Phylogenetic beta diversity, similarity, and differentiation measures based on Hill numbers

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Abstract. Until now, decomposition of abundance-sensitive gamma (regional) phylogenetic diversity measures into alpha and beta (within- and between-group) components has been based on an additive partitioning of phylogenetic generalized entropies, especially Rao’s quadratic entropy. This additive approach led to a phylogenetic measure of differentiation between assemblages: (gamma − alpha)/gamma. We show both empirically and theoretically that this approach inherits all of the problems recently identified in the additive partitioning of non-phylogenetic generalized entropies. When within-assemblage (alpha) quadratic entropy is high, the additive beta and the differentiation measure (gamma − alpha)/gamma always tend to zero (implying no differentiation) regardless of phylogenetic structures and differences in species abundances across assemblages. Likewise, the differentiation measure based on the phylogenetic generalization of Shannon entropy always approaches zero whenever gamma phylogenetic entropy is high. Such critical flaws, inherited from their non-phylogenetic parent measures (Gini-Simpson index and Shannon entropy respectively), have caused interpretational problems. These flaws arise because phylogenetic generalized entropies do not obey the replication principle, which ensures that the diversity measures are linear with respect to species addition or group pooling. Furthermore, their complete partitioning into independent components is not additive (except for phylogenetic entropy). Just as in the non-phylogenetic case, these interpretational problems are resolved by using phylogenetic Hill numbers that obey the replication principle. Here we show how to partition the phylogenetic gamma diversity based on Hill numbers into independent alpha and beta components, which turn out to be multiplicative. The resulting phylogenetic beta diversity (ratio of gamma to alpha) measures the effective number of completely phylogenetically distinct assemblages. This beta component measures pure differentiation among assemblages and thus can be used to construct several classes of similarity or differentiation measures normalized onto the range [0, 1]. We also propose a normalization to fix the traditional additive phylogenetic similarity and differentiation measures, and we show that this yields the same similarity and differentiation measures we derived from multiplicative phylogenetic diversity partitioning. We thus can achieve a consensus on phylogenetic similarity and differentiation measures, including N-assemblage phylogenetic generalizations of the classic Jaccard, Sørensen, Horn, and Morisita-Horn measures. Hypothetical and real examples are used for illustration.

Key words: beta diversity; differentiation; Hill numbers; phylogenetic diversity; phylogenetic entropy; quadratic entropy; replication principle; similarity.

INTRODUCTION

Measures of beta diversity, similarity, and differentiation are basic tools of ecological analyses (Magurran 2004, Magurran and McGill 2011). Most of these measures assume that all species are equally distinct, ignoring phylogenetic and functional differences between them. These measures hide the evolutionary dimension of assemblages. For example, these measures would show a maximal level of differentiation between the primate assemblages of Amazonia and Pacific South America, because these assemblages share no species. These measures would show the same high level of differentiation between the Amazonian and Madagascan primate assemblages, since these also share no species. Yet, the first pair of assemblages share most genera and all subfamilies, and are derived from a relatively recent common ancestor, while the Amazonian/Madagascan pair of assemblages share no genera or subfamilies, and have been on separate evolutionary paths for a much longer time. The phylogenetic depth of the differentiation between assemblages is obviously important for ecology, conservation biology, evolutionary theories of community assembly, and genetics. McPeek and Miller (1996), Webb (2000), Ricotta (2005a), Webb et al. (2006), Lozupone et al. (2007), Barcaro et...
al. (2007), Ferrier et al. (2007), Hardy and Senterre (2007), Bryant et al. (2008), Graham and Fine (2008), Faith et al. (2009), Pavoine et al. (2009), de Bello et al. (2010), Mouchet and Mouillot (2011), Weiner (2011) and Cavender-Bares et al. (2012), among others, have recognized the need for measures of phylogenetic differentiation that capture this depth of separation between groups to answer evolutionary and ecological questions, and to guide conservation policy. Such measures would be especially useful now that differences between species can be objectively quantified in the form of well-supported phylogenetic trees (Faith 1992, Warwick and Clarke 1995, Crozier 1997, Webb 2000, Ives and Helmus 2010, Pavoine et al. 2010, among others) or functional trees (Tilman 2001, Petchey and Gaston 2002, Weiner 2011, among others). Three special issues in Ecology featured a series of papers on integrating ecology and phylogenetics; see McPeek and Miller (1996), Webb et al. (2006), and Cavender-Bares et al. (2012), and papers in each issue.

Most previous phylogenetic similarity and differentiation measures were based on phylogenetic diversity indices such as Faith’s widely used total branch length measure (Faith 1992), phylogenetic entropy (Allen et al. 2009), and Rao’s quadratic entropy (Rao 1982), unified by Pavoine et al. (2009) into a family of phylogenetic generalized entropies. These are generalizations of their non-phylogenetic counterparts, species richness, Shannon entropy, Gini-Simpson index, and generalized entropies, respectively. Phylogenetic differentiation measures were obtained from these phylogenetic generalized entropies by additively partitioning them into within- and between-group (alpha and beta) components (Ricotta 2005b, Hardy and Senterre 2007, Pavoine et al. 2009, Mouchet and Mouillot 2011), following the traditional additive approach that had been applied to their non-phylogenetic counterparts (Lande 1996, Veech et al. 2002). The mean within-group or alpha value was subtracted from the regional or gamma value (the value for the pooled groups), and the resulting “beta” value, or its complement, was normalized by dividing by the gamma value. This was supposed to produce a normalized measure of differentiation or similarity.

Recently, however, researchers have discovered serious interpretational problems with this traditional additive partitioning approach when diversity is equated with Shannon entropy, the Gini-Simpson index, or most other generalized entropies (Jost 2006, 2007, Jost et al. 2010, Ellison 2010). The main measure of similarity in the additive approach, alpha/gamma, does not actually quantify the compositional similarity of the assemblages under study. This ratio can be arbitrarily close to unity (supposedly indicating high similarity) even when the assemblages being compared have no species in common. This problem arises because Shannon entropy, the Gini-Simpson index, and other generalized entropies do not satisfy the replication principle (Jost 2007), which we discuss in Hill numbers obey the replication principle. The phylogenetic generalizations of these measures, likewise, do not obey the replication principle, so they inherit this fundamental problem with the interpretation of the ratio alpha/gamma. The widely used Rao’s quadratic entropy suffers from another problem: just like the Gini-Simpson index, Rao’s quadratic entropy is nonadditive (it cannot be decomposed into the sum of independent within- and between-group components), so imposing an additive framework on it will produce a measure of “beta” that is confounded with within-group diversity (equivalently, with total diversity). As diversity increases, all these traditional abundance-sensitive differentiation measures approach fixed values independent of tree structure or differences in species abundances between assemblages, so they cease to be biologically informative. We prove all these points in Fixing the additive “beta” of phylogenetic generalized entropies, and illustrate them with examples.

