Unifying Species Diversity, Phylogenetic Diversity, Functional Diversity, and Related Similarity and Differentiation Measures Through Hill Numbers

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Unifying Species Diversity, Phylogenetic Diversity, Functional Diversity, and Related Similarity and Differentiation Measures Through Hill Numbers

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Abstract

Hill numbers or the effective number of species are increasingly used to quantify species diversity of an assemblage. Hill numbers were recently extended to phylogenetic diversity, which incorporates species evolutionary history, as well as to functional diversity, which considers the differences among species traits. We review these extensions and integrate them into a framework of attribute diversity (the effective number of entities or total attribute value) based on Hill numbers of taxonomic entities (species), phylogenetic entities (branches of unit-length), or functional entities (species-pairs with unit-distance between species). This framework unifies ecologists' measures of species diversity, phylogenetic diversity, and distance-based functional diversity. It also provides a unified method of decomposing these diversities and constructing normalized taxonomic, phylogenetic, and functional similarity and differentiation measures, including *N*-assemblage phylogenetic or functional generalizations of the classic Jaccard, Sørensen, Horn, and Morisita-Horn indexes. A real example shows how this framework extracts ecological meaning from complex data.

1. INTRODUCTION

Biodiversity, the variety and variability among living organisms and the ecological complexes in which they occur, is a central concept in the life sciences; this includes diversity within species, between species, and of ecosystems (Gaston 1996). Widespread concern about the impact of human activities on ecosystems has made the measurement and assessment of biodiversity increasingly important topics in recent years. With the remarkable progress in our understanding of phylogenies and species traits in ecosystem function, assessing biodiversity has become more complex. In species diversity, all species are treated as equally different from each other. Pielou (1975, p. 17) was the first to notice that diversity measures could be broadened to incorporate species differences. All else being equal, an assemblage of species that are highly divergent from each other is more diverse than an assemblage consisting of species that are similar to each other. Differences among species can be based on their evolutionary histories, as estimated by taxonomic classification or well-supported phylogenetic trees, or can be based on their different trophic guilds or functional traits. Many researchers have recognized the importance of incorporating species differences into biodiversity (see below). Many of the most pressing and fundamental questions in ecology, evolution, and systematics require robust and meaningful measures of this expanded concept of diversity.

Evolutionary or phylogenetic differences among species have been incorporated into diversity analysis since the 1990s (Faith 1992; Warwick & Clarke 1995; McPeek & Miller 1996; Crozier 1997; Webb 2000; Webb et al. 2002, 2006; Helmus et al. 2007; Graham & Fine 2008; Cavender-Bares et al. 2009, 2012; Pavoine et al. 2009a, 2010; Ives & Helmus 2010, 2011; Vellend et al. 2011). Most phylogenetic diversity measures are generalizations of the classic species diversity measures: species richness, Shannon entropy (Shannon 1948), and the Gini-Simpson index (Simpson 1949). We provide a brief review of the classic measures and their phylogenetic generalizations in Sections 2.1 and 2.2.

When species are described by a set of traits that affect ecosystem functioning, species differences can be measured by the dissimilarity or distances between their trait profiles. Functional diversity or trait diversity, a rapidly growing research field in ecology, refers to the diversity of the value and range of species or organismal traits (Tilman et al. 1997; Díaz & Cabido 2001; Tilman 2001; Petchey & Gaston 2002, 2009; Ricotta 2005; Swenson 2012; Swenson et al. 2012). Functional diversity is regarded as key to understanding ecosystem processes and their response to environmental stress or disturbance (Norberg et al. 2001, Suding et al. 2008, Cadotte et al. 2009, Flynn et al. 2011). A large array of functional diversity measures have been developed in the literature (Walker et al. 1999, Petchey & Gaston 2002, Díaz et al. 2007, Villéger et al. 2008, Poos et al. 2009, Schmera et al. 2009, Laliberte & Legendre 2010, Mouchet et al. 2010, Chiu & Chao 2014). There are three major approaches to functional diversity measures: trait-value based, dendrogram based, and distance based (for reviews, see Cadotte et al. 2011, Weiher 2011, Pla et al. 2012, Mason et al. 2013, Mouillot et al. 2013). In this article, we focus on distance-based functional diversity and provide a brief review in Section 2.3 of some related measures and their decompositions. Throughout this article, we use "functional diversity" to refer to distance-based functional diversity.

How to quantify abundance-based species diversity in an assemblage has been one of the most controversial issues in community ecology (e.g., Hurlbert 1971; Routledge 1979; Patil & Taillie 1982; Purvis & Hector 2000; Jost 2006, 2007; Jost et al. 2010; Chao et al. 2012). There have also been intense debates on the choice of diversity partitioning schemes (see Ellison 2010 and the forum that follows it). All authors in the forum following Ellison (2010) achieved a consensus on the use of Hill numbers, also called the effective number of species, as the best choice to quantify abundance-based species diversity. Here, the effective number of species means the number of

equally abundant species that are needed to give the same value of a diversity measure. Illustration of this concept is provided below. Hill numbers are a parametric family of diversity indexes differing among themselves only by the parameter q that determines sensitivity to species relative abundances. The concept of effective number was first used in genetics by Kimura & Crow (1964) and in ecology by MacArthur (1965, 1972). The parametric family that unifies various effective numbers was found by Hill (1973) and was recently reintroduced to ecologists by Jost (2006, 2007). Hill numbers and the advantages of using Hill numbers as diversity measures are reviewed in Section 3.

The most important property of Hill numbers is that they obey a replication principle. Hill (1973) proved a weak version of the replication principle: If N equally large and completely distinct assemblages (i.e., no species in common) have identical relative abundance distributions, then the Hill number of the pooled assemblage will be N times the diversity of an individual assemblage. Chiu et al. (2014, appendix B) recently proved a strong version of the doubling property: Given N equally diverse, equally large assemblages with no species in common (relative abundance distributions may be different, unlike the weak version), then the diversity of the pooled assemblage will be N times the diversity of a single assemblage. Thus, Hill numbers are linear with respect to this kind of pooling of assemblages. If $N = 2$, the replication principle is referred to as the doubling property. We focus on the strong version and provide an illustrative example in Section 4.

Chao et al. (2010) extended Hill numbers to phylogenetic diversity, which incorporates species evolutionary history or phylogenetic distance between species. Recently, Chiu & Chao (2014) also extended Hill numbers to distance-based functional diversity based on species traits. In this article, we review Hill numbers and their extensions and integrate these into a unified framework of attribute diversity (or the effective total attribute value) in Section 4. For species diversity, all species (as taxonomic entities) are treated as being taxonomically equally distinct, so the attribute value is unity for each species. Thus, ordinary Hill numbers in this case measure the effective number of taxonomic entities. For phylogenetic diversity, the attribute value (or feature) (sensu Faith 1992, 2013) is the length of each branch segment; thus all unit-length branches (as phylogenetic entities) are treated as phylogenetically equally distinct. For functional diversity, the attribute value is the functional distance between each pair of species; thus all species pairs with a unit of species pairwise distance (as functional entities) are treated as functionally equally distinct.

By treating each unit-attribute-value entity as a "species" in ordinary species-based diversity, the taxonomic diversity, phylogenetic diversity, and functional diversity can all be formulated as Hill numbers of the corresponding entities or "species," with each entity weighted by its relative abundance or by a measure of its relative importance. For phylogenetic diversity, Hill numbers measure the effective number of unit-length branch segments. For functional diversity, Hill numbers measure the effective number of species pairs with a unit of species pairwise distance. Most previously proposed measures of phylogenetic and functional diversity (Sections 4.1–4.3) can be transformed into this framework and can be better understood through it. The replication principle was also generalized to phylogenetic diversity and functional diversity; a review of these generalizations is given in Section 4.4. We also adopt Hill numbers as a general framework for partitioning diversities (Section 5) and constructing normalized taxonomic, phylogenetic, and functional similarity and differentiation measures (Section 6). Thus, Hill numbers provide a unified framework for measuring and assessing virtually all aspects of biodiversity.

2. PREVIOUS DIVERSITY MEASURES RELATED TO OUR FRAMEWORK

Since the foundational work by Fisher et al. (1943), an enormous number of diversity indexes and similarity/differentiation measures have been proposed, not only in ecology but also in genetics,

economics, information science, linguistics, physics, and the social sciences. There are two general approaches: parametric and nonparametric. Parametric approaches assume a particular species abundance distribution (e.g., log-series, lognormal, negative-binomial, and Zipf-Mandelbrot models) or a species rank abundance distribution (e.g., broken-stick, Poisson lognormal, and geometric series). Then ecologists use the parameters of the distribution (e.g., Fisher's alpha, a parameter to characterize the log-series) or the variance of the distribution to measure heterogeneity or diversity (for overviews, see Magurran 2004, Magurran & McGill 2011, Legendre & Legendre 2012).

However, the parametric approaches often do not perform well because the observed data are not generally sufficient to determine the true abundance distribution, and the results are uninterpretable unless the "true" species abundance distribution is known (Colwell & Coddington 1994, Chao 2005, Jost 2007, Chao & Chiu 2012). The parametric model also does not permit meaningful comparison of assemblages with different abundance distributions. For example, an assemblage that obeys a lognormal abundance model cannot be compared with an assemblage whose abundance distribution follows a gamma distribution. Moreover, it is difficult to incorporate evolutionary or functional differences among species into this approach. Thus, nonparametric methods are more popular because they make no assumptions about the distributional form of the underlying species abundance distribution. In the following subsections, we review the classic nonparametric diversity measures and their phylogenetic and/or functional generalizations.

2.1. Generalized Entropies and Their Decomposition

The species richness of an assemblage is a simple count of the number of species present. It is the most intuitive and frequently used measure of biodiversity and is a key metric in conservation biology (MacArthur & Wilson 1967, Hubbell 2001, Magurran 2004). However, it does not incorporate any information about the abundances of species, and it is a very hard number to estimate accurately from small samples (Colwell & Coddington 1994, Chao 2005, Gotelli & Colwell 2011).

Shannon entropy is a popular abundance-based diversity index and has been used in many disciplines. Shannon entropy is

$$H_{Sh} = -\sum_{i=1}^{S} p_i \log p_i,$$

1a.

where S is the number of species in the assemblage and p_i is the relative abundance of the ith species. Shannon entropy gives the uncertainty in the species identity of a randomly chosen individual in the assemblage. Another popular measure is the Gini-Simpson index,

$$H_{GS} = 1 - \sum_{i=1}^{S} p_i^2,$$

1b.

which gives the probability that two randomly chosen individuals belong to different species. These two abundance-sensitive measures, along with species richness, can be united into a single family of generalized entropy, parameterized by a variable q that controls the measure's sensitivity to species relative abundances:

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

1c.

