of biodiversity into a single index as I use that approach to integrate the other aspects. (For a recent, general review of abundance-based diversity metrics, see Maurer and McGill 2011.) Central is the idea of number equivalents, the effective number of types in a unit if all types had the same proportional abundance. This idea was first put forward nearly 40 years ago by Hill (1973), who took the idea from information theory (Rényi 1960). The Hill index is:

$$^{q}D = \left(\sum_{i=1}^{S} p_i^{q} \right)^{1/(1-q)} \quad (1)$$

where S is the number of species, p_i is the proportional abundance (n_i/N) of the ith species, and q is a parameter that determines how species abundances are weighed. (See Table 1 for definitions of symbols.) A key property of this index is that it is invariant to changes in absolute numbers; if all species are doubled in abundance, ^{q}D is unchanged. It measures variation in relative abundance, not absolute abundance. It also follows the replication principle, combining two sets of nonoverlapping species that have exactly the same abundance distributions doubles the value of ^{q}D.

^{q}D has values in the range $(1,S]$ for $S > 1$. ^{0}D always equals species richness (R). (Note that $R = S$, but I distinguish between the actual count and the diversity component so that I can expand the concept of richness). When $q = 1$, the index is not defined, but at the limit: $^{1}D = \lim_{q \to 1} {}^{q}D = \exp\left(-\sum_{i=1}^{S} p_i \log p_i \right)$, which is the exponential of the Shannon entropy index. ^{2}D equals the inverse Simpson's index, $^{2}D = 1 / \sum_{i=1}^{S} p_i^2$. As species' abundances get more and more concentrated into a single species, ^{q}D approaches a value of 1. As q increases, more and more weight is given to the most abundant species. At $q = 0$ all species are given equal weight, at $q = 1$ the index gives greater weight to common species, and at $q = 2$ the index gives greater weight to the most abundant species (Fig. 1 in Tuomisto 2011). Values of 0, 1 and 2 are typically used because of their relationship to well-known diversity indices, but examing D as a function of q can also be instructive (Hill 1973, Leinster and Cobbold 2012).

Table 1. Definitions of symbols.

- S: the number of species
- R: richness, the number of objects in a set usually with reference to species
- E: evenness, the extent to which species within a sample have the same abundance, phylogenetic divergence, or functional distinctiveness
- n_i: the number of individuals (abundance) of the ith species
- $N = \Sigma n_i$: the total number of individuals of all species
- $p_i = n_i/N$: the proportional abundance of the ith species
- q: exponent that determines how relative proportions are weighed
- L_j: the length (divergence) of the jth branch of the cladogram
- s_j: the number of species that share the jth branch
- T: the total duration of the cladogram
- $L_{ij} = L_j/s_j$: the proportional length of the jth branch of the ith species
- $L_i = \Sigma L_{ij}$: the lineage divergence the ith species
- $L = \Sigma L_i$: the total lineage divergence of all species
- $l_i = L_i/L$: the proportional lineage divergence of the ith species
- m: the number of traits (dimensions) that define an ecological function space
- s_{ik}: the standardized functional value of the kth trait of the ith species
- $d_{ij} = \sqrt{\sum_k (s_{ik} - s_{jk})^2}$: the functional distance between the ith and jth species
- d_i: the smallest functional distance between the ith species and all other species
- $C_m = \pi^{m/2} \Big/ \Gamma\left(\frac{m}{2} + 1 \right)$: coefficient for the volume of a m-dimensional hypersphere
- $v_i = C_m d_i^m$: the functional volume of the ith species
- $V = \Sigma v_i$: the total functional volume of all species
- $f_i = v_i/V$: the proportional functional volume of the ith species
- e_i: the contribution to a specified ecosystem function of the ith species
- $E = \Sigma e_i$: the total ecosystem function of all species
- $f_i = e_i/E$: the proportional functional contribution of the ith species
- $^{q}D(A) = \left(\sum_{i=1}^{S} p_i^{q} \right)^{1/(1-q)}$: abundance diversity, the effective number of equally abundant species
- $^{q}D(P) = \left(\sum_{i=1}^{S} l_i^{q} \right)^{1/(1-q)}$: phylogenetic diversity, the effective number of equally divergent species
- $^{q}D(F) = \left(\sum_{i=1}^{S} f_i^{q} \right)^{1/(1-q)}$: functional diversity, the effective number of equally distinct species

This index can be divided into two components, richness and evenness: ${}^{q}D = R \times {}^{q}E$ (Smith and Wilson 1996). That is, diversity is the product of species richness (R), the number of species within a sample, and evenness (E), the extent to which those species have equal abundances. ${}^{q}E$ has values in the range (0,1]. The 'q' emphasizes that the measure of evenness depends on how abundances are weighted. As noted by Jost (2010), it is often useful to examine the inverse of evenness, inequality ($I = 1/E$), which has desirable properties for comparing samples; although this paper focuses on evenness, all of the same arguments hold for inequality.

One aspect of abundance-based diversity measures that has spawned much confusion and debate is how to partition diversity as a function of scale. Whittaker (1960, 1972, 1977) proposed a hierarchy depending on the extent of the sample: point (within a community), α (community), γ (landscape), ε (region). The problem is that those extents were never precisely defined. Tuomisto (2010a) wisely collapsed them into just two concepts. γ-diversity (D_γ) is the diversity of a given sample, whatever its extent. α-diversity (D_α) is the mean diversity of a complete set of subsamples at a specified grain within that sample, again independent of any particular length, area, volume, or duration. Because D_α is an average, ${}^{0}D_\alpha$ equals the arithmetic mean species richness of the subsamples and will equal ${}^{0}D_\gamma$ only if all species are present in all communities.

From this formulation comes the solution to the most controversial aspect of these measures, differentiation diversity, how the composition of named objects differs among subsets or partitions of those objects. Because Whittaker (1960) defined β-diversity several different ways, opinions about the best metric have varied over the years (see discussion in Scheiner 2011). In an extensive review, Tuomisto (2010a) showed that all measures are mathematically related, and that the multiplicative partition has useful properties (see also Jost 2007). $D_\gamma = D_\alpha \times D_\beta$ is interpreted as the total diversity of a set of samples (D_γ) is equal to the mean diversity per unit (D_α) times the number (equivalent) of units (D_β). The virtue of this relationship is that it leads to D_β being the numbers equivalent of samples or communities. In contrast, an additive partition leads to D_β being species equivalents, rather than community equivalents.