The solution, just as in the non-phylogenetic case, is to convert the phylogenetic generalized entropies into phylogenetic Hill numbers, which do obey the replication principle. This has been done recently by Chao et al. (2010), Leinster and Cobbold (2012), and Scheiner (2012). We concentrate on Chao et al.’s mean phylogenetic diversity (described in the next section) because this measure can be directly applied to diversity decomposition. Many previous measures of phylogenetic diversity (e.g., Rao 1982, Faith 1992, Allen et al. 2009, Pavoine et al. 2009, Ricotta and Szeidl 2009, de Bello et al. 2010) turn out to be special cases or simple transformations of this mean phylogenetic diversity. Jost (2007) derived a partitioning method to decompose Hill numbers into independent components. Here, we modified his approach to a more general framework and derive a new alpha formula. We used this more general framework to obtain phylogenetic generalizations of alpha and beta diversity, and new phylogenetic generalizations of existing non-phylogenetic similarity and differentiation measures, such as the Jaccard, Sørensen, Horn, and Morisita-Horn similarity indices (Morisita 1959, Horn 1966) and C_qN overlap measures (Chao et al. 2008, 2012). We also show that some of the previous phylogenetic differentiation measures can be corrected by normalization to remove their dependency on the alpha value (or gamma value), and these normalized measures turn out to be identical to the phylogenetic generalizations of the overlap measures that we derive from partitioning phylogenetic Hill numbers. Thus, a consensus can be reached about measures of beta diversity, similarity, and differentiation that incorporates the information contained in a phylogenetic tree.
Phylogenetic Generalizations of Entropies and Hill Numbers

Generalized entropy

In order to understand the problems of previous phylogenetic diversity and differentiation measures, it is helpful to first understand the corresponding problems of non-phylogenetic generalized entropy measures. There are many families of generalized entropies. The generalized entropy most often used in ecology is the so-called Tsallis entropy:

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

where \( S \geq 1 \) is the number of species in the assemblage, and \( p_i \) is the relative abundance of the \( i \)th species, with \( i = 1, 2, \ldots, S \) (Havrda and Charvát 1967, Daróczy 1970, Tsallis 1988, Keylock 2005). When \( q = 0 \), \( qH \) becomes \( S - 1 \); when \( q \) tends to 1, \( qH \) tends to Shannon entropy \( H \).

Phylogenetic generalized entropy

Pielou (1975) was the first to notice that the concept of diversity could be broadened to consider differences among species. The earliest taxonomic diversity measure is the cladistic diversity (CD), which is defined as the total number of nodes in a taxonomic tree that encompasses all of the species in the assemblage (Vane-Wright et al. 1991, Faith 1992). A more informative measure is Faith’s phylogenetic diversity (PD; Faith 1992), which measures total branch length arising from the root node. In both CD and PD, species abundances are not considered.

Rao’s quadratic entropy was the first diversity measure that accounted for both phylogeny and species abundances (Rao 1982):

\[ Q = \sum_{i,j} d_{ij} p_i p_j \]

where \( d_{ij} \) denotes the phylogenetic distance (in years since divergence, number of DNA base changes, or other metrics) between species \( i \) and \( j \). It is an extension of the Gini-Simpson index, and reduces to it in the special case of no phylogenetic structure (all species are equally related to one another), \( d_{ij} = 0 \) and \( d_{ij} = 1 \) (\( i \neq j \)). The phylogenetic entropy \( H_p \) extends Shannon entropy to incorporate phylogenetic distances among species (Allen et al. 2009) as follows:

\[ H_p = -\sum_i L_i a_i \log a_i \]

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 \( i \).

For ultrametric trees, Pavoine et al. (2009) showed that Faith’s PD, Allen et al.’s (2009) \( H_p \), and Rao’s \( Q \) can be united into a single parametric family of phylogenetic generalized entropies:

\[ qI(T) = \left( T - \sum_{t \in B_T} L_i a_i^q \right) / (q - 1). \]
t_M = 0); see Appendix A for an example. Then, the integral simplifies to a simple sum of the ordinary generalized entropies \( \delta H_k, k = 1, 2, \ldots, M \) in the \( M \) intervals, weighted by the duration of that interval. This sum is

\[
q I(T) = \sum_{k=1}^{M} (t_k - t_{k-1})(\delta H_k)
\]

which is equivalent to Eq. 2c. In order to be consistent with our own measures and the graphs in our examples, we reversed the ordering of the intervals used by Pavoine et al. (2009), who indexed the intervals from tips to root. If \( T \) is chosen as the age of the root node of the tree, then \( 0 I(T) = \) Faith’s PD minus the tree height; \( 1 I(T) \) is identical to Allen et al.’s (2009) entropy \( H_p \); and \( 2 I(T) \) is identical to Rao’s quadratic entropy \( Q \). In the special case of \( M = 1 \) (all lineages are completely distinct, i.e., there are no internal nodes) and \( T = 1 \), the phylogenetic generalized entropy reduces to the classical generalized entropy defined in Eq. 1 with species relative abundances \( \{p_1, p_2, \ldots, p_S\} \) as the tip node relative abundances.

**Hill numbers obey the replication principle**

Hill (1973) proposed a class of diversity measures called “Hill numbers,” or “effective number of species,” defined for \( q \neq 1 \) as

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

The parameter \( q \) determines the sensitivity of the measure to the species abundances. When \( q = 0 \), the abundances of individual species do not contribute; only presences are counted, so that \( q D \) is simply species richness. Eq. 3 is undefined for \( q = 1 \), but its limit as \( q \) tends to 1 is the exponential of Shannon entropy, i.e., \( 1D = \exp(1 H) \). \( 1D \) weighs species in proportion to their frequency. When \( q = 2 \), \( 2D \) is the inverse Simpson concentration and places more weight on the frequencies of abundant species and discounts rare species. Investigators should at least report the diversity for all species (\( q = 0 \)), the typical species (\( q = 1 \)), and the dominant species (\( q = 2 \)).

All Hill numbers are in units of “species.” It is thus possible to plot them on a single graph as a continuous function of the parameter \( q \). A complete characterization of the species diversity of an assemblage with \( S \) species and relative abundances \( \{p_1, p_2, \ldots, p_S\} \) is conveyed by a diversity profile: a plot of \( q D \) vs. \( q \) from \( q = 0 \) to \( q = 4 \) or 5 (beyond this it changes little); see Tóthmérész (1995). An example of a diversity profile is shown in Appendix B. Although Hill numbers for \( q < 0 \) can be calculated, they are dominated by the frequencies of rare species and have poor statistical sampling properties. We thus restrict ourselves to the case \( q \geq 0 \) throughout the paper.

Hill numbers differ fundamentally from generalized entropies in that they are linear with respect to species addition or group pooling. That is, they obey the replication principle: When \( N \) completely distinct assemblages with identical diversities of order \( q \) are pooled in equal proportions, the diversity of the pooled assemblage is \( N \) times the diversity of any single assemblage. The \( N \) completely distinct assemblages may have different relative abundances (and, for \( q > 0 \), they can even have different numbers of species). See Appendix B for proof. This property is the strong replication principle (a weaker one was proven by Hill 1973). 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 similarity of the assemblages.

**Phylogenetic Hill numbers**

Since generalized entropies do not obey the replication principle, neither do their phylogenetic generalizations. This can be solved by transforming them into Hill numbers, which obey the replication principle. Chao et al. (2010) generalized Hill numbers to take phylogenies into account for all values of \( q \). Define \( B_T, L_i, \) and \( a_i \) as in Eqs. 2b and 2c. Chao et al. (2010) derived the mean phylogenetic diversity for the interval \([-T, 0]\) (or mean diversity over \( T \) years) as

\[
q D(T) = \left\{ \sum_{i \in B_T} \frac{L_i}{T} a_i^q \right\}^{1/(1-q)}.
\]

\[
= \frac{1}{T} \left\{ \sum_{i \in B_T} \left( \frac{L_i}{T} \right)^q \right\}^{1/(1-q)} \quad q \geq 0 \text{ and } q \neq 1
\]

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

It is interpreted as the effective number of completely distinct lineages (no shared lineages) during the time interval from \( T \) years ago to the present.