Here, $^0H = S - 1$, ^1H (the limit of ^qH when q tends to unity) is identical to Shannon entropy, and ^2H is identical to the Gini-Simpson index. This family of indexes has been found many times in

different disciplines (Havrdra & Charvát 1967, Daróczy 1970, Patil & Taillie 1979, Tsallis 1988, Keylock 2005). There are many other families of generalized entropies, most notably the Rényi entropy (which is a monotonic transformation of ^qH).

Members of this family of generalized entropies use different units (e.g., richness is in units of species, the Gini-Simpson index is a probability, and Shannon entropy is in units of information), so they cannot easily be compared with each other. Although generalized entropies and their special cases have been useful in many disciplines (e.g., see Magurran 2004), when $q \neq 0$ they do not behave in the same intuitive linear way as does species richness, even when all relative abundances are equal. In ecosystems with high diversity, mass extinctions may hardly affect their values (Jost 2007, 2010). They also lead to logical contradictions in conservation biology because they do not measure a conserved quantity even in symmetric situations (e.g., under a given conservation plan, the proportion of "diversity" lost and the proportion preserved can both be 90% or more, even if the assemblage lost and the assemblage preserved are equally large and equally diverse) (Jost 2006, 2007; Jost et al. 2010). Thus, changes in the magnitude of these indexes (if $q \neq 0$) cannot be properly compared or interpreted.

For multiple assemblages, the abundance-sensitive generalized entropies were traditionally decomposed using the additive framework. In this approach, a common similarity measure is the ratio of the within-group or "alpha" diversity divided by the total or "gamma" diversity. However, this similarity measure does not actually quantify the compositional similarity of the assemblages under study; it can be arbitrarily close to unity (supposedly indicating high similarity) even when the assemblages being compared have no species in common (Jost 2006, 2007; Jost et al. 2010). All these problems are consequences of the failure of generalized entropy to satisfy the replication principle. By contrast, Hill numbers obey the replication principle and resolve all these problems (see Section 3).

2.2. Phylogenetic Generalized Entropies and Their Decomposition

The most widely used phylogenetic metric is Faith's phylogenetic diversity (*PD*) (Faith 1992), the sum of the branch lengths of a phylogenetic tree connecting all species in the target assemblage. As shown in Chao et al. (2010), Faith's *PD* can be regarded as a phylogenetic generalization of species richness. Species abundances are not considered in Faith's *PD*.

Rao's quadratic entropy takes account of both phylogeny and species abundances (Rao 1982):

$$Q = \sum_{i=1}^{S} \sum_{j=1}^{S} d_{ij} p_i p_j, \qquad \text{2a.}$$

where d_{ij} denotes the phylogenetic distance (in years since divergence, number of DNA base changes, or other metrics) between species i and j. This index measures the average phylogenetic distance between any two individuals randomly selected from the assemblage. Rao's Q is a phylogenetic generalization of the Gini-Simpson index, because in the special case of no phylogenetic structure (all species are equally related to one another), with $d_{ii} = 0$ and $d_{ij} = 1$ $(i \neq j)$, it reduces to the Gini-Simpson index.

The phylogenetic entropy H_P is a generalization of Shannon entropy to incorporate phylogenetic distances among species (Allen et al. 2009):

$$H_P = -\sum_i L_i a_i \log a_i, \qquad \text{2b.}$$

where the summation is over all branches of a rooted phylogenetic tree, L_i is the length of branch i, and a_i denotes the summed relative abundance of all species descended from branch i.

A tree is called ultrametric if all branch tips are the same distance from the root (the first node). Faith's PD, the H_P of Allen and colleagues, and Rao's Q for an ultrametric tree with depth T (i.e., the age of the root node of the tree) can be united into a single parametric family of phylogenetic generalized entropies (Pavoine et al. 2009a)

$$^qI = \left(T - \sum_i L_i a_i^q\right) /(q - 1).$$

2c.

Here, L_i and a_i are defined as in Equation 2b. Then $^0I =$ Faith's PD minus T, ^1I is identical to the phylogenetic entropy H_P given in Equation 2b, and ^2I is identical to Rao's quadratic entropy Q given in Equation 2a. In the special case when $T = 1$ (the tree depth is normalized to unit length) and all branch segments have unit length, then the phylogenetic generalized entropy reduces to the classic generalized entropy defined in Equation 1c, with species relative abundances $\{p_1, p_2, \dots, p_S\}$ as the tip-node abundances.

Because Shannon entropy and the Gini-Simpson index do not obey even the weak version of the replication principle, neither do their phylogenetic generalizations. These generalizations will, therefore, have the same interpretational problems as their parent measures (for examples, see Chao et al. 2010 and their supplementary material). The measures are not wrong—they accurately measure interesting aspects of population structure. But their metrics do not correspond to intuitive notions of diversity, their ratio comparisons are difficult to interpret correctly, and they cannot be directly compared with each other for different values of q.

As with generalized entropies, the abundance-sensitive phylogenetic generalized entropies (including quadratic entropy and phylogenetic entropy) were traditionally decomposed using the additive framework (Ricotta 2005, Hardy & Senterre 2007, Pavoine et al. 2009a, Mouchet & Mouillot 2011). Chiu et al. (2014) showed both empirically and theoretically that this additive approach has the same mathematical property discussed above for generalized entropies. These traditional differentiation measures, (gamma − alpha)/gamma, will always tend to zero, and the corresponding similarity measures, alpha/gamma, will always tend to the maximum value of unity, whenever gamma is high for phylogenetic entropy (^1I) and whenever alpha is high for quadratic entropy (^2I). Thus, these similarity or differentiation measures cease to reflect either tree structure or differences in species abundances and are not biologically informative. Such problems arise mainly because phylogenetic generalized entropies do not obey the replication principle, which ensures that diversity measures are linear with respect to species addition or group pooling (for the extension of the replication principle to phylogenetic diversity, see Section 4.4).

2.3. Functional Diversity Measures and Their Decomposition

We mainly review the distance-based functional indexes and differentiation measures that are related to Hill numbers. The functional attribute diversity (FAD) (Walker et al. 1999) is the sum of the pairwise distances between species,

$$FAD = \sum_{i=1}^{S} \sum_{j=1}^{S} d_{ij},$$

3a.

where d_{ij} is the functional distance between the ith and jth species, such that $d_{ij} = d_{ji} \geq 0$. This measure does not consider the abundances of the species, which may play an important role in the functioning of ecosystems.

Functional diversity measures combining both functional distance and species abundance have been proposed (Rao 1982; Mason et al. 2003, 2005; Botta-Dukát 2005; Ricotta & Szeidl 2006;

Villéger et al. 2008; Laliberte & Legendre 2010). Rao's quadratic entropy (Rao 1982) defined in Equation 2a (where d_{ij} is replaced by functional distance) is the most widely used measure. Despite its wide application to functional diversity, Q, like the Gini-Simpson index, does not obey the replication principle, causing counterintuitive results in ecological applications (Jost 2008, Ricotta & Szeidl 2009, Chiu et al. 2014). Guiasu & Guiasu (2011, 2012) proposed a weighted Gini-Simpson index for pairs of species as follows:

$$GS_D = \sum_{i=1}^{S} \sum_{j=1}^{S} d_{ij}\, p_i\, p_j (1 - p_i p_j) = Q - \sum_{i=1}^{S} \sum_{j=1}^{S} d_{ij}(p_i p_j)^2. \qquad \text{3b.}$$

The three measures (FAD, Q, and GS_D) are closely related to the measures in our unified framework.

For distance-based functional diversity, nearly all previous decompositions are based on additively partitioning Rao's quadratic entropy Q. As discussed in Section 2.2, this approach cannot lead to biologically meaningful similarity or differentiation measures. Ricotta & Szeidl (2009) and de Bello et al. (2010) transformed Q to the effective number of species with a maximum species pairwise distance $d_{\max}$ (see below), which is the theoretical species richness of a perfectly even assemblage with the same quadratic entropy as the original assemblage. Their effective number of species can be expressed as

$$Q_e = \frac{1}{1 - Q/d_{\max}}, \qquad \text{3c.}$$

where $d_{\max}$ denotes the maximum of species pairwise distances. Equivalently, by dividing each distance by its maximum value in the distance matrix prior to all analyses, they scaled all distances so they are between 0 and 1. Villéger et al. (2012) and Escalas et al. (2013) applied the above formula to obtain the corresponding effective number of species for gamma (denoted here by $Q_{e,\gamma}$) and alpha (denoted by $Q_{e,\alpha}$) quadratic entropies, where the subscript e denotes effective. Based on a multiplicative decomposition, this approach leads to the corresponding beta diversity $Q_{e,\beta} = Q_{e,\gamma}/Q_{e,\alpha}$.

De Bello et al. (2010) transformed this beta diversity into a normalized differentiation measure $Q_{e,\beta}^* = (1 - 1/Q_{e,\beta})/(1 - 1/N)$, so that the resulting measure is in the unit interval [0, 1], where N denotes the number of assemblages. Villéger et al. (2012) further proposed a normalized differentiation measure $Q_{e,\beta}^{**} = (Q_{e,\beta} - 1)/(N - 1)$. In functional diversity analysis, most species pairwise distances based on species traits are not ultrametric. [A distance metric d is ultrametric if it satisfies the criterion $d(x, y) \leq \max\{d(x, z), d(y, z)\}$ for all x, y, and z.] Chiu & Chao (2014) used examples to show that the application of Equation 3c and the associated differentiation measures to nonultrametric distance matrices may yield uninterpretable results because Equation 3c is not valid for nonultrametric matrices. The approach by Chiu & Chao (2014) (reviewed in Section 4.3) is valid for any type of distance matrix.