Using this multiplicative formulation, Tuomisto (2012) provides a simple unification of species richness, evenness and diversity partitions: ${}^{q}D_\gamma = R_\gamma \times {}^{q}E_\gamma$, ${}^{q}D_\alpha = R_\alpha \times {}^{q}E_\alpha$, and ${}^{q}D_\beta = R_\beta \times {}^{q}E_\beta$. Similarly, ${}^{q}D_\gamma = {}^{q}D_\alpha \times {}^{q}D_\beta$, $R_\gamma = R_\alpha \times R_\beta$, and ${}^{q}E_\gamma = {}^{q}E_\alpha \times {}^{q}E_\beta$. The interpretation of the various components and their partitions follows the same logic as given above. For example, R_β is the number of subunits needed if the total number of species (R_γ) were divided so that each subunit contained a unique set of species equal to the average species richness of each subunit (R_α). See Tuomisto (2012) for a more complete discussion of this unification and the meaning of the various partitions of diversity, richness and evenness.

An integrative metric

I now use the framework established for abundance-based measures to define an equivalent set of phylogeny-based and function-based metrics and introduce a more precise notation. In this notation ${}^{q}D(A)$ replaces ${}^{q}D$, where the 'A' indicates that D is a function of abundance. Similarly, ${}^{q}D(P)$ is the phylogeny-based metric and ${}^{q}D(F)$ is the function-based metric; metrics that combine any of these aspects are symbolized as ${}^{q}D(AP)$, ${}^{q}D(AF)$, ${}^{q}D(PF)$ and ${}^{q}D(APF)$. This notation has the advantage of making immediately clear what component(s) of biodiversity is(are) being measured. These measures are in all in units of effective number of species allowing for direct comparisons.

This change in notation solves one terminology problem that I recently raised (Scheiner 2011). The problem is that 'diversity' is used in two senses, as a general concept that encompasses inventory, differentiation and pattern diversity, and as a specific metric of one aspect of inventory diversity, ${}^{q}D(A)$. Because of the desirable mathematical properties of ${}^{q}D(A)$, Jost (2006) termed this 'true diversity,' a usage that raised hackles (Gorelick 2011, Jurasinski and Koch 2011, Moreno and Rodríguez 2011) because of its implication that other metrics are untrue. In Scheiner (2011), I suggested the use of 'diversity sensu lato' and 'diversity sensu strictu' for the two concepts, while admitting that solution was very inelegant. I now propose that we use the term 'abundance diversity' for ${}^{q}D(A)$, making immediately clear what aspect of diversity is being measured. Similarly, ${}^{q}D(P)$ is 'phylogenetic diversity' and ${}^{q}D(F)$ is 'functional diversity'. Combinations such as ${}^{q}D(AP)$ can be referred to using combination names such as abundance-phylogenetic diversity. The use of 'effective number of species' as units for all of these measures further unifies these concepts (Moreno and Rodríguez 2011).

Phylogeny-based measures

The concept of phylogenetic diversity is the extent to which species within a set are closely or distantly related. I distinguish two aspects of phylogenetic diversity, the absolute amount of divergence among species and variation among species in those amounts. In analogy with abundance, the absolute amount of divergence of a given species from other species is similar to n_i, the number of individuals of a given species. ${}^{q}D(A)$, measures variation in the relative number of individuals, not their absolute abundances. Similarly, ${}^{q}D(P)$ should measure variation in species' divergences, not absolute divergence. Divergence is an equally important property to measure, but needs to be distinguished from diversity. Recognizing such a distinction adds clarity to our understanding and insures that metrics of abundance-based and phylogeny-based values are in similar units and on an equivalent scale and so are comparable.

A cladogram denotes a set of phylogenetic relationships assessed within a given time depth (Fig. 1). For simplicity of presentation, I assume that branches of the cladogram that have equal durations represent equal amounts of phylogenetic divergence. In this example the cladogram is ultrametric because all species have equal total lengths from the root to the tip. However, this is not a necessary assumption. All of the formulas given below hold for non-ultrametric cladograms, for example if branch length equaled number of DNA base changes. I use ultrametric cladograms as illustrations in this paper only because they make the presentation more transparent. If neither absolute time nor other

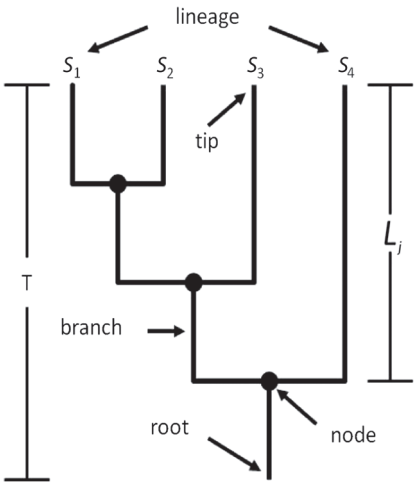

Figure 1. The components of a cladogram. Each species consists of a lineage measured over a total duration T, the time from the tip to the root. Each branch of the cladogram has divergence L_j that may be shared by multiple lineages that coalesce at a given node. This cladogram is ultrametric because all lineages have equal distances from the root to the tips.

branch length measures are available, a cladogram based on Linnean taxonomic categories could be used (e.g. species, genus, family), although this usage assumes that the same taxonomic level in different taxa represents an equal amount of divergence. In general such usage should be avoided as this assumption is likely to be false, even for relatively restricted cladograms.