This mean diversity is invariant to the units used to measure branch lengths. There is a simple relationship between our measures and Rao’s quadratic entropy \( Q \), \( D(T) = 1/(1 - Q(T)) \), and likewise between our measure and Allen et al.’s (2009) phylogenetic entropy \( H_p \), \( D(T) = \exp(H_p)/T \). See Chao et al. (2010) for a proof. When lineages are completely distinct over the time interval \([-T, 0]\) (so that all branch lengths are equal to \( T \), and thus, all lineages are equally distinct), the mean diversity \( D(T) \) reduces to the non-phylogenetic Hill numbers \( D = (\sum a_i^q)^{1/(1-q)} \). This includes the special case when \( T \) tends to zero, which means that we ignore phylogeny and only consider the present-day assemblage.
The branch or phylogenetic diversity \( q^{\text{PD}}(T) \) of order \( q \) during the time interval from \( T \) years ago to the present is defined as the product of \( \bar{D}(T) \) and \( T \). That is, \( q^{\text{PD}}(T) = T \times q^{\bar{D}}(T) \), which quantifies the amount of evolutionary “work” done on the system over the interval \([-T, 0]\), or the effective number of lineage-years (or other tree units) contained in the tree on the interval \([-T, 0]\). If \( q = 0 \), \( q^{\text{PD}}(T) \) reduces to Faith’s phylogenetic diversity, regardless of abundances. Two types of profiles completely characterize phylogenetic diversity.

(1) A diversity profile is obtained by plotting \( q^{\text{PD}}(T) \) or \( q^{\bar{D}}(T) \) as functions of \( T \) for \( q = 0, 1, \) and \( 2 \); see Fig. B2 (Appendix B) or Chao et al. (2010: Fig. 3) for examples. (2) The other type of diversity profile is obtained by plotting \( q^{\text{PD}}(T) \) or \( q^{\bar{D}}(T) \) as a function of order \( q \), for a selected value of temporal perspective \( T \). See Fig. B3 (Appendix B) for examples.

In many applications, the measure of evolutionary work is based on the number of nucleotide base changes at a selected locus, or the amount of functional or morphological differentiation from a common ancestor. In these cases, the lengths from tips to the root of the phylogenetic tree are not necessarily all equally long, so the tree is not ultrametric. In these cases, the time parameter \( T \) should be replaced by \( \bar{T} \), the weighted arithmetic mean of the distances from the tree base to each of the terminal branch tips (i.e., the mean evolutionary change per species over the interval of interest):

\[
\bar{T} = \sum_{i \in B_T} L_i a_i.
\]

In other words, \( \bar{T} \) is the mean tree height. Here, \( B_T \) denotes the set of branches connecting the chosen tree base to all the branch tips (species) in the assemblage. See Fig. 1 in Chao et al. (2010) for an illustrative example. As shown by Chao et al. (2010), the mean phylogenetic diversity and branch diversity for a non-ultrametric assemblage have the same form as those for an ultrametric tree, except that \( T \) must be replaced by the mean tree height \( \bar{T} \) (if abundance data are available so that it can be obtained). Therefore, if the diversity of a non-ultrametric assemblage is \( z \), then its diversity is the same as the diversity of an ultrametric assemblage consisting of \( z \) equally abundant and completely distinct lineages all with branch length \( \bar{T} \). Although our derivation and presentation for the rest of the paper are focused on ultrametric trees, all results and conclusions for our proposed measures are also valid for non-ultrametric trees if \( T \) is substituted for \( \bar{T} \).

Unlike previous phylogenetic diversity measures developed in the literature, the mean diversity and the amount of evolutionary work done on the assemblage depend explicitly on \( T \), the temporal perspective of the investigator. However, the time \( T \) does not need to be the age of the oldest node; it may be less (though this would throw away phylogenetic information and would rarely be done) or it may be greater than the age of the root node. Often, the most appropriate and least arbitrary choice is the divergence time between the group under study and its nearest outgroup; the sampling protocol (for example, the decision to keep orchids but not other families) uniquely determines this number. This contrasts with the traditional approach using the root node as the reference point. In that approach, the age of the root node can depend on the vagaries of sampling success, so the traditional phylogenetic measures will often change with sampling effort, and cannot be directly compared between studies. Diversities of different assemblages should generally be compared using the same \( T \) for all of them. It is easy to convert results to different \( T \) values; see the Discussion.

**Phylogenetic Hill numbers obey the replication principle**

The replication principle for Hill numbers can be generalized to phylogenetic diversity in the following sense: when we combine \( N \) equally weighted, completely phylogenetically distinct assemblages (no lineages
shared among assemblages in the interval \([-T, 0]\); see Fig. 1), each with the same mean diversity \(q\mathcal{D}(T) = X\) in the time interval \([-T, 0]\), the pooled assemblages must have mean diversity \(q\mathcal{D}(T) = N \times X\). Also, the amount of evolutionary work \(q\mathcal{P}(T)\) done on the pooled assemblages is \(N\) times the amount of evolutionary work done on a single assemblage. The same temporal perspective (or for non-ultrametric trees, the same mean quantity \(\bar{T}\)) must be used for all \(N\) assemblages, but they may have different numbers of species and totally different tree structures. Most previous phylogenetic diversity measures do not obey the replication principle, but the phylogenetic Hill numbers proposed here do obey it. See Appendix B or Chao et al. (2010) for proofs. This intuitive property sets our phylogenetic diversity measures apart from the phylogenetic generalized entropy measures.

**Partitioning Hill Numbers and their Phylogenetic Generalizations into Alpha and Beta Components**

**Partitioning Hill numbers into alpha and beta components**

The formulas for alpha, beta, and gamma depend on the question under investigation. We consider a fixed set of \(N\) assemblages. The total diversity of the pooled assemblage (gamma diversity) can be decomposed multiplicatively into independent alpha and beta components. Assume that there are \(S\) species in the pooled assemblages. Let \(y_{ij} \geq 0\) denote any measure of species importance of the \(i\)th species in the \(j\)th assemblage, \(i = 1, 2, \ldots, S; j = 1, 2, \ldots, N\). Throughout the paper, we will refer to \(y_{ij}\) as measures of “abundance.” They can be absolute abundances, relative abundances, incidence, or any other importance measure (e.g., biomass, coverage of plants or corals, basal area of plants). Any transformation of these measures can also be used for \(y_{ij}\); see Lengendre and Legendre (2012) for various transformations. Our goal was to quantify the species-by-species resemblance or differentiation of the \(N\) sets of abundances, \((y_{1j}, y_{2j}, \ldots, y_{Sj}), j = 1, 2, \ldots, N\).

Let \(y_{ij} = \sum_{j=1}^{N} y_{ij}\) be the total abundance in the region, and let \(y_{ij} = \sum_{j=1}^{N} y_{ij}\) be the assemblage size of the \(j\)th assemblage. In order to link our approach to previous work in the literature, we first re-express the value \(y_{ij}\) as

\[
y_{ij} = y_{ij} \left( \frac{y_{ij}}{y_{jj}} \right) = y_{ij} \frac{y_{ij}}{y_{jj}} w_{pj} \tag{5a}
\]

where \(p_{ij} = y_{ij}/y_{ij}\) is the relative abundance of the \(i\)th species in the \(j\)th assemblage, and \(w_{j} = y_{ij}/y_{jj}\) (relative assemblage size or the weight of the \(j\)th assemblage), with \(\sum_{j=1}^{N} w_{j} = 1\). Thus, comparing the \(N\) sets of vectors \((y_{1j}, y_{2j}, \ldots, y_{Sj}), j = 1, 2, \ldots, N\), is equivalent to comparing the \(N\) sets of vectors \((w_{p1j}, w_{p2j}, \ldots, w_{pSj}), j = 1, 2, \ldots, N\). If our goal is to compare the \(N\) sets of relative abundance vectors \((p_{1j}, p_{2j}, \ldots, p_{Sj}), j = 1, 2, \ldots, N\), we can simply define \(y_{ij}\) to be the species relative abundance in the \(j\)th assemblage. In this special case, \(y_{ij} = 1, y_{jj} = N\), then assemblage weight naturally becomes \(1/N\), an equal-weight case.