2.4. Other Unified Approaches

Leinster & Cobbold (2012) derived a parametric class of measures based on species similarity. Scheiner (2012) also proposed a metric that integrates abundance, phylogeny, and function. Because the approaches of both Leinster & Cobbold (2012) and Scheiner (2012) are based on a framework of Hill numbers and their measures are in units of species equivalents, it is important to distinguish these two previous approaches from ours (for detailed discussions, see **Supplemental Appendix 1;** for all **Supplemental Material**, follow the link from the Annual Reviews home page at **http://www.annualreviews.org**). We find that the measure proposed by Leinster &

▶ Supplemental Material

Cobbold (2012) may not be sensitive to species abundances when the similarity matrix is computed from species traits in functional analysis. If the species similarity matrix deviates greatly from a naive identity matrix, then their measure typically yields very low diversity values especially for assemblages with many species; this causes problems for the interpretation of species equivalents in their approach. Reeve et al. (2014) recently proposed a partitioning of the Leinster & Cobbold (2012) diversity measure. In **Supplemental Appendix 1**, we also give an example to show that their gamma diversity may be less than their proposed alpha diversity even in an equal-weight case. Scheiner's (2012) measure cannot be directly linked to most of the previous phylogenetic and functional measures reviewed in Sections 2.2 and 2.3. Scheiner's approach and our measures have different meanings of species equivalents and thus quantify different aspects and properties of ecosystems. Neither the measures proposed by Leinster & Cobbold (2012) nor those proposed by Scheiner (2012) have been developed to construct normalized similarity (or differentiation) measures that can be applied to compare multiple sets of assemblages.

3. ADVANTAGES OF USING HILL NUMBERS

Shannon entropy and the Gini-Simpson index can be easily converted to the effective number of species (the number of equally common species that would be needed to produce the given Shannon entropy or Gini-Simpson index) (MacArthur 1965). Shannon entropy can be converted by taking its exponential, and the Gini-Simpson index can be converted by the formula $1/(1-H_{GS})$. The converted measures use the same units as species richness. Hill (1973) integrated species richness and the converted Shannon and Gini-Simpson measures into the class of diversity measures called Hill numbers of order q, or the effective number of species, defined as

$$^{q}D = \left(\sum_{i=1}^{S} p_i^q \right)^{1/(1-q)}, \quad q \geq 0, \quad q \neq 1. \qquad 4a.$$

This measure is undefined for $q = 1$, but its limit as q tends to unity exists and is

$$^{1}D = \lim_{q \to 1} {}^{q}D = \exp\left(-\sum_{i=1}^{S} p_i \log p_i \right) = \exp(H_{Sb}). \qquad 4b.$$

The relationship between Hill number of order q ($q \neq 1$) and the generalized entropy can be expressed as

$$^{q}D = [1 - (q - 1)(^{q}H)]^{1/(1-q)}. \qquad 4c.$$

There are two essential assumptions in the ordinary species-based Hill numbers. First, all species are assumed to be equally distinct. Second, only species relative abundances, $\{p_1, p_2, \ldots, p_S\}$ with $\sum_{i=1}^{S} p_i = 1$, are involved in Equation 4a; thus species abundances or weights must be properly normalized to calculate Hill numbers. The parameter q determines the sensitivity of the measure to the relative frequencies of the species. When $q = 0$, the species abundances do not count at all and $^{0}D = S$ is obtained. When $q = 1$, the species are weighed in proportion to their frequencies and the measure ^{1}D (in Equation 4b) can be interpreted as the effective number of common or typical species (i.e., species with typical abundances) in the assemblage. When $q = 2$, abundant species are favored and rare species are discounted; the measure ^{2}D becomes the inverse Simpson concentration. The measure ^{2}D can be interpreted as the effective number of dominant or very abundant species in the assemblage.

In general, if $^{q}D = x$, then the diversity of order q of this assemblage is the same as that of an idealized assemblage with x equally abundant species. This is why Hill numbers are referred to as the effective number of species or as species equivalents. All Hill numbers are in units of species.
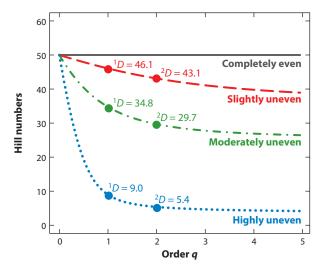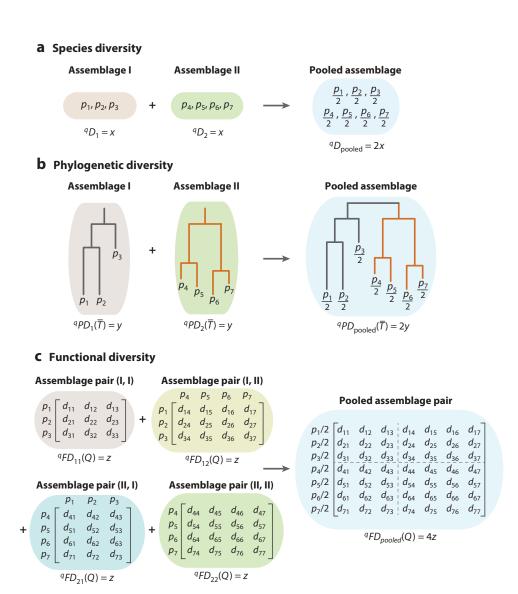
Figure 1

Diversity (Hill numbers) profile for assemblages of differing evenness. The x axis is the order q, $0 \leq q \leq 5$. The y axis is the Hill number (the effective number of equally abundant species). Each of the four assemblages has exactly 50 species and 500 individuals, but they differ in their relative evenness. Completely even assemblage (*solid black line*): Each species is represented by 10 individuals; slightly uneven assemblage (*long-dashed red line*): 25 species each represented by 14 individuals and 25 species each represented by 6 individuals (this structure is denoted as $\{25 \times 14, 25 \times 6\}$); moderately uneven assemblage (*dash-dotted green line*): $\{20 \times 20, 15 \times 5, 10 \times 2, 5 \times 1\}$; highly uneven assemblage (*dotted blue line*): $\{1 \times 150, 1 \times 120, 1 \times 80, 1 \times 50, 6 \times 10, 40 \times 1\}$. For $q = 0$, the Hill number is species richness, which is equal to 50 for all assemblages. The diversity profile curve is a nonincreasing function of q. The slope of the curve reflects the unevenness of species relative abundances. The more uneven the distribution of relative abundances, the more steeply the curve declines. For completely even relative abundances, the curve is a constant at the level of species richness. The two solid dots on each curve denote the Hill numbers of order $q = 1$ and 2. For example, in the highly uneven assemblage, $^{1}D = 9$, implying that the Shannon diversity of the assemblage is the same as that of an assemblage with 9 equally abundant species. For $q = 2$, $^{2}D = 5.4$, implying that the Simpson diversity of the assemblage is the same as that of an assemblage with 5.4 equally abundant species. Similar interpretation applies to other assemblages.

It is thus possible to plot them on a single graph as a continuous function of the parameter q. This diversity profile characterizes the species abundance distribution of an assemblage and provides complete information about its diversity. The steepness of its slope graphically illustrates the degree of dominance in the assemblage (for examples illustrating the concept of the effective number of species, see **Figure 1**). As proved by Chao et al. (2014b), a diversity profile conveys the same information as the species accumulation curve of an assemblage.

Hill numbers offer six distinct advantages over other diversity indexes. First, as discussed in Section 1, Hill numbers of a given order q obey an intuitive replication principle or doubling property implicit in biologists' concept of diversity: Suppose there are N equally large, equally diverse assemblages with no shared species are pooled. The diversity of the pooled assemblage is N times the diversity of any single assemblage (see **Figure 2a**). Most other diversity indexes do not obey this property. Because Hill numbers obey this replication principle, changes in their magnitude have simple interpretations, and the ratio of alpha diversity to gamma diversity accurately reflects the compositional similarity of the assemblages. The property has been extensively discussed by many authors (MacArthur 1965, 1972; Whittaker 1972; Hill 1973; Peet 1974; Routledge 1979; Jost 2006, 2007, 2009; Ricotta & Szeidl 2009; Jost et al. 2010) and has been extended to phylogenetic and functional diversity measures (Chao et al. 2010, Chiu & Chao 2014) (see Section 4.4).

Second, all Hill numbers are expressed in intuitive units of effective numbers of species. There-fore, they can be directly compared across orders q to extract information about dominance and other assemblage characteristics (see **Figure 1**). Third, key diversity indexes proposed in the litera-ture, including the widely used Shannon entropy and the Gini-Simpson index, can be converted to Hill numbers by simple algebraic transformations. Fourth, they can be easily partitioned into inde-pendent within- and between-group components. Fifth, in comparisons of multiple assemblages, there is a direct link between Hill numbers and species compositional similarity (or differentiation) among assemblages (Jost 2007, Chao et al. 2014b). This property unites diversity and similarity (or differentiation). Sixth, and most relevant to this review, Hill numbers and their partitioning can be generalized to taxonomic, phylogenetic, and functional diversities, so they provide a unified framework for measuring biodiversity.

a Species diversity

Assemblage I: p_1, p_2, p_3 + Assemblage II: p_4, p_5, p_6, p_7 → Pooled assemblage: $\frac{p_1}{2}, \frac{p_2}{2}, \frac{p_3}{2}$ $\frac{p_4}{2}, \frac{p_5}{2}, \frac{p_6}{2}, \frac{p_7}{2}$

$^qD_1 = x$ $^qD_2 = x$ $^qD_{\text{pooled}} = 2x$

b Phylogenetic diversity

$^qPD_1(\overline{T}) = y$ $^qPD_2(\overline{T}) = y$ $^qPD_{\text{pooled}}(\overline{T}) = 2y$

c Functional diversity

Assemblage pair (I, I):
$^qFD_{11}(Q) = z$

Assemblage pair (I, II):
$^qFD_{12}(Q) = z$

Assemblage pair (II, I):
$^qFD_{21}(Q) = z$

Assemblage pair (II, II):
$^qFD_{22}(Q) = z$

Pooled assemblage pair:
$^qFD_{pooled}(Q) = 4z$

4. A UNIFIED FRAMEWORK: ATTRIBUTE DIVERSITY BASED ON HILL NUMBERS

Consider an assemblage of S species with relative abundances (or any measure of relative importance) $\{p_1, p_2, \ldots, p_S\}$, $\sum_{i=1}^{S} p_i = 1$. Assume these species are connected through a (possibly nonultrametric) phylogenetic tree and a matrix of pairwise distances between species based on functional traits. The species diversity, phylogenetic diversity, and functional diversity can each be formulated as the attribute diversity (Hill numbers) of the equally distinct entities (taxonomic entities, phylogenetic entities, and functional entities, as briefly introduced in the Introduction and discussed in this section), with each entity weighted by its relative abundance or by a measure of relative importance (for a summary, see **Table 1**).