The total lineage divergence represented by the cladogram in Fig. 1 is simply the sum of the branch lengths ($L = \Sigma L_j$). To provide units for this example, assume that for species 1 the length of the branch from the tip to its first node is 2, so the total lengths of the branches of the entire cladogram is 20. This value, L, is analogous to the total number of individuals, N, and thus, needs to be partitioned among the lineages. I do so by first dividing the divergence of a given branch, L_j, equally among lineages that share that branch (s_j), so that the proportional share for the ith species of a given branch is $L_{ij} = L_j/s_j$. The amount of divergence of the ith species (L_i) is then the sum of those proportional branches. For example, in Fig. 1, species 1 has a total divergence of $(2/1 + 2/2 + 2/3 + 2/4) = 4.17$ time units. Similarly, species 4 has a total divergence of $(6/1 + 2/4) = 6.50$ time units. If none of the species share a node within the duration under consideration (i.e. are unrelated) and the cladogram is ultrametric, then $L = S \times T$, the number of species (lineages) multiplied by the total duration (T). Isaac et al. (2007) also proposed the use of L_i as a measure of divergence, termed evolutionary distinctiveness.

Table 2. Lineage divergences (in units of time) and phylogenetic diversities (in units of numbers of equivalent species) for the cladograms shown in Fig. 2.

	Cladogram			
	A	B	C	D
L_1	4.50	4.17	3.67	4.00
L_2	4.50	4.17	3.67	4.00
L_3	6.50	5.17	3.67	4.00
L_4	6.50	6.50	5.00	4.00
l_1	0.20	0.21	0.23	0.25
l_2	0.20	0.21	0.23	0.25
l_3	0.30	0.26	0.23	0.25
l_4	0.30	0.33	0.31	0.25
L	22	20	16	16
$^0D(P)$	4.00	4.00	4.00	4.00
$^1D(P)$	3.93	3.93	3.96	4.00
$^2D(P)$	3.87	3.86	3.92	4.00

Each species accounts for a proportion of the total divergence, $l_i = L_i/L$, and the metric of phylogenetic diversity is:

$$^qD(P) = \left(\sum_{i=1}^{S} l_i^q \right)^{1/(1-q)} \quad (2)$$

This metric has all of the same properties as $^qD(A)$. Values of $^qD(P)$ range in the interval $(1,S]$ for $S > 1$. $^0D(P) = R$, and if all species are equally divergent, $^qD(P) = R$ for all q. Conversely, $^qD(P)$ converges towards 1 if the cladogram consists of several very closely related species and one very divergent species.

Table 2 and Fig. 2 give examples of cladograms that differ in the amounts of divergence among the species. Cladogram D consists of four equally divergent species and has a phylogenetic diversity of 4.0 for all values of q. The total divergence of the set of species is not necessarily related to the phylogenetic diversity. Both C and D have a total divergence of 16, but C has three species that are more closely related than the fourth, and so is less diverse. Figure 3

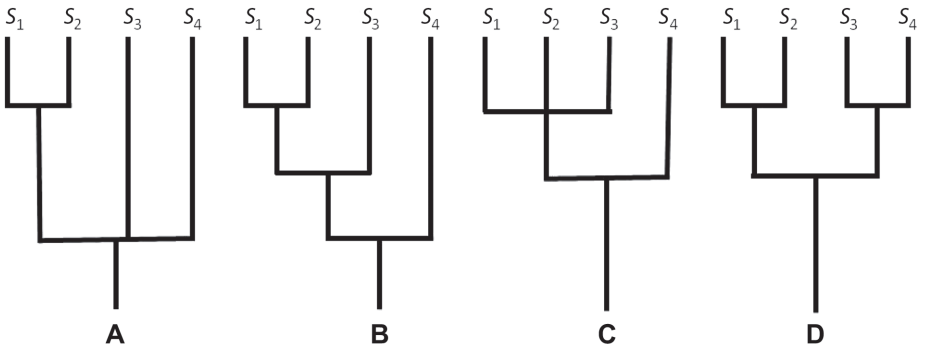

Figure 2. Four cladograms that differ in the amount of variation among species in lineage divergences.

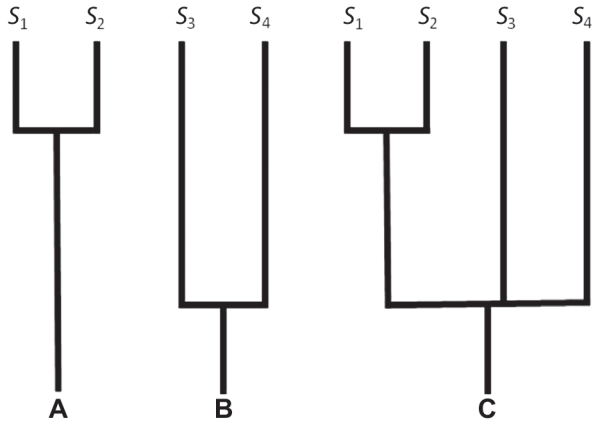

Figure 3. Cladograms A and B have the same diversity [^{2}D(P) = 2], but differ in their amount of divergence [A: L = 10; B: L = 14]. Combining these two produces cladogram C with a value of 3.92, rather than 4, because of that difference in divergence. Combining A with a second, identical cladogram would produce a cladogram with ^{2}D(P) = 4.

further illustrates the difference between diversity and divergence; cladograms A and B differ in their amount of divergence but have the same diversities [^{2}D(P) = 2].

This metric is related to measures of tree symmetry or balance (Mooers and Heard 1997, Vellend et al. 2011). If only dichotomous branching is allowed (i.e. cladograms B and D), then a symmetrical tree will consist of equally diverged species and ^{q}D(P) = R for all q. However, if polytomies are allowed, then it is possible for the cladogram to be symmetrical overall, but not symmetrical at every node and have a lower phylogenetic diversity. A measure of cladogram symmetry is given by phylogenetic evenness, ^{q}E(P) = ^{q}D(P)/R; if all species are equally divergent, ^{q}E(P) = 1 for all q and converges towards 0 as ^{q}D(P) converges towards 1.

^{q}D(P) has the same doubling and replicating properties as ^{q}D(A). For example, doubling the lengths of the branches of all species does not change the value of ^{q}D(P), even though it doubles the value of L, just as doubling the abundances of all species in a community doubles N, but does not change ^{q}D(A). If a community is doubled in its number of species by joining two identically-shaped clades at the root (i.e. two unrelated sets of species), the value of ^{q}D(P) doubles, with no change in the value of ^{q}E(P). This doubling property can be understood by considering a counterexample (Fig. 3). Combining cladograms A and B into cladogram C does not produce a diversity of 4.0 because of the greater total divergence in cladogram B as compared to cladogram A. Rather, combining A with an identical cladogram would produce a cladogram with a diversity of 4.0.