For the gamma diversity, we simply pool species abundances over assemblages, and let \(y_{j+} = \sum_{j=1}^{N} y_{ij} = y_{j+} \sum_{j=1}^{N} w_{pj}\) be the total value of the \(i\)th species in the region. The gamma diversity of order \(q\) is the Hill number based on the relative abundance \(\hat{p}_{ij} = y_{ij}/y_{j+} = \sum_{j=1}^{N} w_{pj}\) in the pooled assemblage (Routledge 1979, Jost 2006, 2007) as follows:

\[
q\mathcal{D}_q = \left\{ \sum_{j=1}^{N} \left( \frac{y_{ij}}{y_{j+}} \right)^q \right\}^{1/(1-q)} = \left\{ \sum_{j=1}^{N} \left( \sum_{i=1}^{S} w_{pj} y_{ij} \right)^q \right\}^{1/(1-q)} \quad q \neq 1. \tag{5b}
\]

When \(q\) tends to 1, we have

\[
1\mathcal{D}_q = \lim_{q \to 1} q\mathcal{D}_q = \exp \left\{ -\sum_{i=1}^{S} \left( y_{ij}/y_{j+} \right) \log(y_{ij}/y_{j+}) \right\} = \exp \left\{ -\sum_{i=1}^{S} \left( \sum_{j=1}^{N} w_{pj} y_{ij} \right) \log \left( \sum_{j=1}^{N} w_{pj} y_{ij} \right) \right\}. \tag{5c}
\]

In Appendix C, we derive the following new formula for alpha diversity, which is interpreted as “the effective number of species per assemblage”:

\[
q\mathcal{D}_a = \frac{1}{N} \left\{ \sum_{j=1}^{N} \left( \frac{y_{ij}}{y_{j+}} \right)^q \right\}^{1/(1-q)} = \frac{1}{N} \left\{ \sum_{j=1}^{N} \left( \sum_{i=1}^{S} w_{pj} y_{ij} \right)^q \right\}^{1/(1-q)} \quad q \neq 1. \tag{6a}
\]

The formula when \(q\) tends to 1 is

\[
1\mathcal{D}_a = \lim_{q \to 1} q\mathcal{D}_a = \exp \left\{ -\sum_{i=1}^{S} \left( y_{ij}/y_{j+} \right) \log(y_{ij}/y_{j+}) - \log N \right\} = \exp \left\{ -\sum_{i=1}^{S} \sum_{j=1}^{N} w_{pj} y_{ij} \log(w_{pj}) - \log N \right\}. \tag{6b}
\]

For any arbitrary weights, our gamma is always greater than or equal to the alpha for all orders \(q \geq 0\). The beta component is \(q\mathcal{D}_b = q\mathcal{D}_a - q\mathcal{D}_a\), which is always between unity (when all assemblages are identical in species absolute abundances) and \(N\) (when the \(N\) assemblages have no species in common); see Appendix C for proofs. The beta diversity can be interpreted as the effective number of completely distinct assemblages in the region (i.e., assemblage diversity).
Routledge (1979) and Jost (2007) each derived a mathematical formula for alpha diversity. For equal-weight case, all the three alpha formulas are identical. They differ, however, when assemblage weights are not equal due to different assumptions used in deriving each alpha formula. These three alpha formulas will be compared elsewhere. Previous approaches to alpha diversity led to a beta that can only be used to produce differentiation measures to compare species relative abundances, but not absolute abundances. Our approach expands the conventional concept of alpha so that beta can quantify the differentiation among \( N \) sets of vectors \( (y_{1j}, y_{2j}, \ldots, y_{Nj}) j = 1, 2, \ldots, N \) for any measure of species importance \( y_{ij} \), including absolute abundances. See Appendix C for the mathematical properties of our proposed new alpha and beta diversities.

Our alpha component is independent of beta and contains only the within-group information, and the beta component contains only the between-group information. Neither component, taken by itself, imposes any mathematical constraints on the other component; if we know only the value of one component, we cannot infer anything about the other component. This ensures that beta is not confounded with alpha, an essential prerequisite for much biological reasoning about diversity and differentiation. The precise meaning of independence for alpha and beta components has been the subject of debate and misunderstanding (e.g., Baselga 2010, Ellison 2010, Jost 2010, Ricotta 2010, Veech and Crist 2010); see Chao et al. (2012) for a detailed resolution.

**Partitioning mean phylogenetic diversity into alpha and beta components**

The mean phylogenetic diversity \( \bar{D}(T) \) (Eqs. 4a and 4b) can be decomposed into independent phylogenetic alpha and beta diversities. Here, we take into account the phylogenetic distances among species in comparing assemblages. We need to introduce some additional notation conventions for phylogenetic trees. See Fig. 2 for an example. A pooled tree is first constructed for the regional assemblage. For this pooled assemblage in the time interval \([-T, 0]\), define \( B_T \) as the set of all branches, and \( L_i \) be the length of branch \( i \), \( i \in B_T \). The tip nodes represent those species in the present-day assemblage. For the \( j \)th assemblage, \( j = 1, 2, \ldots, N \), let \( z_{ij} \) denote the total abundances descended from branch \( i \), \( i \in B_T \), although \( z_{ij} \) can be any quantitative measure of species importance as discussed in the preceding section. (Here, the index \( i \) can correspond to both tip node and internal node; if \( i \) is a tip node, then \( z_{ij} \) represents data of the current assemblage and is analogous to \( y_{ij} \) in Partitioning Hill diversity.)
numbers into alpha and beta components). As shown in Fig. 2, the diversity for each individual assemblage can be easily computed from the pooled tree structure. Only the node abundances vary with assemblages.

Our goal here is to quantify the node-by-node resemblance (or differentiation) among the $N$ abundance sets $\{z_{ij}; i \in B_T\}$, $j = 1, 2, \ldots, N$. Let $a_g = z_{ij}/z_{ij}$ (here the “$+$” sign in $z_{ij}$ denotes a sum over the tip nodes only) be the corresponding relative abundances descended from branch $i$ in the $j$th assemblage, and $z_{ij} = \sum_{j=1}^N z_{ij}$. For the pooled assemblage, it follows from Eq. 5a that we have a similar expression, $z_{ij} = z_{ij} + w_j a_i$, where $w_j = z_{ij}/z_{ij}$ (relative assemblage size) is the weight for the $j$th assemblage. In the pooled assemblage, the node abundance for branch $i$ becomes $z_{i+} = z_{i+} + \sum_{j=1}^N w_j a_i$, and the corresponding relative abundance is $a_{i+} = z_{i+}/z_{i+} = \sum_{j=1}^N w_j a_i$.