1. In species diversity, all species are taxonomically equally distinct, and thus the taxonomic entities are species. Each species has an attribute value of unity and is weighted by its relative abundance. Species diversity measures the effective number of these species or entities (see Section 4.1).

2. In phylogenetic diversity, the attribute value for each branch segment is its length. A unit-length branch segment is defined as a phylogenetic entity. All entities are phylogenetically equally distinct with an attribute value of unity for each entity. Instead of species, we are measuring the effective number of phylogenetic entities, equivalently, the effective total of the attribute values. In other words, "species" are replaced by phylogenetically equally distinct entities (Faith 1992, 2013). For example, a branch of 5-unit length is counted as 5 "species" (i.e., 5 phylogenetic entities). Each entity is weighted by the corresponding branch abundance, the summed relative abundance of all species descended from the branch (see Section 4.2).

3. In functional diversity, the attribute value of each pair of species is the functional trait distance between the pair of species. A species-pair with a unit of distance between the two species is defined as a functional entity. All entities are functionally equally distinct with an attribute

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Figure 2

A strong version of the replication principle or quadratic replication principle for the attribute diversity in the special case of two assemblages (for the direct extension to N assemblages, see Section 4.4). Assume there are two equally large assemblages. Assemblage I (with phylogenetic tree in *black*) includes three species with species relative abundances $\{p_1, p_2, p_3\}$, and Assemblage II (with phylogenetic tree in *orange*) includes four completely distinct species with species relative abundances $\{p_4, p_5, p_6, p_7\}$. The pooled assemblage includes seven species with abundances $\{p_1/2, p_2/2, \ldots, p_7/2\}$. Background colors are simply for clearer presentation. (*a*) Replication principle for ordinary Hill numbers: When two assemblages with no shared species and with the same diversity are pooled, the diversity of the pooled assemblage is twice the diversity of either one of the single assemblages. The relative abundance distributions are allowed to be different between the two assemblages. For $q > 0$, the two assemblages may have a different number of species. (*b*) Replication principle for the phylogenetic diversity $^qPD(\bar{T})$ (Equation 6a) for two assemblages with totally different tree structures: If the two assemblages are completely phylogenetically distinct as shown (no branches shared between assemblages, though branches within an assemblage may be shared) and they have identical mean branch lengths (i.e., $\bar{T}_1 = \bar{T}_2 \equiv \bar{T}$) and identical phylogenetic diversities (i.e., $^qPD_1(\bar{T}) = ^qPD_2(\bar{T}) \equiv y$), then the phylogenetic diversity $^qPD(\bar{T})$ of the pooled assemblage will be double that of each individual assemblage. (*c*) Quadratic replication principle for the functional diversity $^qFD(Q)$ (Equation 7a): Assume the mean species pairwise distances for the four assemblage pairs, (I, I), (I, II), (II, I), and (II, II), are identical (i.e., $Q_{11} = Q_{12} = Q_{21} = Q_{22} \equiv Q$), and assume the functional diversities for the four assemblage pairs are also identical (i.e., $^qFD_{11}(Q) = ^qFD_{12}(Q) = ^qFD_{21}(Q) = ^qFD_{22}(Q) \equiv z$). The quadratic replication principle implies that the functional diversity of the pooled assemblage will be quadruple that of each individual assemblage.

Table 1 A unified framework for quantifying species diversity, phylogenetic diversity, and functional diversity on the basis of Hill numbers (by treating each entity as a "species" with its relative abundance as indicated in the table)

Type of diversity	Element in collection C	Attribute value	Entity	Relative abundance of an entity	Attribute diversity (effective number of entities or total attribute value)	Generalized Hill numbers (effective number of species or lineages)
Attribute diversity (unified framework)	Element u in collection C, $u \in C$	v_u	An entity is an element with a unit of attribute value	$a_u/\bar{V}$, where a_u = weight or abundance, $\bar{V} = \sum_{u \in C} v_u a_u$	$^q AD(\bar{V}) =$ $\left[\sum_{u \in C} v_u \times \left(\frac{a_u}{\bar{V}} \right)^q \right]^{1/(1-q)}$	Generalized Hill numbers $^q D(\bar{V}) = \left[\frac{^q AD(\bar{V})}{\bar{V}} \right]^{1/\lambda}$ $\lambda = 1$ or $\lambda = 2$ (see below)
Species diversity	Species i, $C = \{1, \dots, S\}$	Unity for species i	Taxonomic entity (species)	p_i; species relative abundance ($\bar{V} = 1$)	Species diversity (Hill numbers, effective number of species) $^q D = \left[\sum_{i=1}^S 1 \times \left(\frac{p_i}{\sum_{k=1}^S p_k} \right)^q \right]^{1/(1-q)}$	Hill numbers $^q D$
Phylogenetic diversity	Branch segment i, $C = \{1, \dots, B\}$	Branch length L_i for branch i	Phylogenetic entity (branch of unit-length)	$a_i/\bar{T}$, where $a_i =$ branch abundance, $\bar{T} = \sum_{j=1}^B L_j a_j$	Phylogenetic diversity (effective total branch-length) $^q PD(\bar{T}) = \left[\sum_{i=1}^B L_i \times \left(\frac{a_i}{\bar{T}} \right)^q \right]^{1/(1-q)}$	Phylogenetic Hill numbers $^q \bar{D}(\bar{T}) = \frac{^q PD(\bar{T})}{\bar{T}}$
Functional diversity	Species-pair (i,j), $C = \{(i,j); i,j = 1, \dots, S\}$	Distance d_{ij} for species-pair (i,j)	Functional entity (species-pair of unit-distance)	$p_i p_j /Q$, where $Q = \sum_{i,j=1}^S d_{ij} p_i p_j$	Functional diversity (effective sum of species pairwise distances) $^q FD(Q) = \left[\sum_{i,j=1}^S d_{ij} \times \left(\frac{p_i p_j}{Q} \right)^q \right]^{1/(1-q)}$	Functional Hill numbers $^q D(Q) = \left(\frac{^q FD(Q)}{Q} \right)^{1/2}$

value of unity for each entity. Instead of species, we are measuring the effective number of functional entities, or equivalently, the effective sum of functional distances between two species. Here, "species" are replaced by functionally equally distinct entities. For example, a species-pair with distance of 5 units is counted as 5 "species" (i.e., 5 functional entities). The weight for each entity is determined by the product of the relative abundances of the two species involved (see Section 4.3).

In this article, we integrate the three types of diversities into a unified framework. Let C denote the original collection of species (in species diversity), phylogenetic tree branch segments (in phylogenetic diversity), or species pairs (in functional diversity). For each element u in the collection, assume its attribute value is denoted by v_u and its weight or measure of importance is denoted by a_u (biomass, cover area, relative or absolute abundance, or incidence frequency in a set of sample plots, or any other measure). We refer to a_u as the abundance or weight of element u for simplicity. The mean attribute value (weighted by abundance) is

$$\bar{V} = \sum_{u \in C} v_u a_u. \qquad \text{5a.}$$

In species diversity, all species in the original collection are equally distinct. However, the branch segments or species pairs in the collections of the other two types of diversities are not equally distinct. Our approach to unify these three types of diversities is to first consider a new collection of equally distinct entities, i.e., taxonomic entities in species diversity, phylogenetic entities in phylogenetic diversity, and functional entities in functional diversity. Any element in the original collection with attribute value of v_u is counted as v_u entities in this new collection. Because all entities are equally distinct in the new collection, they can be regarded as "species" in ordinary species-based Hill numbers. Note that in our unified framework, the number of entities is allowed to be any real number, not necessarily an integer.

Next we determine the relative abundance of each entity in the new collection by proper normalization. Note that the mean attribute value $\bar{V}$ is also the total abundance of entities, implying each of the v_u entities has relative abundance $a_u/\bar{V}$. It follows from the definition of $\bar{V}$ that the sum of all relative abundances of entities is unity, i.e., $\sum_{u \in C} v_u(a_u/\bar{V}) = 1$ so that we can apply the concept of Hill numbers to this new collection of entities for all three types of diversities. Two illustrative examples are provided in **Supplemental Appendix 2**. The proposed attribute diversity of order q is the Hill number of order q of this new collection of entities:

▶ Supplemental Material

$$^qAD(\bar{V}) = \left[\sum_{u \in C} v_u \times \left(\frac{a_u}{\bar{V}} \right)^q \right]^{1/(1-q)} = \left[\sum_{u \in C} v_u \times \left(\frac{a_u}{\sum_{b \in C} v_b a_b} \right)^q \right]^{1/(1-q)}. \qquad \text{5b.}$$

This is interpreted as the effective number of entities or the effective total of the attribute values because each entity has attribute value of unity. Thus, by considering the new collection of entities, the attribute diversity is a genuine Hill number in units of attribute value. It is dependent on the units used to measure the attribute. It is independent of the units used to measure abundances because it is only a function of the relative abundances $a_u/\bar{V}$ (the units are cancelled out in both numerator and denominator). We express the attribute diversity as a function of the mean attribute value $\bar{V}$ to emphasize its important role in the construction of other measures (see Equation 5c) and in the proof of the replication principle (discussed in Section 4.4).

For species diversity, the measure $^qAD(\bar{V})$ reduces to ordinary Hill numbers (in units of species). For phylogenetic diversity, it reduces to the branch diversity (in units of branch length) derived in Chao et al. (2010). For functional diversity, it reduces to the total-distance diversity

(in units of functional distance) proposed recently in Chiu & Chao (2014) (for a summary, see **Table 1**) (also see Sections 4.1–4.3).

When $q = 0$ or all abundances are identical ($a_u \equiv a$), ${}^0 AD(\bar{V}) = \sum_{u \in C} v_u$ (the actual total of the attribute values), which is independent of species abundance (only species incidences are involved) and represents the maximum possible value of the attribute diversity. The attribute diversity of order 0 reduces to species richness (in species diversity), Faith's *PD* (in phylogenetic diversity), and Walker's *FAD* (in functional diversity). From this view, Faith's *PD* (the actual number of phylogenetic entities) and Walker's *FAD* (the actual number of functional entities) can be regarded as phylogenetic richness and functional richness, respectively. When $q = 1$, the attribute diversity formula is defined by letting q tend to 1:

$$ {}^1 AD(\bar{V}) = \lim_{q \to 1} {}^q AD(\bar{V}) = \exp\left(-\sum_{u \in C} v_u \frac{a_u}{\bar{V}} \log \frac{a_u}{\bar{V}} \right). $$

When $q = 2$, ${}^2 AD(\bar{V}) = 1 / \sum_{u \in C} v_u (a_u / \bar{V})^2$.