If the cladogram can be subdivided into smaller sets of taxa (clades), we can define measures of α-, β- and γ-diversity analogous to those given above: ^{q}D(P)$_\gamma$ is the phylogenetic diversity (effective number of species) of the total set, ^{q}D(P)$_\alpha$ is the mean effective number of species of the subsets, and ^{q}D(P)$_\beta$ is the effective number of equally divergent clades within the entire set of species. If a Linnean classification were used, ^{q}D(P)$_\beta$ might be the effective number of equally speciose genera within a family, for example.

Measures of ^{q}D(P) depend on the time depth considered. At a very shallow time depth, none of the branches might converge on a node, and ^{q}D(P) = R. As time depth increases, phylogenetic diversity will decline as some of the species converge. Once all of the species have converged at the deepest node, phylogenetic diversity increases again towards R as the cladogram appears increasingly to consist of a set of equally, closely-related species.

Because ^{q}D(P) is time dependent, comparisons among sets of species should be done at equal time depths, or equal taxonomic levels if a Linnean classification is being used. This constraint does not hold if an independent measure of divergence is used (e.g. DNA base changes) so that the cladograms are non-ultrametric, although it is still necessary that the two sets be comparable in some sense. For example, you would not compare a set of mammals with another consisting of plants and fungi as the time depth and amount of divergence differs greatly between those two sets. This standardization is analogous to comparing communities that have been equally sampled, for example over the same area or the same number of individuals.

In a recent review of phylogenetic diversity measures, Vellend et al. (2011) distinguish between two general classes, those based on phylogenetic information from a larger set of species than those for which the index will be calculated (type I) and those based on just the set of species being considered (type II). It is difficult to relate their type I indices to the metric proposed here, except to note that ^{q}D(P)$_\alpha$ provides a measure of diversity of subsets of species. Their type II indices differ from my metric in a critical way. All previous proposed measures are based on information about the distance of tips from each other on the cladogram, rather than variation in amounts of divergence. Thus, they capture aspects that are closer to L than ^{q}D(P), and L exactly equals Faith's (1992) phylogenetic diversity index (PD). A better terminology for all of those metrics would be phylogenetic divergence. Another way to appreciate that diversity and divergence measure different properties is to consider their units. ^{q}D(P) is in units of equivalent numbers of species, similar to ^{q}D(A); in contrast, divergences are in units of change over time (e.g. DNA base changes per million years). This difference in units means that direct comparisons of abundance-based and phylogeny-based measures of diversity are questionable.

Integrating abundance and phylogeny

Because ^{q}D(A) and ^{q}D(P) are constructed using analogous metrics, it is simple to construct an analogous, integrated measure:

$$^q\mathrm{D(AP)} = \left(\sum_{i=1}^{S} \left(\frac{n_i L_i}{\Sigma n_i L_i} \right)^q \right)^{1/(1-q)} \quad (3)$$

This integrated metric has properties similar to those previous described, e.g. it varies within the interval [1,S]. Examples of how this index separately varies as a function of abundance and phylogeny and captures information about covariation among those components are shown in Table 3. Table 3A shows measures of ^{q}D(A) for four communities. Communities 2 and 3 have equal values of ^{q}D(A)

Table 3. (A) Species abundances and abundance diversities of four communities. (B) Assemblage diversity of order q = 1 of the 16 combinations of cladograms (Table 2) and communities (Table 3A). (C) Assemblage diversity of order q = 2 of the 16 combinations of cladograms (Table 2) and communities (Table 3A).

(A)

	Community			
	1	2	3	4
n_1	5	10	2	30
n_2	5	6	2	6
n_3	5	2	6	2
n_4	5	2	10	2
p_1	0.25	0.50	0.10	0.75
p_2	0.25	0.30	0.10	0.15
p_3	0.25	0.10	0.30	0.05
p_4	0.25	0.10	0.50	0.05
${}^0D(A)$	4.00	4.00	4.00	4.00
${}^1D(A)$	4.00	3.22	3.22	2.23
${}^2D(A)$	4.00	2.78	2.78	1.69

(B) ${}^1D(AP)$

	Cladogram			
Community	A	B	C	D
1	3.93	3.93	3.96	4.00
2	3.49	3.46	3.33	3.22
3	2.96	2.88	2.95	3.22
4	2.43	2.40	2.31	2.23

(C) ${}^2D(AP)$

	Cladogram			
Community	A	B	C	D
1	3.87	3.86	3.92	4.00
2	3.11	3.07	2.91	2.78
3	2.52	2.38	2.43	2.78
4	1.83	1.82	1.75	1.69

because their species' abundances are simply reversed in order but not changed in magnitude.

Table 3B–C show values of ${}^qD(AP)$ for q = 1 and q = 2, respectively, for the 16 combinations of cladograms and communities. Only for the combination D1 where the species have equal abundances and equal divergences is ${}^qD(AP) = 4$ for all values of q. All combinations with cladogram D equal those of ${}^qD(A)$ (Table 3A), and all combinations with community 1 equal those of ${}^qD(P)$ (Table 2). A comparison of combinations with communities 2 and 3 demonstrate the effect of having the most abundant species be closely related (cladogram B) or distantly related (cladogram C) to the other species. The latter is less diverse because numerical abundance and evolutionary divergence is concentrated in the same species.

Chao et al. (2010) proposed a measure of phylogenetic diversity based on Hill numbers that combines information on species abundances and branch length and which generalizes previous measures (Rao 1982, Faith 1992, Allen et al. 2009, Pavoine et al. 2009, Ricotta and Szeidl 2009) (the abundance-weighted phylogenetic diversity category of Vellend et al. 2011). Their metric does not combine abundance-based and phylogeny-based diversities as defined here. Rather it is a time-averaged measure of ${}^qD(A)$; if all abundances are equal, it is an abundance-weighted measure of variation in branch lengths (L_j) rather than proportional lineage divergences (l_i). The meaning of a time-averaged measure is not clear as the community that is being measured did not necessarily exist in the past, and certainly the species' abundances varied over time. Other integrative metrics (Cadotte et al. 2010) do not have the desirable properties of those based on Hill numbers; see Jost (2006) and Chao et al. (2010) for detailed discussions of those properties.