The phylogenetic gamma diversity of order $q$ can be calculated from Eq. 4a as

$$
q\bar{D}_i(T) = \frac{1}{T} \left\{ \sum_{i \in B_T} L_i \left( \frac{z_{ij}/z_{ij}}{T} \right)^q \right\}^{1/(1-q)} = \frac{1}{T} \left\{ \sum_{i \in B_T} L_i \left( \frac{\sum_{j=1}^N w_j a_i}{T} \right)^q \right\}^{1/(1-q)}
$$

$q \geq 0$ and $q \neq 1$. \hspace{1cm} (7a)

The limit when $q$ approaches unity exists and is equal to

$$
1\bar{D}_i(T) = \lim_{q \to 1} q\bar{D}_i(T) = \exp \left[ -\sum_{i \in B_T} \left( \frac{\sum_{j=1}^N w_j a_i}{T} \right) \log \left( \frac{\sum_{j=1}^N w_j a_i}{T} \right) \right].
$$

The gamma diversity is the effective number of completely distinct lineages over the interval $[-T, 0]$ in the pooled assemblage. In Appendix C, we derive the following phylogenetic alpha diversity for $q \geq 0$ and $q \neq 1$ as

$$
q\bar{D}_a(T) = \frac{1}{N} \left\{ \sum_{i \in B_T} L_i \left( \frac{z_{ij}/z_{ij}}{T} \right)^q \right\}^{1/(1-q)} = \frac{1}{N} \left\{ \sum_{i \in B_T} L_i \left( \frac{\sum_{j=1}^N w_j a_i}{T} \right)^q \right\}^{1/(1-q)}.
$$

For $q = 1$, we have

$$
1\bar{D}_a(T) = \lim_{q \to 1} q\bar{D}_a(T) = \exp \left[ -\sum_{i \in B_T} \left( \frac{\sum_{j=1}^N w_j a_i}{T} \right) \log \left( \frac{\sum_{j=1}^N w_j a_i}{T} \right) - \log(NT) \right].
$$

The alpha diversity is interpreted as the effective number of completely distinct lineages over the interval $[-T, 0]$ for an individual assemblage.

Gamma diversity should not be smaller than alpha diversity. As in the case of our non-phylogenetic decomposition of Hill numbers, our phylogenetic gamma (Eqs. 7a and 7b) and alpha (Eqs. 8a and 8b) components satisfy this property for all $q \geq 0$ and any arbitrary weights (see Appendix C). The complete partitioning of phylogenetic gamma diversity into independent within- and between-group (alpha and beta) diversities is multiplicative. The phylogenetic beta diversity is the ratio of gamma diversity to alpha diversity:

$$
\frac{q\bar{D}_b(T)}{q\bar{D}_a(T)} = \frac{q\bar{D}_i(T)}{q\bar{D}_a(T)} \quad q \geq 0.
$$

This is equivalent to the ratio of gamma branch diversity to alpha branch diversity, i.e., $\frac{q\bar{D}_b(T)}{q\bar{D}_a(T)} = \frac{q\bar{D}_{b,i}(T)}{q\bar{D}_{a,i}(T)}$. When the $N$ assemblages are identical in species identities and species abundances, then $\frac{q\bar{D}_b(T)}{q\bar{D}_a(T)} = 1$ for any $T$. When the $N$ assemblages are completely phylogenetically distinct (no shared lineages), then $\frac{q\bar{D}_b(T)}{q\bar{D}_a(T)} = N$, no matter what the diversities or tree shapes of the assemblages. The phylogenetic beta diversity $\frac{q\bar{D}_b(T)}{q\bar{D}_a(T)}$ quantifies assemblage diversity and is the effective number of completely phylogenetically distinct assemblages in the interval $[-T, 0]$. See Fig. 1 for examples of completely phylogenetically distinct assemblages. This interpretation is conceptually the same as the beta diversity for ordinary Hill numbers, but incorporates the relatedness of species. When all lineages in the pooled assemblage are completely distinct in the interval $[-T, 0]$, the phylogenetic alpha, beta, and gamma diversities reduce to those based on ordinary Hill numbers. This includes the limiting case that $T$ tends to zero, so that phylogeny is ignored. If our goal is to quantify the node-by-node resemblance among the $N$ relative abundance sets $\{a_g; i \in B_T\}$, $j = 1, 2, \ldots, N$, then we just redefine $z_{ij}$ to be $a_g$, implying that assemblage weights become equal ($w_j = 1/N$) in Eqs. 7a, 7b, 8a, 8b, and 9.

When $q = 0$, we have $\frac{q\bar{D}_b(T)}{q\bar{D}_a(T)} = L_a(T)/L_a(T)$, where $L_a(T)$ denotes the total branch length of the pooled tree, and $L_a(T)$ denotes the average length of an individual tree. When $q = 1$, the phylogenetic beta diversity of order 1 is

$$
\frac{1}{N} \exp \left[ (H_{P,\gamma} - H_{P,\alpha})/T + \sum_{j=1}^N w_j \log w_j + \log(NT) \right]
$$

(10a)

where $H_{P,\gamma}$ and $H_{P,\alpha}$ denote, respectively, the gamma and alpha phylogenetic entropy. When assemblage weights are equal, this implies an additive decomposition for phylogenetic entropy $H_p$ (Pavoine et al. 2009, Mouchet and Mouillot 2011), as for ordinary Shannon entropy (Jost 2007). When $q = 2$ and
assemblages are equally weighted, the phylogenetic beta diversity of order 2 is as follows (see Appendix C for proof):

$$2\bar{D}_b(T) = (1 - Q_T/T)^{-1}/(1 - Q_\alpha/T)^{-1}$$

(10b)

where $Q_T$ and $Q_\alpha$ denote, respectively, the gamma and alpha quadratic entropy.

Since our alpha and gamma phylogenetic diversities both obey the replication principle, the beta diversity formed by taking their ratio is replication-invariant (see Appendix C for proof). That is, when assemblages are replicated, the beta diversity does not change. This property is related to the condition that alpha and beta must be independent. A consequence is that beta can be easily converted into normalized similarity and differentiation measures by transformations that do not depend on alpha or gamma diversity. We make use of this property in the following section. Another consequence is consistency when pooling equally distinct sub-trees, such as pooling equally ancient subfamilies. If all subfamilies show the same beta diversity, the beta diversity is unchanged by pooling the subfamilies.

As with ordinary Hill numbers, the \textit{lineage excess} $\bar{D}_a(T) - \bar{D}_\alpha(T)$ can be interpreted as the effective number of regional lineages not contained in a typical local assemblage, or the absolute number of lineages gained in going from the local to the regional scale. The lineage excess and the phylogenetic beta together contain the same information as phylogenetic alpha and gamma diversities. The measure $[(\bar{D}_a(T) - \bar{D}_\alpha(T))/(N - 1)]$ quantifies the lineage turnover rate per assemblage (i.e., the effective number of lineages unique to a typical local assemblage). The relative lineage turnover rate per assemblage can be measured by $[(\bar{D}_a(T) - \bar{D}_\alpha(T))/(N - 1)(\bar{D}_\alpha(T))] = (\bar{D}_b(T) - 1)/(N - 1)$ This is one class of measures proposed in the next section.

**Normalized Similarity/Differentiation Measures and Their Phylogenetic Generalizations**

**Normalized similarity/differentiation measures based on Hill numbers**

Based on the gamma diversity (Eqs. 5b and 5c) and the new alpha formula (Eqs. 6a and 6b), our beta diversity as a ratio of gamma and alpha is independent of alpha and always lies in the range $[1, N]$ for any arbitrary weights and all orders $q \geq 0$ (Appendix C). Since the range depends on $N$, the beta diversity cannot be used to compare species differentiation across multiple regions with different numbers of assemblages. To remove the dependence on $N$, we follow Jost (2006, 2007) and Chao et al. (2008, 2012), who proposed several transformations to measure local overlap, regional overlap, homogeneity, and turnover. A summary of these non-phylogenetic measures and their relationship with previous measures is shown in Table 1. See Appendix D for details.