The attribute diversity can be transformed to the following generalized Hill numbers in units of the effective number of equally common, equally distinct species or lineages (or simply the effective number of species or species equivalents):

$$ {}^q D(\bar{V}) = \left[\frac{{}^q AD(\bar{V})}{\bar{V}} \right]^{1/\lambda}, \qquad\qquad 5c. $$

where $\lambda = 1$ (for species diversity and phylogenetic diversity) and $\lambda = 2$ (for functional diversity). For species diversity, the measure ${}^q D(\bar{V})$ reduces to ordinary Hill numbers. For phylogenetic diversity, it reduces to phylogenetic Hill numbers (Chao et al. 2010). For functional diversity, it reduces to functional Hill numbers (Chiu & Chao 2014). The generalized Hill numbers (in Equation 5c) are independent of not only the units used to measure abundances but also the units used to measure attribute value. We include a parameter λ in Equation 5c so that all these types of Hill numbers are in the same units of species equivalents for all three types of diversities (see **Table 1**). The measure ${}^q AD(\bar{V})/\bar{V}$ in functional diversity quantifies the effective number of species pairs.

These attribute diversities are "effective" numbers, in the following sense: If the attribute diversity of the actual assemblage with a mean attribute value of $\bar{V}$ is ${}^q AD(\bar{V})$, then the attribute diversity of this actual assemblage is the same as that of an idealized assemblage having ${}^q AD(\bar{V})/\bar{V}$ equally abundant and equally distinct species, lineages, or species pairs (corresponding to the three types of diversities) with a constant attribute value of $\bar{V}$ for each species, lineage, or species pair. In the new collection of entities, the interpretation is exactly the same as that of ordinary Hill numbers. That is, the attribute diversity of the collection of entities is the same as that of an idealized collection with ${}^q AD(\bar{V})$ equally abundant entities.

4.1. Species Diversity

Consider the collection of species (entities are equivalent to species), with each species indexed by $i \in C = \{1, 2, \ldots, S\}$. The abundances $\{a_1, a_2, \ldots, a_S\}$ are set to be $\{p_1, p_2, \ldots, p_S\}$, $\sum_{k=1}^{S} p_k = 1$. The attribute value here is the same (unity) for all species, so the mean attribute value is unity and the attribute diversity in Equation 5b reduces to ordinary Hill numbers:

$$ {}^q D = \left[\sum_{i=1}^{S} 1 \times \left(\frac{p_i}{\sum_{k=1}^{S} p_k} \right)^q \right]^{1/(1-q)} = \left(\sum_{i=1}^{S} p_i^q \right)^{1/(1-q)}. $$

4.2. Phylogenetic Diversity

Consider the collection of all branch segments in a phylogenetic tree. Let B denote the number of branch segments in the tree, with each branch indexed by $i \in C = \{1, 2, \ldots, B\}$. Let L_i denote the length of branch i, $i = 1, 2, \ldots, B$, and a_i denote the branch abundance (the summed relative abundance of all species descended from the branch i). The mean attribute value is $\bar{V} = \sum_{i=1}^{B} L_i a_i$, i.e., the mean branch length, which is denoted by $\bar{T}$ in Chao et al. (2010). We use the notation $\bar{T}$ hereafter for mean attribute value in the formula of the phylogenetic diversity. For an ultrametric tree, $\bar{T}$ simply reduces to the tree depth.

For each branch segment with length L_i, $i = 1, 2, \ldots, B$, the new collection in our unified approach consists of L_i phylogenetically equally distinct entities. The total abundance over all entities (the number of entities in the collection is Faith's PD) is $\bar{T}$. Each entity thus has relative abundance $a_i/\bar{T}$ such that $\sum_{i=1}^{B} L_i(a_i/\bar{T}) = 1$. This type of normalization for phylogenetic diversity was first proposed by Chao et al. (2010) with an illustrative example in figure 1 of their paper. More details are provided in **Supplemental Appendix 2**. For both ultrametric and nonultrametric trees, the attribute diversity in Equation 5b reduces to the phylogenetic or branch diversity of Chao et al. (2010):

$$^{q}PD(\bar{T}) = \left[\sum_{i=1}^{B} L_i \times \left(\frac{a_i}{\sum_{j=1}^{B} L_j a_j} \right)^q \right]^{1/(1-q)} = \left[\sum_{i=1}^{B} L_i \times \left(\frac{a_i}{\bar{T}} \right)^q \right]^{1/(1-q)} ; \qquad 6a.$$

$$^{1}PD(\bar{T}) = \lim_{q \to 1} {}^{q}PD(\bar{T}) = \exp\left[-\sum_{i=1}^{B} L_i \frac{a_i}{\bar{T}} \log\left(\frac{a_i}{\bar{T}} \right) \right].$$

The measure $^{q}PD(\bar{T})$ is interpreted as the effective total branch length. When the temporal perspective is taken to be the age of the tree's most basal node, $^{0}PD(\bar{T})$ is Faith's PD. $^{1}PD(\bar{T})$ can be linked to the phylogenetic entropy H_p (in Equation 2b) by the formula $^{1}PD(\bar{T}) = \bar{T} \exp(H_P/\bar{T})$. $^{2}PD(\bar{T})$ can be linked to Rao's quadratic entropy Q (in Equation 2a) by $^{2}PD(\bar{T}) = \bar{T}/(1 - Q/\bar{T})$ (for proofs, see Chao et al. 2010). Faith & Richards (2012) and Faith (2013) subsequently extended the phylogenetic diversity to other applications.

The phylogenetic Hill numbers (or the mean phylogenetic diversity of Chao et al. 2010) in units of the effective number of equally abundant and equally distinct lineages based on Equation 5c are

$$^{q}\bar{D}(\bar{T}) = \frac{^{q}PD(\bar{T})}{\bar{T}} = \left[\sum_{i=1}^{B} \frac{L_i}{\bar{T}} a_i^q \right]^{1/(1-q)}, \quad q \geq 0, \quad q \neq 1; \qquad 6b.$$

$$^{1}\bar{D}(\bar{T}) = \lim_{q \to 1} {}^{q}\bar{D}(\bar{T}) = \exp\left[-\sum_{i=1}^{B} \frac{L_i}{\bar{T}} a_i \log a_i \right].$$

Because $^{q}\bar{D}(\bar{T}) = {}^{q}PD(\bar{T})/\bar{T}$, the phylogenetic Hill numbers can also be linked to Faith's PD: $^{0}\bar{D}(\bar{T}) = $ Faith's $PD/\bar{T}$, which can be interpreted as lineage richness. Thus, Faith's PD can be regarded as a phylogenetic generalization of species richness. Phylogenetic diversity can also be connected to H_P and Q, under the temporal perspective described in the preceding paragraph.

4.3. Functional Diversity

Consider the collection of all pairs of species. Each pair is indexed by $u = (i, j)$, $u \in C = \{(i, j); i, j = 1, 2, \ldots, S\}$. (Here we have S^2 pairs because same-species pairs are included so that

intraspecific variability can be considered; if there is no intraspecific variability, the distance for a same-species pair is set to be 0.) The attribute value for each pair $u = (i, j)$ is the species pairwise distance, i.e., $v_u = d_{ij}$ (distance between species i and j) and its abundance a_u is $p_i p_j$. The mean attribute value can be expressed as $\bar{V} = \sum_{u \in C} v_u a_u = \sum_{i,j} d_{ij} p_i p_j$, which is Rao's quadratic entropy Q, the notation we use hereafter for mean distance between species in functional diversity.

For each species pair (i, j), $i, j = 1, 2, \ldots, S$, the new collection in our unified approach consists of d_{ij} functionally equally distinct entities. The total abundance over all entities (the number of entities in the collection is Walker's FAD) is Rao's Q, implying each entity has relative abundance $p_i p_j / Q$ such that $\sum_{i,j} d_{ij}(p_i p_j / Q) = 1$. An illustrative example is given in **Supplemental Appendix 2**. Equation 5b reduces to the distance-based functional diversity (Chiu & Chao 2014):

$$
\begin{aligned}
{}^q FD(Q) &= \left[\sum_{u \in C} v_u \times \left(\frac{a_u}{\sum_{b \in C} v_b a_b} \right)^q \right]^{1/(1-q)} \\
&= \left[\sum_{i,j=1}^{S} d_{ij} \times \left(\frac{p_i p_j}{\sum_{k,m=1}^{S} d_{km} p_k p_m} \right)^q \right]^{1/(1-q)} = \left[\sum_{i,j=1}^{S} d_{ij} \times \left(\frac{p_i p_j}{Q} \right)^q \right]^{1/(1-q)} .
\end{aligned}
$$

7a.

The measure is interpreted as the effective sum of the functional distances between species. For $q = 0$, this measure reduces to FAD (in Equation 3a). For $q = 2$, this measure can be linked to the weighted Gini-Simpson index (in Equation 3b) by the equation ${}^2 FD(Q) = Q^2/(Q - GS_D)$. It follows from Equation 5c that the functional Hill number of order q in units of the effective number of equally abundant and (functionally) equally distinct species is

$$
{}^q D(Q) = \left(\frac{{}^q FD(Q)}{Q} \right)^{1/2} .
$$

7b.

This can also be linked to FAD and GS_D. A summary of our unified attribute diversity and the above three types of diversities is given in **Table 1**.

Note that, in functional diversity, we can extend the mean attribute value (or mean distance between species) Q, our functional diversity ${}^q FD(Q)$, and functional Hill numbers ${}^q D(Q)$ to a pair of assemblages (say, Assemblage I and II). Assume there are S species in the combined assemblage. Let the two sets of relative abundances be denoted by $(p_{11}, p_{21}, \ldots, p_{S1})$ and $(p_{12}, p_{22}, \ldots, p_{S2})$ for Assemblage I and II, respectively; some of the p_{ij} may be zero. Using a derivation parallel to that for a single assemblage except that we now use $a_u = p_{i1} p_{j2}$ for any pair of species $u = (i, j)$ where i refers to a species in Assemblage I and j refers to a species in Assemblage II, we obtain the abundance-weighted mean distance over all possible such species pairs:

$$
Q_{12} = \sum_{i=1}^{S} \sum_{j=1}^{S} d_{ij} p_{i1} p_{j2}.
$$

This equation extends Rao's Q to a pair of assemblages (Chiu & Chao 2014), so it is referred to as mean distance between species of Assemblage I and Assemblage II. Similarly, we can obtain the functional diversity ${}^q FD(Q_{12})$ and the functional Hill numbers ${}^q D(Q_{12})$ for the assemblage pair (I, II). The former is interpreted as the effective sum of pairwise distances between a species of Assemblage I and a species in Assemblage II, with a constant distance Q_{12} between any such pair of species. The latter is interpreted as the corresponding effective numbers of equally abundant and equally distinct species in each of the two assemblages. These measures are used to present the replication principle.