Function-based measures

Current function-based measures of diversity suffer from both the conceptual confusion described above (i.e. confounding diversity and divergence), and from problems with the methodological approaches used in its calculation. Defining a measure of ecological function that is suitable for use in a diversity measure is not straightforward for two reasons. First, unlike abundance and phylogeny that are indexed by a single variable (n_i and L_i, respectively), ecological function is not embodied in a single variable. Rather it is a result of multiple traits or characteristics of an organism such as leaf size and photosynthetic mode for a plant or prey type and time of day when foraging for an animal. (See Petchey and Gaston 2006 for a detailed discussion of how to identify those traits.) If each species is measured for m characteristics or traits, those traits define an m-dimensional hyperspace within which the species are arrayed as a set of points.

Second, ecological function is context dependent. 'Function' implies function with respect to something. What we want to capture in an index of functional diversity is the extent to which a given species contributes to some specified community property (e.g. total productivity, nitrogen cycling). Thus, a given trait does not have a single functional value, but depends on which ecological function is being considered. In contrast, both ${}^qD(A)$ and ${}^qD(P)$ depend only on the area, volume, or duration sampled. Neither depends on reference to some function external to the species themselves. Adding yet more complexity, this functional value may depend on ecological interactions with other species in the community. Although p_i and l_i are relative measures, the effect of other species is strictly additive within the context of the metric. Although species abundances and phylogenetic relationships are caused by ecological interactions, the functions of the species are a direct cause of the ecological function under consideration.

We are, thus, faced with two concepts of function: 'function of' and 'function for'. 'Function of' focuses on an organism's traits and how they determine the role of that individual in a community. 'Function for' focuses on the effects of those roles on community and ecosystem processes. There are two possible solutions to reconciling these differing aspects of function. The first solution integrates these two aspects into a single metric. The second solution defines separate metrics for each aspect. There are benefits and costs to each approach.

Solution 1: an integrated metric

I begin by defining an integrated measure of functional diversity. First, all traits are standardized to a mean of zero

and standard deviation of 1 (the standard z-transformation) as recommended by Petchey and Gaston (2006) and Villéger et al. (2008). The z-transformation has the advantage of putting all traits on the same scale. Otherwise, the *m*-dimensional space could be distorted (i.e. seem to be larger along one axis than another) simply due to the units used to measure a trait.

A second standardization, however, is key. The traits are further standardized by the effect that each has on the ecological function under consideration. For example, as determined by multiple regression, variation among species in leaf area might account for 10% of the variation among species in g C fixed per day, and variation in root length might account for 15% of that variation. So the standardized leaf area values would be multiplied by 0.10 and root length values multiplied by 0.15. Without this second standardization, functional diversity devolves to being a measure of trait variation, which may not provide any more information than phylogenetic diversity. Petchey and Gaston (2006) suggest a similar approach by using additional weighting of the traits by importance based on general knowledge of species' ecologies, e.g. some traits would be multiplied by 2. Although similar in spirit to the weighting scheme that I propose, their method has the limitation that such weightings can be arbitrary, especially in the absence of precise information on trait effects.

Functional diversity should capture some sense of each species' distinctiveness from the other species. If all species have very similar trait values, we would not consider them to be very distinct. We also want a measure that will differentiate between a group of very similar species, such a group with one additional very different species, and a group where all of the species are very different. As with phylogenetic measures, we also want to distinguish between the total amount of functional distinctiveness among the species and the amount of variation in that distinctiveness.

I define the function of a given species as the volume surrounding its point in the hyperspace. To measure distinctiveness, I define this function as a hypersphere with a radius equal to half the distance from the nearest other species. (Because the diversity metric uses proportions, the factor of 1/2 drops out of the final calculation.) Half the distance to the nearest species is used because that defines a unique, nonoverlapping volume occupied by each species (Fig. 4). No other distance measure would define a unique volume. It is this unique volume that measures the distinctiveness of each species.

The distance is given by $d_{ij} = \sqrt{\sum_k (s_{ik} - s_{jk})^2}$, where d_{ij} is the functional distance between the *i*th and *j*th species, and s_{ik} is the functional value of the *k*th trait of the *i*th species scaled to its effect on the particular ecological function under consideration as described above. Next, we find the minimum distance $[d_i = \min(d_{ij})]$ of the *i*th species to any other species. The functional volume of the *i*th species is given by $v_i = C_m d_i^m$, where $C_m = \pi^{m/2} \Big/ \Gamma\left(\frac{m}{2}+1\right)$ and Γ is the gamma function. The total functional volume of all species is $V = \Sigma v_i$, and the proportional functional volume of the *i*th species is $f_i = v_i/V$.

From this, the metric of functional diversity is:

$$^{q}D(F) = \left(\sum_{i=1}^{S} f_i^{q}\right)^{1/(1-q)} \quad (4)$$

This metric is the effective number of equally distinct species, that is species that affect ecological function to a similar extent but through different combinations of trait values. If all species are equally distinct, that is they are arrayed an equal distance from each other on the surface of the hypersphere, then $^{q}D(F) = R$ for all q, just as with the other metrics. $^{q}D(F)$ tends towards 1 as the set of species converges to $S - 1$ very similar species and one extremely different species. Variation in distinctiveness is measured as functional evenness, $^{q}E(F) = {}^{q}D(F)/R$. As with the phylogeny-based metric, $^{q}D(F)$ separates the total effect of the species on ecological function (V), from the variation in distinctiveness among the species.