This framework reveals that many of the most popular measures in an ecologist’s toolbox, including the Jaccard, Sørensen, Horn, and Morisita-Horn measures of similarity for two assemblages (Morisita 1959, Horn 1966), are transformations of multiplicative beta diversity. The multiplicative beta diversity can be calculated for any number of assemblages, so the beta-transformation viewpoint led to multiple-assemblage generalizations of the classic measures (Jost 2006, 2007, Chao et al. 2008). Nearly all of the previous similarity measures in the literature based on Hill numbers can only be used for comparing relative abundances. For all $q \geq 0$, our new beta diversity using the new alpha formula (Eq. 6a) is valid for any weights, so the beta-transformation viewpoint also leads to one kind of weighted generalizations of the classic measures. This enables us to compare absolute abundance sets (by using relative sizes as assemblage weights), in addition to relative abundance sets (by using equal weights). As Clarke and Warwick (2001) concluded, a suitable similarity (or differentiation) measure should have the flexibility to reflect resemblance (or difference) in absolute abundances, not just relative abundances; see also Magurran (2004:174). Anderson et al. (2006:692) also indicated “… differences in absolute abundances can also be important ecologically, as they may correspond to differences in an ecosystem’s productivity or responses to a pollutant or other impact.”

**Phylogenetic generalizations of normalized similarity/differentiation measures**

Since our phylogenetic beta diversity has the same mathematical properties as the multiplicative beta diversity based on ordinary Hill numbers, we can now generalize all of those non-phylogenetic similarity measures in Table 1 to include phylogenetic similarities between assemblages. All of the transformation formulas are still valid, with the ordinary multiplicative beta diversity replaced by our phylogenetic beta diversity (which is a function of $T$, the temporal perspective of the investigator). Of course, all these measures are also mathematically independent of alpha diversity, a property that most existing phylogenetic similarity measures lack.

Table 2 summarizes the four classes of phylogenetic similarity measures derived from our approach. The corresponding differentiation measures are the one-complements of the similarity measures. The formulas for the special cases for $q = 0, 1, 2$ are also displayed there. All derivation details are provided in Appendix D, and a brief description is given below:

1. **Lineage overlap from a local perspective.**—This class of measures takes the following form:

$$C_{\phi_N}(T) = \frac{N^{1-q} - (\bar{D}_b(T))^{1-q} - 1}{N^{1-q} - 1}.$$  (11a)
Table 1. Four classes of non-phylogenetic similarity measures and their special cases, based on the beta diversity from partitioning Hill numbers.

<table>
<thead>
<tr>
<th>Measure</th>
<th>Turnover-complement ( V_{\phi N} = \frac{N - N_D}{N - 1} )</th>
<th>Homogeneity measure ( S_{\phi N} = \frac{1}{1 - \frac{D_0}{N}} )</th>
</tr>
</thead>
<tbody>
<tr>
<td>( q = 0 )</td>
<td>( S) Sorenson ( \frac{N - S/\bar{S}}{N - 1} )</td>
<td>( \bar{S}/S - 1/N )</td>
</tr>
<tr>
<td>( q = 1 ) (equal weight)</td>
<td>( \cdots )</td>
<td>( \cdots )</td>
</tr>
<tr>
<td>( q = 1 ) (general weight)</td>
<td>( \cdots )</td>
<td>( \cdots )</td>
</tr>
<tr>
<td>( q = 2 ) (equal weight)</td>
<td>( \text{Regional-overlap} 1 - \frac{H_{GS,T} - H_{GS,S}}{(N - 1)(1 - H_{GS,S})} )</td>
<td>( \text{Morisita-Horn} 1 - \frac{H_{GS,T} - H_{GS,S}}{(1 - 1/N)(1 - H_{GS,S})} )</td>
</tr>
<tr>
<td>( q = 2 ) (general weight)</td>
<td>( 1 - \frac{\sum_{i=1}^{N} \sum_{j=1}^{N} (w_{ij} - w_{ik})^2}{(N - 1) \sum_{i=1}^{N} \bar{p}_{ji}^2} )</td>
<td>( 1 - \frac{\sum_{i=1}^{N} \sum_{j=1}^{N} (w_{ij} - w_{ik})^2}{(N - 1) \sum_{i=1}^{N} \bar{w}_{ji}^2} )</td>
</tr>
</tbody>
</table>

Notes: The corresponding differentiation measures are the one-complements of the similarity measures. To quantify the resemblance of absolute abundance sets, use relative assemblage sizes as weights; to quantify the resemblance of relative abundance sets, use equal weight. \( D_0 = D_p(T) \) where \( D_0(T) = \frac{1}{1 - \frac{\bar{p}_i}{\bar{q}_i}} \) and \( \bar{p}_i \) is the relative abundance of the \( i \)th species in the \( T \)th assemblage; \( w_j \) is the relative abundance size in set; \( \bar{w}_{ji} \) = \( \sum_{i=1}^{N} w_{ij} \); see Eqs. 5b, 5c, 6a, and 6b for details (in subsection Partitioning Hill numbers into alpha and beta components). \( \bar{S} \) is the alpha species richness (average species richness per assemblage); \( H_i \) and \( H_s \) are gamma and alpha Shannon entropy, respectively; and \( H_{GS,T} \) and \( H_{GS,S} \) are gamma and alpha Gini-Simpson indices, respectively. Ellipses (\ldots) indicate that the equation is not displayed because it cannot be linked to any other conventional measures.

Table 2. Four classes of phylogenetic similarity measures and their special cases, based on the phylogenetic beta diversity from partitioning mean phylogenetic diversity.

<table>
<thead>
<tr>
<th>Measure</th>
<th>Phylo-turnover-complement, ( \tilde{V}<em>{\phi N}(T) = \frac{N - \bar{N}</em>{Dh}(T)}{N - 1} )</th>
<th>Phylo-homogeneity, ( \tilde{S}_{\phi N}(T) = \frac{1}{1 - \frac{\bar{D}_h(T)}{1/N}} )</th>
</tr>
</thead>
<tbody>
<tr>
<td>( q = 0 )</td>
<td>( \text{Phylo- Sorenson} \frac{N - L_{w}(T)/L_{s}(T)}{N - 1} )</td>
<td>( \text{Phylo-Jaccard} \frac{L_{w}(T)/L_{s}(T) - 1/1/N}{1 - 1/N} )</td>
</tr>
<tr>
<td>( q = 1 ) (equal weight)</td>
<td>( \cdots )</td>
<td>( \cdots )</td>
</tr>
<tr>
<td>( q = 1 ) (general weight)</td>
<td>( \cdots )</td>
<td>( \cdots )</td>
</tr>
<tr>
<td>( q = 2 ) (equal weight)</td>
<td>( \text{Phylo-regional-overlap} 1 - \frac{Q_{ij} - Q_{ij}}{(N - 1)(1 - Q_{ij})} )</td>
<td>( \text{Phylo-Morisita-Horn} 1 - \frac{Q_{ij} - Q_{ij}}{(1 - 1/1/N)(1 - Q_{ij})} )</td>
</tr>
<tr>
<td>( q = 2 ) (general weight)</td>
<td>( 1 - \frac{\sum_{i \in B} \sum_{j=1}^{N} (w_{ij}a_{ij} - w_{ik}a_{ik})^2}{(N - 1) \sum_{i \in B} \bar{a}_{ji}^2} )</td>
<td>( 1 - \frac{\sum_{i \in B} \sum_{j=1}^{N} (w_{ij}a_{ij} - w_{ik}a_{ik})^2}{(N - 1) \sum_{i \in B} \bar{w}_{ji}^2} )</td>
</tr>
</tbody>
</table>