4.4. Replication Principle

The replication principle for ordinary Hill numbers was extended to the phylogenetic diversity measures (Equation 6a) in Chao et al. (2010) and to the distance-based functional diversity measures (Equation 7a) in Chiu & Chao (2014). We review these two extensions separately using the unified attribute diversities (see **Figure 2**). To begin, suppose there are N phylogenetically completely distinct assemblages (no shared branches across assemblages, though branches within an assemblage may be shared, as shown in **Figure 2b**). Assume these assemblages are equally large and have identical mean branch lengths (i.e., $\bar{T}_1 = \bar{T}_2 = \cdots = \bar{T}_N \equiv \bar{T}$) and identical phylogenetic diversities [i.e., $^qPD_1(\bar{T}) = {}^qPD_2(\bar{T}) = \cdots = {}^qPD_N(\bar{T}) \equiv y$]. If these assemblages are pooled, then the pooled assemblages must have phylogenetic diversity $N \times y$. A similar replication principle is also valid for the phylogenetic Hill number (in units of species equivalents); here the mean branch lengths can be allowed to be different for these N assemblages (Chao et al. 2014a).

Our functional diversity $^qFD(Q)$ obeys a quadratic replication principle. Suppose we have N equally large and completely distinct assemblages (no shares species). For all pairs of assemblages (k, m), $k, m = 1, 2, \ldots, N$, assume identical mean distances (i.e., $Q_{km} \equiv Q$ for $k, m = 1, 2, \ldots, N$) and identical functional diversities [i.e., $^qFD_{km}(Q) \equiv z$ for $k, m = 1, 2, \ldots, N$]. When these equally large and completely distinct assemblages are pooled, the functional diversity of the pooled assemblage is $N^2 \times z$. Why we have $N^2 \times z$ instead of $N \times z$ can be explained by considering a simple case of pooling two assemblages (say, I and II) (see **Figure 2c**). In the combined assemblage, we need to consider the species pairwise distances for four combinations of assemblages: (I, I), (I, II), (II, I), and (II, II). Thus, we have a quadrupling property instead of a doubling property in the special case of $N = 2$. Because the functional Hill number is a square root of $^qFD(Q)/Q$, i.e., $^qD(Q) = [^qFD(Q)/Q]^{1/2}$ (Equation 5c), the replication principle is still valid for the functional Hill numbers; here the mean distances Q_{km} for $k, m = 1, 2, \ldots, N$ are allowed to be different (Chiu & Chao 2014).

4.5. Dendrogram-Based Versus Distance-Based Measures

Because we can always obtain a distance matrix from a phylogenetic tree or dendrogram, one may wonder how the results of the two approaches (dendrogram-based in Equation 6a and distance-based in Equation 7a) are compared for a given tree. Notice that for a dendrogram, we know species relations not only for a pair of species but also for every possible combination of three species, four species, or any subset of the species. The dendrogram-based phylogenetic diversity makes use of all such species interrelations. However, the distance-based diversity uses only species pairwise distances, and we only need to supply the relation between two species to obtain distance-based diversity. From this perspective, the distance-based approach is more widely applicable than the tree approach, because less information is needed. By contrast, the distance-based approach is less complete than a tree approach when the data truly have a tree structure, because distance approaches throw away multispecies information. Because the dendrogram- and distance-based diversities are based on different information, the two measures are not directly comparable.

In assessing the evolutionary relationships among species, common descent necessarily produces a true tree structure (in the absence of horizontal gene transfer) for any given gene. A reliable estimate of the structure of this true phylogenetic tree can often be constructed based on hypotheses such as maximum parsimony. Thus, given the inherent tree structure of phylogenies, we recommend the use of dendrogram-based phylogenetic diversity and related measures, because all species interrelations can be incorporated. Some information would be

lost if we use the distance-based measures by converting the dendrogram to a pairwise distance matrix.

In functional diversity analysis, one of the commonly used approaches, Petchey & Gaston (2002, 2009) construct a functional dendrogram by applying a clustering algorithm to the species pairwise distance matrix. Then a class of dendrogram-based functional diversity measures (Equation 6a) can be obtained. Given a distance matrix based on species traits, an unavoidable issue in a dendrogram-based approach to functional analysis is how to select a clustering algorithm to construct a dendrogram. Different clustering methods may lead to different conclusions (Poos et al. 2009). Using the distance-based functional diversity (Equation 7a) and related measures in functional studies based on species traits, we can avoid arbitrariness due to choice of clustering algorithms to obtain dendrograms from data that is not necessarily inherently tree-like.

5. A UNIFIED DIVERSITY DECOMPOSITION

For N assemblages defined by the investigator, diversity decomposition of gamma into alpha and beta components for ordinary Hill numbers and phylogenetic diversity have been developed by Jost (2006, 2007) and Chiu et al. (2014). Functional diversity decomposition was recently proposed by Chiu & Chao (2014). With the attribute diversity as a unified measure, the previous decomposition can be integrated in a unified partitioning scheme that decomposes the attribute gamma diversity of the pooled assemblage into independent alpha and beta components, using a derivation developed by Chiu et al. (2014). Similar decomposition can be done for the corresponding generalized Hill numbers. We describe the partitioning procedures of the attribute diversity in this section because this partitioning is recommended for practical applications.

Assume there are S species in the pooled assemblage, and their phylogenetic tree and functional distance matrix can be constructed. We start with the attribute gamma diversity. This gamma diversity depends only on the species relative abundances in the pooled assemblage. However, how species relative abundances in the pooled assemblage should be defined depends on how we pool data over assemblages. The pooling scheme depends on the objective of the study. If the objective is to compare absolute abundances among assemblages (given the total abundance in the pooled assemblage), we should pool individuals over assemblages. If the objective is to compare relative abundances among assemblages, we should pool relative abundances of individual assemblages. These two kinds of pooling lead to different relative abundances in the pooled assemblage. (The former pooling is equivalent to an assemblage-size-weighted pooling scheme for relative abundances, whereas the latter pooling naturally reduces to equal weight.) Because the pooling concept has been a debated issue in the literature (Hardy & Senterre 2007, Hardy & Jost 2008, Villéger & Mouillot 2008, de Bello et al. 2010) and is essential in diversity analysis, we give a numerical example in **Supplemental Appendix 3** to explain the difference between the two pooling schemes and describe the objective for each scheme (for other examples, see de Bello et al. 2010).

To adapt to both kinds of pooling schemes for multiple assemblages, we define z_{ik} as any measure of species importance of the ith species in the kth assemblage, $i = 1, 2, \ldots, S$, $k = 1, 2, \ldots, N$. Some of the z_{ik} may be zero. The measure z_{ik} can be absolute abundances, relative abundances, incidence, biomasses, cover areas, or any other species importance measure. For simplicity, we refer to z_{ik} as abundance of the ith species in the kth assemblage in the following presentation.

Define $z_{+k} = \sum_{i=1}^{S} z_{ik}$ as the size of the kth assemblage. Let $z_{++} = \sum_{k=1}^{N} z_{+k}$ be the total abundance in pooled assemblage and $z_{i+} = \sum_{k=1}^{N} z_{ik}$ be the total abundances of the ith species in the pooled assemblage. Then the species relative abundance set in the pooled assemblage is

$\{z_{i+}/z_{++}; i = 1, 2, \dots, S\}$. If we pool relative abundances over assemblages instead of absolute abundances, we have the special case in which $z_{+k} = 1$ and $z_{++} = N$. Assume the attribute value of a species, branch segment, or species-pair u in the pooled assemblage is v_u. Now we can follow the same procedure as in Section 4 by considering various collections C and their corresponding entities in the pooled assemblage. For phylogenetic diversity, z_{ik} and z_{i+} are extended to branch abundances for any branch i, as described in Section 4.2.

In species diversity and phylogenetic diversity, it follows from Equation 5b that the attribute gamma diversity of order q can be written as

$$^qAD_\gamma(\bar{V}) = \left[\sum_{i \in C} v_i \times \left(\frac{z_{i+}/z_{++}}{\bar{V}} \right)^q \right]^{1/(1-q)}, \quad q \geq 0, \quad q \neq 1, \qquad 8a.$$

where $\bar{V} = \sum_{i \in C} v_i z_{i+}/z_{++}$ denotes the mean attribute value in the pooled assemblage. The attribute gamma diversity is interpreted as the effective total attribute value in the pooled assemblage. In functional diversity, Equation 7a leads to the functional gamma diversity, a special case of $^qAD_\gamma(\bar{V})$:

$$^qAD_\gamma(\bar{V}) = {}^qFD_\gamma(Q) = \left[\sum_{i,j=1}^S d_{ij} \times \left(\frac{z_{i+}z_{j+}/z_{++}z_{++}}{Q} \right)^q \right]^{1/(1-q)}, \quad q \geq 0, \quad q \neq 1, \qquad 8b.$$

where $Q = \sum_{i,j=1}^S d_{ij} z_{i+} z_{j+}/z_{++}z_{++}$ denotes the mean species pairwise distance (quadratic entropy) in the pooled assemblage.

To evaluate the attribute alpha diversity, first note that the entities in each individual assemblage are a subset of those in the pooled assemblage. The attribute diversity of each individual assemblage can be calculated from the entities of the pooled assemblage, and only the abundances vary with assemblages. For taxonomic entities and functional entities, this can be readily understood. Chiu et al. (2014, their figure 2) showed that the phylogenetic diversity for each individual assemblage can be computed from the pooled tree structure and only the node abundances vary with assemblages. The alpha formulas derived by Chiu et al. (2014) for species diversity and phylogenetic diversity can be integrated into the following attribute alpha diversity:

$$^qAD_\alpha(\bar{V}) = \frac{1}{N} \left[\sum_{i \in C} v_i \sum_{k=1}^N \left(\frac{z_{ik}/z_{++}}{\bar{V}} \right)^q \right]^{1/(1-q)}, \quad q \geq 0, \quad q \neq 1. \qquad 9a.$$

This attribute alpha diversity is interpreted as the effective total attribute value per assemblage. In the attribute alpha formula, $\bar{V}$ denotes the mean attribute value in the pooled assemblage. The functional alpha diversity, a special case of $^qAD_\alpha(\bar{V})$, can be expressed as (Chiu & Chao 2014)

$$^qAD_\alpha(\bar{V}) = {}^qFD_\alpha(Q) = \frac{1}{N^2} \left[\sum_{k,m=1}^N \sum_{i,j=1}^S d_{ij} \times \left(\frac{z_{ik}z_{jm}/z_{++}z_{++}}{Q} \right)^q \right]^{1/(1-q)}, \quad q \geq 0, \quad q \neq 1.$$
$$9b.$$

Here Q denotes the quadratic entropy in the pooled assemblage. This functional alpha diversity is interpreted as the effective total functional distance between species of a pair of assemblages.