To see how the metric behaves, consider the simplest situation of species measured for just a single trait (Table 4). If there are only two species in the community, the diversity is 2.0 for all values of q. If a third species is added, the value of diversity depends on the distinctiveness of that species. If the third species has a trait value exactly midway between the other two (community 2), then diversity is 3.0 for all values of q because the species are maximally distinct. As

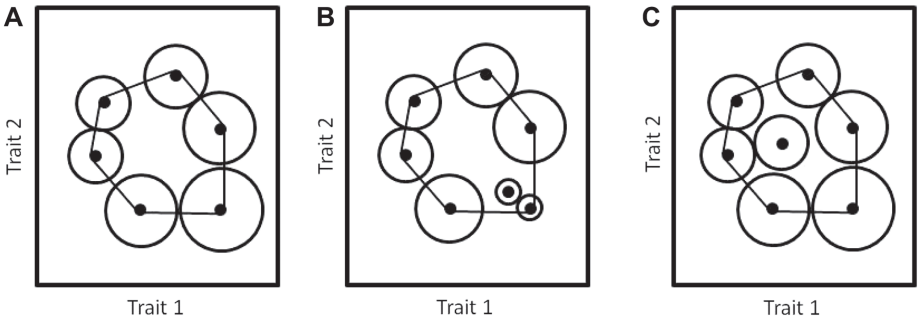

Figure 4. Three communities measured for two traits showing both the volumes for each species as defined by the minimum distance to the other species and the convex hull volume. The three communities have values of V of 7.31, 5.78 and 8.10 (in units of trait values), respectively, and values of $^{2}D(F)$ of 5.85, 6.21, and 6.81 (in units of number of equivalent species), respectively; all have the same value of FRic. Community B has a lower value of V than community A because the additional species is very similar in trait value to an existing species, while community C has a greater value because the new species is substantially different from the other species.

Table 4. Species mean trait values (s_i), minimum distances (d_i), and functional diversities of four communities consisting of two or three species where each species is measured for just a single trait.

	Community			
	1	2	3	4
s_1	1	1	1	1
s_2	9	5	3	2
s_3	NA	9	9	9
d_1	4.0	2.0	1.0	0.5
d_2	4.0	2.0	1.0	0.5
d_3	NA	2.0	3.0	3.5
${}^0D(A)$	2.00	3.00	3.00	3.00
${}^1D(A)$	2.00	3.00	2.59	1.98
${}^2D(A)$	2.00	3.00	2.27	1.59

two of the species become more similar (communities 3 and 4), the variance in distinctiveness increases and diversity decreases as expected.

Standardizing trait values against a particular ecological function facilitates comparisons of functional diversities among sets of species. Such comparisons are meaningful only if the same ecological function is being compared. Because all traits are standardized to the same units (e.g. prey mass consumed per unit time), comparisons of V are meaningful because they are in the same units. Such a standardization avoids the need to only compare functional diversity for species that are measured for the same traits (cf. Petchey and Gaston 2009). Comparisons could be made among sets that contain completely different types of species, if the ecological function were comparable. For example, you could compare plants and birds if the function were productivity (g C biomass fixed within those species per unit time).

This index accomplishes the goals set by Mason et al. (2005) for a set of measures of functional diversity by dividing it into three components – richness, evenness and divergence – multivariate measures of which are provided in Villéger et al. (2008). My measures of ${}^qD(F)$ and ${}^qE(F)$ meet the criteria listed in Villéger et al. (2008), Table 1, except that while ${}^qE(F)$ ranges from (0,1], ${}^qD(F)$ ranges from (1,S]. Their measures of functional evenness and functional diversity are related conceptually to ${}^qE(F)$ and ${}^qD(F)$, respectively, except that their metrics do not have the properties of Hill numbers, nor are they directly related to each other, as are ${}^qE(F)$ and ${}^qD(F)$.

Because ${}^qD(F)$ is based on proportions, the coefficient C_m drops out of the calculation, so ${}^qD(F)$ can be thought of simply in terms of proportional minimum distances. However, using just minimum distances fails to define the functional volume (V), and thus fails to capture a key aspect of functional diversity. Villéger et al. (2008) define functional richness (FRic) as the amount of functional space filled by the community and measure it as the volume of the convex hull that encompasses all species in that space (see their Fig. 1b). That measure is conceptually similar to my measure of V, except that it fails to capture the amount of filling of the hull. The addition of species to the interior of the hull does not change their measure of functional richness, but might increase or decrease V, depending on the exact arrangement of the species in the hyperspace (Fig. 4). V does not suffer from the limitations of FRic. The latter requires that the number of species be greater than the number of traits so that the number of dimensions of the space be greater than the number of points within it, and it is undefined if all of the species are arrayed along a single line.

My approach differs from current proposed metrics of functional diversity that are based on hierarchical clustering techniques (reviewed by Petchey and Gaston 2006). Such clustering produces a dendrogram, superficially similar to a cladogram without a root. Functional diversity is then measured as a sum of distances between species along branches of the dendrogram, superficially similar to cladistic measures of phylogenetic diversity, although much more closely allied to phenetic measures (Sneath and Sokal 1973). The problem with such dendrogram-based techniques is that the distribution of species in the trait-defined hyperspace is continuous so that the hierarchical clusters defined by the dendrogram are arbitrary. Two species that are close to each other in the hyperspace can end up on distant branches of the dendrogram depending on the distance measure and clustering method and as a function of minor changes in trait values. My approach measures distance directly, avoiding this problem. Although the logic for a dendrogram-based approach is based on those used for measures of phylogenetic diversity, there is a fundamental difference between a dendrogram and a cladogram. A cladogram is based on an evolutionary branching process that uniquely defines a set of actual relationships (ignoring errors in estimating those relationships). The relationships in a dendrogram are mathematically, rather than biologically, defined. Finally, dendrogram-based techniques do not provide a measure of variation of distinctiveness in function. Rather, they provide a measure closer to V, the total volume of the hyperspace defined by the set of species. The units of these other measures of functional diversity are not numbers of species, but multivariate trait units. So, as with current measures of phylogenetic diversity, direct comparisons with abundance-based measures of diversity are questionable.

If the set of species can be subdivided into guilds, we can define measures of α-, β- and γ-diversity analogous to those described above. In particular, ${}^qD(F)_\beta$ is the effective number of equally distinct guilds within the entire set of species. One difference of my approach from dendrogram-based methods is that subsets of guilds can be flexibly defined. For dendrogram-based methods, such subsets are sets of species that cluster on the same branch of the dendrogram and, presumably, are near each other in the hypervolume. Under my scheme, such subsets could be defined based on taxonomy, or a single trait (e.g. night-time vs day-time foragers), providing a richer picture of how functional effects are distributed among species.