Notes: The corresponding differentiation measures are the one-complements of the similarity measures. When all lineages are completely distinct (this includes \( T = 0 \), ignoring phylogeny), the phylogenetic measures reduces to the corresponding non-phylogenetic versions in Table 1. (All measures can also be applied to non-ultrametric trees if \( T \) is substituted for \( T \).) First row: All measures are functions of \( \bar{N}_{Dh}(T) \), where \( \bar{N}_{Dh}(T) = \bar{D}_h(T)/\bar{L}_{w}(T) \), \( \bar{D}_h(T) = (1/1/T)(\sum_{i \in B} L_i \sum_{j=1}^{N} (w_{ij}a_{ij}/T)^{1/(1-\eta)} \), and \( \bar{L}_{w}(T) = (1/1/T)(\sum_{i \in B} L_i \sum_{j=1}^{N} (w_{ij}a_{ij}/T)^{1/(1-\eta)} \). \( B \) is the set of all branches in the time interval \([T, 0] \), \( L_i \) is the length of branch \( i \); \( a_{ij} \) is the the total relative abundance descended from branch \( i \) in the \( j \)th assemblage; \( w_j \) is relative assemblage size for quantifying the resemblance of species absolute abundances among assemblages (\( w_j = 1/N \) for quantifying the resemblance of species relative abundances); and \( \bar{a}_{ji} = \sum_{j=1}^{N} w_{ij}a_{ij} \); see Eqs. 7a, 7b, 8a, and 8b for details (in the subsection Partitioning mean phylogenetic diversity into alpha and beta components). Second row: \( L_w(T) \) and \( L_s(T) \) are, respectively, the gamma and alpha Faith’s phylogenetic diversity (PD; total lineage length). Third and fourth rows: \( H_{G,T} \) and \( H_{G,S} \) are the gamma and alpha phylogenetic entropy. Fifth row: \( Q_{ij} \) and \( Q_{ij} \) are the gamma and alpha quadratic entropy. Ellipses (\ldots) indicate that the equation is not displayed because it cannot be linked to any other conventional measures.
derived in Chao et al. (2008) to phylogenetic and similarity measures extends the lineages in an individual assemblage. This class of It gives the effective average proportion of shared

common and completely distinct lineages in the interval \([-T, 0]\), with exactly \(A\) lineages shared by all of them, and the remaining lineages of each assemblage are not shared by any other assemblages, then \(\bar{C}_{qN}(T)\) gives the lineage overlap \(A/S\) for all orders of \(q\). The differenti-

<table>
<thead>
<tr>
<th>Local-overlap (C_{qN})</th>
<th>Regional-overlap (U_{qN})</th>
</tr>
</thead>
<tbody>
<tr>
<td>(\frac{(1/4D_B)q^{-1} - (1/N)^q}{1 - (1/N)^q})</td>
<td>(\frac{(1/4D_B)q^{-1} - (1/N)^q}{1 - (1/N)^q})</td>
</tr>
<tr>
<td>(\frac{N - S/S}{N - 1})</td>
<td>(\frac{S/S - 1/N}{1 - 1/N})</td>
</tr>
<tr>
<td>Horn overlap (1 - \frac{H_s - H_s}{\log N})</td>
<td>Horn overlap (1 - \frac{H_s - H_s}{\log N})</td>
</tr>
<tr>
<td>(H_s - H_s - \sum_{j=1}^{N} w_j \log w_j)</td>
<td>(H_s - H_s - \sum_{j=1}^{N} w_j \log w_j)</td>
</tr>
<tr>
<td>(\log N)</td>
<td>(\log N)</td>
</tr>
<tr>
<td>Morisita-Horn (1 - \frac{H_{GS,Y} - H_{GS,Y}}{(1 - 1/N)(1 - H_{GS,Y})})</td>
<td>Regional-overlap (1 - \frac{H_{GS,Y} - H_{GS,Y}}{(N - 1)(1 - H_{GS,Y})})</td>
</tr>
<tr>
<td>(\sum_{i=1}^{N} \sum_{j=1}^{N} (w_i p_{ij} - w_i p_{ai})^2)</td>
<td>(\sum_{i=1}^{N} \sum_{j=1}^{N} (w_i p_{ij} - w_i p_{ai})^2)</td>
</tr>
<tr>
<td>(1 - \frac{N}{(N - 1) \sum_{j=1}^{N} \overline{p}_{ai}^2})</td>
<td>(1 - \frac{N}{(N - 1) \sum_{j=1}^{N} \overline{p}_{ai}^2})</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Phylo-local-overlap (\bar{C}_{qN}(T))</th>
<th>Phylo-regional-overlap (\bar{U}_{qN}(T))</th>
</tr>
</thead>
<tbody>
<tr>
<td>(\frac{N - L_c(T)/L_s(T)}{N - 1})</td>
<td>Phoyo-Jaccard (\frac{L_c(T)/L_s(T) - 1/N}{1 - 1/N})</td>
</tr>
<tr>
<td>Phylo-Horn overlap (1 - \frac{H_{p,f} - H_{p,a}}{T \log N})</td>
<td>Phylo-Horn overlap (1 - \frac{H_{p,f} - H_{p,a}}{T \log N})</td>
</tr>
<tr>
<td>(H_{p,a} - H_{p,f} - T \sum_{j=1}^{N} w_j \log w_j)</td>
<td>(H_{p,a} - H_{p,f} - T \sum_{j=1}^{N} w_j \log w_j)</td>
</tr>
<tr>
<td>(T \log N)</td>
<td>(T \log N)</td>
</tr>
<tr>
<td>Phylo-Morisita-Horn (1 - \frac{Q_T - Q_s}{(1 - 1/N)(T - Q_s)})</td>
<td>Phylo-regional-overlap (1 - \frac{Q_T - Q_s}{(N - 1)(T - Q_s)})</td>
</tr>
<tr>
<td>(\sum_{i \not= T} \sum_{j=1}^{N} \overline{w_i p_{ij} - w_i p_{ai}}^2)</td>
<td>(\sum_{i \not= T} \sum_{j=1}^{N} \overline{w_i p_{ij} - w_i p_{ai}}^2)</td>
</tr>
<tr>
<td>(1 - \frac{2}{(N - 1) \sum_{j=1}^{N} \overline{d}_{ai}^2})</td>
<td>(1 - \frac{2}{(N - 1) \sum_{j=1}^{N} \overline{d}_{ai}^2})</td>
</tr>
</tbody>
</table>

**Table 1.** Extended.
ation measure \(1 - \bar{C}_q(N, T)\) thus quantifies the effective average proportion of unique lineages in an assemblage.