Chiu et al. (2014) and Chiu & Chao (2014) proved that the attribute gamma diversity (Equations 8a and 8b) is always greater than or equal to the attribute alpha diversity (Equations 9a and 9b) for all $q \geq 0$ regardless of species abundances and attributes. Based on a multiplicative partitioning,

the attribute beta diversity is the ratio of attribute gamma diversity to attribute alpha diversity:

$$^qAD_\beta(\bar{V}) = \frac{^qAD_\gamma(\bar{V})}{^qAD_\alpha(\bar{V})}, \quad q \geq 0. \qquad \text{10a.}$$

A similar decomposition can be applied to generalized Hill numbers (**Supplemental Appendix 3**), and the corresponding beta component has a relation with attribute beta diversity:

$$^qD_\beta(\bar{V}) = [^qAD_\beta(\bar{V})]^{1/\lambda}, \qquad \text{10b.}$$

where $\lambda = 1$ (for species diversity and phylogenetic diversity) or 2 (for functional diversity). All formulas of the alpha, beta, and gamma diversities in the decomposition of attribute diversity or generalized Hill numbers are tabulated in **Supplemental Appendix 3**.

For all orders of q, the attribute beta component $^qAD_\beta(\bar{V})$ is between unity and N^λ, where λ is defined in the preceding paragraph. These ranges for $^qAD_\beta(\bar{V})$ depend only on N. Thus, they are independent of their corresponding attribute alpha diversity, implying that alpha and beta components are unrelated (or independent) (for a rigorous discussion of unrelatedness and independence of the two measures, see Chao et al. 2012).

When the N assemblages are identical in species identities and species abundances (i.e., $z_{i1} = z_{i2} = \cdots = z_{iN}$ for all species i), $^qAD_\beta(\bar{V}) = 1$ for all types of diversities. When the N assemblages are completely distinct (no shared species or no shared branches), $^qAD_\beta(\bar{V}) = N$ for species diversity and phylogenetic diversity and $^qAD_\beta(\bar{V}) = N^2$ for functional diversity. Thus, the attribute beta diversity $^qAD_\beta(\bar{V})$ quantifies the effective number of equally large and completely distinct assemblages in the case of species diversity (no shared species) and phylogenetic diversity (no shared branches between assemblages); the functional beta diversity $^qAD_\beta(\bar{V})$ quantifies the effective number of equally large and completely distinct pairs of assemblages (no shared species pairs). Our interpretation of beta diversity as the effective number of assemblages or assemblage pairs is just one of many other types of beta diversities proposed in the literature (for recent reviews of various beta diversity measures, see Anderson et al. 2011, Legendre & De Cáceres 2013).

6. NORMALIZED SIMILARITY AND DIFFERENTIATION MEASURES

For species diversity, the most commonly used similarity measures include N-assemblage generalizations of the Jaccard, Sørensen, Horn (1966) and Morisita-Horn (Morisita 1959) measures. Jost (2006, 2007), Chao et al. (2008, 2012), and Chiu et al. (2014) have demonstrated that all the above measures are monotonic transformations of beta diversity based on ordinary Hill numbers. As discussed in Section 3.1, this is an advantage of using the framework of Hill numbers: A direct link exists between diversity and similarity (or differentiation) among assemblages. Chiu et al. (2014) and Chiu & Chao (2014) extended this framework by proposing four classes of similarity (or differentiation) measures that are monotonic functions of beta diversity, whether derived from species, phylogenetic, or functional diversity. Our unified framework here integrates all these.

The attribute beta diversity, $^qAD_\beta(\bar{V})$, quantifies pure differentiation among the N assemblages, and it lies in the range $[1, N^\lambda]$ for all orders $q \geq 0$; again, here $\lambda = 1$ (for species diversity and phylogenetic diversity) or 2 (for functional diversity). Because the range depends only on N, we can apply several transformations to normalize the beta component onto the interval [0, 1] to measure local attribute overlap, regional attribute overlap, attribute homogeneity, and attribute turnover. Here, local refers to a property of an individual assemblage, whereas regional refers to a property of the pooled assemblage. In **Table 2**, we tabulate these formulas for the two most important classes (local and regional attribute overlap); the formulas for the special cases for $q = 0$, 1, and 2; and the relationship with previous measures [for formulas of the other two classes of similarity measures (attribute homogeneity and attribute turnover), see Chiu & Chao 2014, Chiu et al. 2014].

Table 2 Two classes of attribute overlap (or similarity) measures and their special cases for three types of diversities

Order	Type of diversity	Local attribute overlap $C_{qN}^*(\bar{V}) = \dfrac{N^{\lambda(1-q)} - [{}^qAD_\beta(\bar{V})]^{1-q}}{N^{\lambda(1-q)} - 1}$	Regional attribute overlap $U_{qN}^*(\bar{V}) = \dfrac{[1/{}^qAD_\beta(\bar{V})]^{1-q} - (1/N)^{\lambda(1-q)}}{1 - (1/N)^{\lambda(1-q)}}$
$q = 0$	Species diversity	Classic Sørensen[a] $C_{0N} = \dfrac{N - S/\bar{S}}{N - 1}$	Classic Jaccard[a] $U_{0N} = \dfrac{\bar{S}/S - 1/N}{1 - 1/N}$
	Phylogenetic diversity	Phylo-Sørensen[a] ($=$ PhyloSør for $N = 2$) $\bar{C}_{0N}(T) = \dfrac{N - PD_\gamma/PD_\alpha}{N - 1}$	Phylo-Jaccard[a] ($= 1 -$ UniFrac for $N = 2$) $\bar{U}_{0N}(T) = \dfrac{PD_\alpha/PD_\gamma - 1/N}{1 - 1/N}$
	Functional diversity	Func-Sørensen[a] $C_{0N}^*(Q) = \dfrac{N^2 - N^2(FAD_\gamma/FAD_{pair})}{N^2 - 1}$	Func-Jaccard[a] $U_{0N}^*(Q) = \dfrac{FAD_{pair}/FAD_\gamma - 1}{N^2 - 1}$
$q = 1$	Species diversity	Classic Horn[b] $C_{1N} = U_{1N} = \dfrac{H_{Sb,\alpha} - H_{Sb,\gamma} - \sum_{k=1}^{N} \frac{z_{+k}}{z_{++}} \log\left(\frac{z_{+k}}{z_{++}}\right)}{\log N}$; $1 - \dfrac{H_{Sb,\gamma} - H_{Sb,\alpha}}{\log N}$ (if $z_{+k} = 1, z_{++} = N$)	
	Phylogenetic diversity	Phylo-Horn[b] $\bar{C}_{1N}(T) = \bar{U}_{1N}(T) = \dfrac{H_{P,\alpha} - H_{P,\gamma} - T\sum_{k=1}^{N} \frac{z_{+k}}{z_{++}} \log\left(\frac{z_{+k}}{z_{++}}\right)}{T \log N}$; $1 - \dfrac{H_{P,\gamma} - H_{P,\alpha}}{T \log N}$ (if $z_{+k} = 1, z_{++} = N$)	
	Functional diversity	Func-Horn[b] $C_{1N}^*(Q) = U_{2N}^*(Q) = 1 - \dfrac{\log[{}^1FD_\gamma(Q)] - \log[{}^1FD_\alpha(Q)]}{2 \log N}$	
$q = 2$	Species diversity	Classic Morisita-Horn[c] $C_{2N} = 1 - \dfrac{\sum_{i=1}^{S} \sum_{m>k} (z_{im} - z_{ik})^2}{(N-1)\sum_{i=1}^{S}\sum_{k=1}^{N} z_{ik}^2}$; $1 - \dfrac{H_{GS,\gamma} - H_{GS,\alpha}}{(1-1/N)(1 - H_{GS,\alpha})}$ (if $z_{+k} = 1, z_{++} = N$)	Classic regional overlap[c] $U_{2N} = 1 - \dfrac{\sum_{i=1}^{S} \sum_{m>k} (z_{im} - z_{ik})^2}{(N-1)\sum_{i=1}^{S} z_{i+}^2}$; $1 - \dfrac{H_{GS,\gamma} - H_{GS,\alpha}}{(N-1)(1 - H_{GS,\gamma})}$ (if $z_{+k} = 1, z_{++} = N$)
	Phylogenetic diversity	Phylo-Morisita-Horn[c] $\bar{C}_{2N}(T) = 1 - \dfrac{\sum_{i=1}^{B} L_i \sum_{m>k}^{N} (z_{im} - z_{ik})^2}{(N-1)\sum_{i=1}^{B} L_i \sum_{k=1}^{N} z_{ik}^2}$; $1 - \dfrac{Q_\gamma - Q_\alpha}{(1-1/N)(T - Q_\alpha)}$ (if $z_{+k} = 1, z_{++} = N$)	Phyloregional overlap[c] $\bar{U}_{2N}(T) = 1 - \dfrac{\sum_{i=1}^{B} L_i \sum_{m>k}^{N} (z_{im} - z_{ik})^2}{(N-1)\sum_{i=1}^{B} L_i z_{i+}^2}$; $1 - \dfrac{Q_\gamma - Q_\alpha}{(N-1)(T - Q_\gamma)}$ (if $z_{+k} = 1, z_{++} = N$)
	Functional diversity	Func-Morisita-Horn $C_{2N}^*(Q) = \dfrac{\sum_{i,j=1}^{S} d_{ij} \sum_{k,m=1}^{N} \left[\left(\frac{z_{i+}z_{j+}}{N}\right)^2 - (z_{ik}z_{jm})^2\right]}{(N^2-1)\sum_{i,j=1}^{S} d_{ij} \sum_{k,m=1}^{N} (z_{ik}z_{jm})^2}$	Functional regional overlap $U_{2N}^*(Q) = \dfrac{\sum_{i,j=1}^{S} d_{ij} \sum_{k,m=1}^{N} \left[\left(\frac{z_{i+}z_{j+}}{N}\right)^2 - (z_{ik}z_{jm})^2\right]}{(1-1/N^2)\sum_{i,j=1}^{S} d_{ij}(z_{i+}z_{j+})^2}$

Note: The corresponding differentiation measures are the only complements of the overlap measures. In the formulas, $\lambda = 1$ (for species diversity and phylogenetic diversity) and 2 (for functional diversity). Notation: $z_{ik} =$ the abundance (or any species importance measure) of the ith species in the kth assemblage, $z_{+k} = \sum_{i=1}^{S} z_{ik}$ (the assemblage size of the kth assemblage), $z_{i+} = \sum_{k=1}^{N} z_{ik}$ (the total abundance of the ith species in the pooled assemblage), and $z_{++} = \sum_{i=1}^{S} \sum_{k=1}^{N} z_{ik}$ (the total abundance in the pooled assemblage). If z_{ik} represents species relative abundance, then in all formulas $z_{+k} = 1$, $z_{++} = N$. For phylogenetic diversity, z_{ik} and z_{i+} are extended to branch abundances for any branch $i = 1, 2, \ldots, B$.