This measure of functional diversity, as well as all others, contains an important, implicit assumption, that functional diversity is a quantity that can be added up among species. We know that on a strict basis this is not true. If it is mostly true, then a measure of functional diversity is likely to provide useful information. If instead the function of a species in an ecosystem is highly dependent on non-additive interactions and greatly changed with the exact identities of the

other species, then measures of functional diversity will not contain useful information. For example, one might wish to manage a community to preserve the subset of species that will maximize future functional diversity. If functional diversity is highly context dependent, current estimates provide no information about future values.

Solution 2: separate metrics

An alternative solution is to separate ecosystem effect from trait values. To create a measure of functional diversity based on ecosystem effect, the only values that are measured are the ecological property of a given species (e.g. g C biomass fixed per unit time), notated as e_i. The total function is now $E = \Sigma e_i$, and the proportional function is now $f_i = e_i/E$. Functional diversity is calculated as in Eq. 4. This metric is notated as ${}^qD(E)$ to indicate that it is a measure of ecosystem effect. This approach has several advantages. First, it makes functional diversity similar to abundance diversity and phylogenetic diversity as an index of variation of a single species property. Second, it eliminates the problem of having to relate trait values to ecological functions. Measuring just the former is much simpler. Third, it allows for comparisons within a single community of the functional diversity of different ecological properties, for example, a comparison of diversity in g C fixed and g N fixed. On the other hand, this alternative approach fails to capture information about the basis for that variation in ecosystem function. Of course, the same could be said of abundance diversity and phylogenetic diversity. Both measure aggregate outcomes of complex ecological and evolutionary processes. Perhaps we should treat functional diversity in a similar fashion. For all three diversity measures, additional models are then necessary to link those aggregate measures to those processes.

Similarly, a trait-based metric, ${}^qD(T)$, can be defined using the distance method described above, except that the traits would not be standardized by their ecological effect. This approach has two advantages: It allows a broader definition of function that encompasses what is usually consider the species niche. It also obviates the need to measure the relationship between trait values and functional effect. This approach has the disadvantage of leaving the choice of traits to the expert opinion of the researcher (Petchey and Gaston 2006). Expert opinion may be correct, but it runs the risk of either missing critical traits, or worse including traits that do not affect ecosystem function. These errors would, respectively, underestimate or overestimate the apparent functional diversity.

These two metrics can still be combined as:

$$ {}^qD(ET) = \left(\sum_{i=1}^{S} \left(\frac{e_i v_i}{\sum e_i v_i} \right)^q \right)^{1/(1-q)} \quad (5) $$

The critical difference between ${}^qD(F)$ and ${}^qD(ET)$ is how each combines information on trait values and functional effects. For ${}^qD(F)$, the covariance between traits and effects is determined within individuals among traits. For ${}^qD(ET)$, that covariance is determined among species. The latter potentially allows separation of the role of a species within a community from the effect of that species on ecological functions, while the former provides a mechanistic link between traits and functions.

Leinster and Cobbold (2012) recently proposed an approach for combining information about species functional differences with abundances within the Hill framework. Their metric weighs abundances by species trait similarities and is, thus, akin to the approach of Chao et al. (2010) that weighs abundances by phylogenetic distance.

A metric of biodiversity

Because in the above metrics all three aspects of biodiversity – abundance, phylogeny and function – are measured in the same fashion, an integrated metric is immediately apparent:

$$ {}^qD(APF) = \left(\sum_{i=1}^{S} \left(\frac{n_i L_i v_i}{\sum n_i L_i v_i} \right)^q \right)^{1/(1-q)} \quad (6) $$

If the alternative approach to functional diversity is preferred, e_i can be substituted for v_i or combined with a unweighted measure of v_i as in Eq. 5. This metric has all of the same properties of others based on Hill numbers, including measures of evenness and partitions into subsets. We can combine these three components into a single metric even though the underlying quantities are measured on very different scales because the metric is based on proportions. This is another way of reiterating one of the properties of the Hill number, that it is invariant to multiplication (e.g. doubling the abundance of all species leaves the same value of ${}^qD(A)$). Because each of these aspects of biodiversity – abundance, productivity, and function – is a different property of each species it is only through the use of proportions that can we create a composite index with similar units – the effective number of species.

Because all versions of this metric have similar units – the effective number of species – and scale to the same interval – $(1,S]$ – the measures are comparable and differences are interpretable. It allows, for example, a comparison of ${}^qD(APF)$ with ${}^qD(A)$, ${}^qD(P)$, and ${}^qD(F)$ measured for the same set of species leading to an understanding of the extent to which diversity is due to equality in abundance, phylogeny, or function. Devictor et al. (2010) provide an example of a comparison of these components (using an index related to a Hill number of order $q = 2$ and using a dendrogram-based measure of functional diversity), although they do not compare those values to ones based on a composite index.

One aspect of diversity patterns captured by this combined index is the covariation of the various diversity components as demonstrated in the earlier example of ${}^qD(AP)$ (Table 2). In general, the product of the individual proportions does not equal the proportion of the product [i.e. $\sum_{i=1}^{S} (p_i l_i f_i) \neq \sum_{i=1}^{S} \left(\frac{n_i L_i v_i}{\sum n_i L_i v_i} \right)$]. Currently we do not know whether these components tend to covary across communities, for example whether the most abundant species tend to be closely or distantly related to the other species in a community. The theory of limiting similarity predicts that the most abundant species should be distantly related

(Abrams 1983), while the neutral theory makes the opposite prediction (Hubbell 2001).

Recent attempts to quantify differentiation diversity for combined diversity metrics include Stegen and Hurlbert (2011), who present a metric combining all three components using cladogram- and dendrogram-based distance methods. That metric uses the product of the proportional values of each component (i.e. p_i, l_i and f_i), rather than the proportion of the product (Eq. 5). Besides failing to account for component covariance, their index is not based on Hill numbers, although it can be related to values of ${}^{q}D(APF)_{\beta}$. Similarly, Swenson et al. (2011) use a dendrogram-based measure of functional diversity combined with a measure of abundance, again based on a product of the proportional values.

The greatest impediment to using the proposed metric is being able to accurately measure all three components. This ability depends on a number of factors. One factor is the geographic extent of the samples. Measures of abundance are relatively straightforward at ecological extents (communities to landscapes) but much more difficult at biogeographic extents (regions to continents) (Chiarucci et al. 2011). If abundance data is not available, frequency or presence/absence data can be substituted (e.g. number of grid cells covered by a species' range).

Phylogenetic information is becoming much more available (e.g. vertebrates, vascular plants), but is still missing at the level of species for many groups (e.g. insects, fungi). Phylogenetic information may also be incomplete, for example existing for some insect families in a sample and not others. In such instances a hybrid approach could be taken, calculating diversity using the complete phylogenetic information for a subset of the taxa and comparing that to diversity using Linnean information for the full data set. In such a case, the Linnean-based measure would tend to have a higher value of ${}^{q}D(P)$ because of the large number of polytomies. I emphasize, though, that the latter is just a stop-gap until more complete phylogenetic information can be generated. Such a stop gap could be justified if one is faced with time-sensitive management decisions.

The toughest challenge is measuring ecological function. Linking trait values to function is difficult for a single species, much less an entire community. The current practice is to use best judgment to choose the traits to include in the analysis, with perhaps a crude weighting of importance (Petchey and Gaston 2006). Given the practical limitations on measuring actual effects, work is needed to determine the accuracy and bias associated with such cruder estimates. Using the alternative strategy of using separate measures of ecosystem effect and trait values avoids this problem.

Work is also needed to develop estimates of measurement error. Such estimates exist for ${}^{q}D(A)$ (Zar 1999), but not for phylogeny-based or function-based metrics. A cladogram has error associated with estimates of its branch pattern and lengths, but all ecological metrics fail to take that error into account. However that error structure is generally understood, so incorporating it into these diversity metrics should be straightforward. The same is true of function-based metrics where errors associated with estimation of trait values or ecological functions are well understood. Linking trait values to ecological function is a simple scaling and, thus, does not alter estimates of error.

Scale

The diversity of a system changes with the extent over which it is measured. For abundance-based measures, increasing the span of space or time that is encompassed will alter the number of species observed and their relative abundances. What is meant by the extent of a sample differs for phylogeny-based and function-based measures. For phylogeny, the extent is the time depth of the cladogram. As noted above, estimates of diversity can fall and then rise as time depth increases. This is a different sense of time than the time span of abundance measures. In the latter, increasing the sampling time increases the number of individuals encountered. In the former, increasing the time depth does not change the species observed, but does change their apparent relationships.

For function-based measures, the extent is the number of traits considered. For ${}^{q}D(T)$ in particular, including more traits can make species appear to be more similar or more different. To take a simple example, consider a community consisting of rodents and birds and within each group some species are granivores and some insectivores. Depending on whether you included diet, mode of locomotion, or body size in the analysis, the perceived differences in trait values could end up making either all of the birds most similar to each other, or make some of the birds more similar to some of the rodents. Those analyses are not more or less correct, they simply differ in the scale being measured. (Note that adding an invariant trait – e.g. homeothermy in this example – has no effect on these measures.) Thus, we must always be explicit about the extent of any sample and make sure that comparisons among samples acknowledge any differences in extent.

Conclusion

Biodiversity has a variety of components. The measure that I propose gathers three of those components – abundance, phylogeny and function – into a single metric. Such an integrated metric allows for more complex and comprehensive comparisons within and among ecological units and expands ecological theory. Current theories of diversity focus on species richness or abundance-based metrics (Scheiner and Willig 2011). Having a more comprehensive metric with well-understood properties can provide a foundation for theory expansion. Conservation and management of diversity is clearly enhanced by having an integrated metric. There has been much discussion of the need to take all of these aspects of diversity into account when making management decisions. The metric proposed here allows for these aspects to be measured separately and together, thus permitting a more informed decision. In one sense, though, I have not produced a new metric. Rather, I have taken our current abundance-based metric and shown how other aspects of species can be measured in a similar fashion. In this way my efforts are part of a larger movement towards unification and simplification of the current bewildering array of diversity indices.

This metric is just one way to measure biodiversity. For example, the index of phylogenetic diversity of Chao et al. (2010) is also based on Hill numbers with all of its desirable properties. It combines information on abundance and phylogenetic relationships in a different way than I propose and, thus, measures a different property. Similarly dendrogram-based measures of functional diversity (Petchey and Gaston 2006, Villéger et al. 2008) measure different properties. The metric that I present here measures variation in lineage divergence and functional distinctiveness. Total divergence and distinctiveness are equally desirable properties to assess. These other metrics take those totals into account and should continue to be explored in that context, especially in ways that follow the lead of Chao et al. (2010) and Leinster and Cobbold (2012).

The two alternatives that I put forward for measuring functional diversity can be thought of as a focus on outcomes (e_i) versus inputs (v_i). Either is legitimate, although the former makes the measure closer to what is captured by the abundance-based and phylogeny-based metrics. We need a discussion of the theoretical underpinnings and practical aspects of both formulations so as to decide which is more useful. My purpose here is to show what is needed for each approach so that we can have that discussion.

More development is needed in three regards. First, the value of an integrated metric is that it accounts for covariance among the individual components (e.g. whether the most phylogenetically divergent species is also the one with the greatest distinctiveness in effect on ecosystem function). This metric provides a summary of that covariance, but its mathematical dissection would be useful, especially if we wish to connect the metric to mechanistic models. This covariance is potentially complex if the functional value of a given species depends on the identities of other species in the community, and such dependence may render moot trait-based measures of functional diversity. Second, the error structure of the metric needs to be determined to facilitate comparisons among ecological units. Third, work is needed on the practical aspects of measuring all of the components of the metric so as to make it useful. The ongoing need to manage biodiversity in the face of global change adds urgency to these efforts.

Acknowledgements – I thank Mary Ann Horn for mathematical insights, Ann Chao, Catherine Graham and Maureen Kearney for illuminating comments, Alan Tessier for provocative conversations, Hanna Toumisto and Lou Jost for insightful reviews. The development of these ideas was facilitated by my participation of the PRONEX symposium at the Univ. Federal da Bahia, Brazil; I thank Charbel El-Hani for that invitation. This manuscript is based on work done while serving at the US Natl Science Foundation. The views expressed in this paper do not necessarily reflect those of the National Science Foundation or the United States Government.

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