Abbreviations: FAD, Walker's functional attribute diversity (sum of the pairwise distances between species); $FD(Q)$, functional diversity (Equations 8b and 9b); Phylo, phylogenetic; Func, functional; PD, Faith's phylogenetic diversity (total branch length).

[a] $S =$ species richness in the pooled assemblage; $\bar{S} =$ average species richness per assemblage; $PD_\gamma, PD_\alpha =$ gamma and alpha total branch length (i.e., Faith's PD); $FAD_\gamma =$ sum of the pairwise distances between species in the pooled assemblage; $FAD_{pair} =$ sum of FAD over all possible pairs of assemblages (there are N^2 pairs of assemblages).

[b] $H_{Sb,\gamma}, H_{Sb,\alpha} =$ gamma and alpha Shannon entropy; $H_{P,\gamma}, H_{P,\alpha} =$ gamma and alpha phylogenetic entropy; ${}^1FD_\gamma(Q), {}^1FD_\alpha(Q) =$ gamma and alpha functional diversity of order 1 (formulas obtained by letting $q \to 1$ in Equations 8b and 9b).

[c] $H_{GS,\gamma}, H_{GS,\alpha} =$ gamma and alpha Gini-Simpson index; $Q_\gamma, Q_\alpha =$ gamma and alpha quadratic entropy.

For species diversity and phylogenetic diversity, the local attribute overlap measures (**Table 2**) quantify the effective average proportion of the total attribute value of an individual assemblage that is shared with all other assemblages. For functional diversity, they quantify the effective average proportion of the species pairwise distances in a pair of local assemblages that are shared with all other pairs of assemblages. This class of measures unifies the taxonomic local species overlap measure C_{qN} for ordinary Hill numbers (Chao et al. 2008), the phylogenetic local lineage overlap measure $\bar{C}_{qN}(\bar{T})$ (Chiu et al. 2014), and the functional local distance overlap measure $C_{qN}^*(Q)$ (Chiu & Chao 2014). The corresponding differentiation measure is $1 - C_{qN}^*(\bar{V})$, which quantifies the effective average proportion of the total nonshared attribute value in a local individual assemblage (for species diversity and phylogenetic diversity), or in a pair of local assemblages (for functional diversity).

For $q = 0$, this overlap measure yields Sørensen-type similarity measures, which are referred to as classic Sørensen, phylo-Sørensen, and func-Sørensen in **Table 2**. For phylo-Sørensen, when $N = 2$ and $q = 0$, it reduces to the popular measure PhyloSør developed by Bryant et al. (2008) and Ferrier et al. (2007). For $q = 1$, this overlap measure extends Horn's (1966) two-assemblage measure to phylogenetic and functional versions for N assemblages. For $q = 2$, this overlap measure extends Morisita's (1959) two-assemblage Morisita-Horn measure to phylogenetic and functional versions for N assemblages.

The regional attribute overlap measures (**Table 2**) differ from the local attribute overlap measures by taking a regional perspective. For species and phylogenetic diversity, they quantify the effective proportion of the total attribute value in the pooled assemblage that is shared with all local assemblages. For functional diversity, they quantify the effective proportion of the species pairwise distances in the pooled assemblage that are shared with all pairs of local assemblages. This class of measures unifies the taxonomic regional species overlap measure U_{qN} for ordinary Hill numbers (Chiu et al. 2014), the phylogenetic regional lineage overlap measure $\bar{U}_{qN}(\bar{T})$ (Chiu et al. 2014), and the functional regional distance overlap measure $U_{qN}^*(Q)$ (Chiu & Chao 2014). The corresponding differentiation measure is $1 - U_{qN}^*(\bar{V})$, which quantifies the effective proportion of the total nonshared attribute value in the pooled assemblage.

For $q = 0$, this overlap measure yields Jaccard-type similarity measures, which are referred to as the classic Jaccard, phylo-Jaccard, and func-Jaccard measures in **Table 2**. For phylo-Jaccard, when $N = 2$ and $q = 0$, its complement reduces to the UniFrac measure developed by Lozupone & Knight (2005) and the PD-dissimilarity measure developed by Faith et al. (2009). For $q = 1$, local and regional attribute overlap measures coincide.

Similar transformations can also be applied to the beta generalized Hill number ${}^qD_\beta(\bar{V})$ (Equation 10b) to construct similarity and differentiation measures among assemblages. The two beta diversities, ${}^qAD_\beta(\bar{V})$ and ${}^qD_\beta(\bar{V})$, differ only in functional diversity. The similarity measures in functional diversity based on ${}^qAD_\beta(\bar{V})$ quantify distance overlap from different perspectives. By contrast, the similarity measures based on ${}^qD_\beta(\bar{V})$ quantify species overlap from different perspectives (for species overlap measures, see **Supplemental Appendix 4**).

We applied various diversity and similarity/differentiation measures to the real data discussed in Ricotta et al. (2012). The example shows that choosing the proper diversity and similarity/differentiation measures is critical. The example also shows that some previous taxonomic, phylogenetic, and functional differentiation measures may give biologically incorrect interpretations (see the sidebar, A Real Example and **Supplemental Appendix 5**). In the sidebar, A Real Example, we regard the observed species richness and abundances as the "true" parameters of the complete assemblage for illustrative purposes. In practice, when only a sample is taken from an assemblage, statistical estimation is needed (see sidebar, Statistical Estimation Issues).

Supplemental Material

A REAL EXAMPLE

Forty-three vascular plant species were collected from vegetation plots in three dune habitats: embryo dunes, mobile dunes, and transition dunes (for details, see Carboni et al. 2010, 2011, 2013; for relevant discussion, also see Ricotta et al. 2012). A phylogenetic tree of the 43 species was constructed using the software PHYLOMATIC (Webb & Donoghue 2005). All species were further characterized by a set of 16 functional traits, and a functional distance matrix was calculated (Pavoine et al. 2009b). All previous abundance-sensitive differentiation measures (especially those measures based on decomposing the Gini-Simpson index and the quadratic entropy) show very low taxonomic, phylogenetic, and functional differentiation between any two habitats. The low values do not reflect biological reality but are inescapable consequences of a mathematical property of these measures. The measures obtained by decomposing the attribute diversity (summarized in **Table 2**) show moderate to high differentiation and yield the biologically expected ranking of differentiation among the habitats, whereas the previous measures do not (for details, see **Supplemental Appendix 5**).

STATISTICAL ESTIMATION ISSUES

In this article, all diversity measures and similarity/differentiation indexes are in terms of the true population values of species richness and species abundances in an assemblage. In practice, the true values are unknown and must be estimated from samples. For ordinary Hill numbers, the estimation of species richness ($q = 0$) is a very difficult issue (Chao 2005, Chao & Chiu 2012). The estimation of the exponential of Shannon entropy ($q = 1$) is also surprisingly nontrivial (see Chao et al. 2013), but for $q = 2$, there is a nearly unbiased estimator based on statistical estimation theory. How the diversity profile should be estimated as a continuous function of the order q is a challenging statistical issue. Similar estimation issues exist for the phylogenetic and functional diversities, but with added sources of uncertainty. Alternatively, to make fair comparisons among samples, ecologists have used rarefaction and extrapolation to compare species richness at a standardized sampling effort or sample completeness (as measured by sample coverage) (for a review, see Chao & Jost 2012, Colwell et al. 2012). This was recently extended to Hill numbers (Chao et al. 2014b), and it merits further extension to the unified framework of the attribute diversity.

SUMMARY POINTS

1. By considering different attributes and entities (taxonomic entities, phylogenetic entities, and functional entities) and treating entities as equally distinct "species" in a framework of Hill numbers, the concept of attribute diversity provides a unified approach to quantifying species diversity, phylogenetic diversity, and functional diversity. In these three types of diversities, the attribute diversity quantifies the effective number of species, effective total branch length with respect to some preselected reference point, and effective sum of species pairwise distances, respectively (for a summary, see **Table 1**; for plots of attribute diversity profiles, also see the example in **Supplemental Appendix 5**).

2. Transforming the attribute diversity to the generalized Hill numbers (Equation 5c) (**Table 1**), we then respectively obtain Hill numbers, phylogenetic Hill numbers, and functional Hill numbers derived in the literature, all in the units of the effective number

▶ Supplemental Material

of species or lineages (see **Table 1**; for plots of profiles for the generalized Hill numbers, also see the example in **Supplemental Appendix 5**).

3. The attribute diversity and the generalized Hill numbers have direct links to many widely used diversity measures (see Section 4). The most important feature of the attribute diversity measures and the generalized Hill numbers is that they satisfy a strong version of replication principle or quadratic replication principle (see **Figure 2**) while most of the previous measures do not, making their values difficult to interpret.

4. When there are N assemblages defined by the investigator, the attribute diversity of the pooled assemblage can be decomposed into independent alpha and beta components. We can use the beta component to construct several classes of attribute overlap (or similarity) measures and their corresponding differentiation measures, which extend many popular similarity/differentiation measures to phylogenetic and functional versions (for a summary, see **Table 2**; for plots of the two major classes of attribute differentiation measures, also see **Supplemental Appendix 5**).

DISCLOSURE STATEMENT

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