For \(q = 0\), this similarity measure is referred to as the “phylo-Sørensen” \(N\)-assemblage overlap measure because for \(N = 2\), it reduces to the measure PhyloSor (phylo-Sørensen) developed by Bryant et al. (2008) and Ferrier et al. (2007). For \(q = 1\), this measure \(\bar{C}_{1, N}(T)\) is called the “phylo-Horn” \(N\)-assemblage overlap measure because it extends Horn (1966) two-assemblage measure to incorporate phylogenies and weights for \(N\) assemblages. For \(q = 2\), \(\bar{C}_{2, N}(T)\) is called the “phylo-Morisita-Horn” \(N\)-assemblage similarity measure because it extends Morisita-Horn measure (Morisita 1959) to incorporate phylogenies and weights for \(N\) assemblages. The differentiation measure \(1 - \bar{C}_{2, N}(T)\) for the equal-weight case reduces to the measure proposed by de Bello et al. (2010). Their measure is valid only for ultrametric trees (de Bello et al. 2010: 7). For \(q = 2\), Eq. 11a as applied to equally weighted non-ultrametric trees reduces to the following (see Table 2):

\[
1 - \bar{C}_{2, N}(\bar{T}) = \frac{1 - \frac{1}{1 - 1/N} \left[ \sum_{i \in R_q} \sum_{j \neq k} (w_{i,aj} - w_{i,ak})^2 \right]}{1 - (1/N)(T - Q_2)}
\]  

(11b)

where \(Q_2\) and \(Q_3\) are, respectively, gamma and alpha quadratic entropy, and \(T\) is the mean base change. This is the phylogenetic generalization of Jost’s (2008) genetic differentiation measure \(D\). See the Discussion for more information about its application to genetics. A general form taking into account assemblage weights (so that absolute abundances can be compared) is

\[
1 - \bar{C}_{2, N}(\bar{T}) = \frac{\sum_{i \in R_q} \sum_{j = 3}^N (w_{i,aj} - w_{i,ak})^2}{(N - 1) \sum_{i \in R_q} \sum_{j = 1}^N w_{i,a_j}^2 a_j^2}
\]  

(11c)

This generalizes Jost’s measure \(D\) to assess differences in both phylogenies and assemblage weights. The above expression shows that the similarity index \(\bar{C}_{2, N}(\bar{T})\), as in all our similarity measures, is unity if and only if \(w_{i,aj} = w_{i,ak}\) (i.e., absolute abundances are identical) for all node \(i\) in the branch set and for any two assemblages \(j\) and \(k\). This reveals that the index compares absolute abundances node by node among the \(N\) assemblages. Therefore, when absolute abundances differ, there can be nonzero differentiation even if all assemblages have identical species relative abundances. If our target is to compare node-by-node relative abundances, we simply change our measure of species importance to relative abundances and thus equal weights are naturally obtained. Then the differentiation index is zero if and only if all assemblages have identical node-by-node relative abundances.

2. Lineage overlap from a regional perspective.—This class of measures takes the form

\[
\bar{U}_{q, N}(T) = \frac{\frac{1}{\bar{C}_q(T)}^{1/q} - (1/N)^{1/q}}{1 - (1/N)^{1/q}}.
\]  

(12a)

This class of measures quantifies the effective proportion of shared lineages in the pooled assemblage. Assume each of the \(N\) assemblages has only completely distinct lineages and the phylogenetic trees for all assemblages are identical. If there are \(S\) completely distinct, equally abundant lineages in the pooled assemblage, with exactly \(R\) lineages shared by all \(N\) assemblages, and with the remaining \(S - R\) lineages evenly distributed in \(N\) assemblages, then this measure equals the lineage overlap \(R/S\) in the pooled assemblage. In this case, the measure \(1 - \bar{U}_{q,N}(T) = 1 - R/S\) is a complementarity measure for all orders of \(q\).

For \(q = 0\), this measure is called the “phylo-Jaccard” \(N\)-assemblage measure because for \(N = 2\) the measure \(1 - \bar{U}_{0,2}(T)\) reduces to the Jaccard-type UniFrac measure developed by Lozupone and Knight (2005) and the PD-dissimilarity measure developed by Faith et al. (2009). For \(q = 1\), this measure is identical to the “phylo-Horn” \(N\)-assemblage overlap measure \(\bar{C}_{1, N}(T)\); see Table 2. For \(q = 2\), we refer to the measure \(\bar{U}_{2, N}(T)\) as a “phylo-regional-overlap” measure. For equally weighted non-ultrametric trees, we have

\[
1 - \bar{U}_{2, N}(T) = \frac{N - 2\bar{D}_p(T)}{N - 1} = \frac{Q_2 - Q_3}{(N - 1)(T - Q_1)}.
\]

(12b)

See Table 2 for a more general formula with assemblage weights.

3. Phylogenetic homogeneity.—This class of measures takes the form

\[
\bar{S}_{q, N}(T) = \frac{1/\bar{C}_q(T) - 1/N}{1 - 1/N}
\]  

(12b)

This measure is linear in the proportion of regional diversity contained in the typical assemblage. For \(q = 0\), it is the “phylo-Jaccard” \(N\)-assemblage measure \(\bar{U}_{0, N}(T)\). For \(q = 2\), this measure is identical to \(\bar{C}_{2, N}(T)\), the “phylo-Morisita-Horn” \(N\)-assemblage similarity measure. Thus, we have \(\bar{S}_{0, N}(T) = \bar{U}_{0, N}(T)\) and \(\bar{S}_{2, N}(T) = \bar{C}_{2, N}(T)\) see Table 2. However, for \(q = 1\), this measure does not reduce to the “phylo-Horn” overlap measure.

4. Complement of phylogenetic turnover rate.—This class of measures takes the form

\[
\bar{V}_{q, N}(T) = \frac{N - q\bar{D}_p(T) - 1}{N - 1} = 1 - \frac{q\bar{D}_p(T) - 1}{N - 1}.
\]  

(12c)

The corresponding differentiation measure \(\frac{q\bar{D}_p(T) - 1}{N - 1}\) is the relative lineage turnover rate per assemblage. This differentiation measure is linear in beta and measures the relative lineage turnover rate per assemblage. When \(q = 0\), the measure \(\bar{V}_{0, N}(T)\) is identical to the “phylo-Sørensen” \(N\)-assemblage measure. For \(q = 2\), this measure is identical to \(\bar{U}_{2, N}(T)\), the “phylo-regional-overlap” measure. That is, we have \(\bar{V}_{0, N}(T) = \bar{C}_{0, N}(T)\) and \(\bar{V}_{2, N}(T) = \bar{U}_{2, N}(T)\).
For $q = 1$, the corresponding inequality is
\[
0 \leq I_b(T) \leq \lim_{q \to 1} \left( \frac{1 - N^{1-q}}{q - 1} \right) \left( T - (q-1)I_a(T) \right) = T \log N.
\]

See Appendix E for proofs. When all species are completely distinct and $T = 1$, the measure $Q_b$ reduces to the generalized entropy (in Eq. 1), so Eq. 13b reduces to its non-phylogenetic version (Jost et al. 2010). These inequalities show why the traditional phylogenetic similarity and differentiation measures produce counterintuitive results, and also how to fix them. We discuss the three most commonly used special cases ($q = 0, 1, 2$).

1. $q = 2$.—Eq. 13b shows that the “beta” quadratic entropy $Q_b$ is confounded with alpha quadratic entropy $Q_a$ through the constraint $Q_b \leq (1 - 1/N)(T-Q_a)$. A high alpha quadratic entropy means that $Q_a \to T$, so that additive “beta” is necessarily to be small, even if the assemblages share no lineages whatsoever. This implies that, when $Q_a$ is high (close to $T$), the “differentiation” measure $J_{\bar{z}_a}(T)$ is necessarily going close to 0, and the “similarity” measure $1-J_{\bar{z}_a}(T)$ is close to its maximum value of unity, for any set of assemblages, even assemblages that share no species or lineages. So the additive “beta” does not measure pure differentiation among assemblages, and the “similarity” and “differentiation” measures also do not really measure phylogenetic similarity and differentiation. The low values do not reflect reality, but are inescapable mathematical consequences of Eq. 13b. In Examples we demonstrate this by means of hypothetical and real examples, and compare the measure $J_{\bar{z}_a}(T)$ with our proposed measures. See Hardy and Senterre (2007) for another real example; in this case, the authors later recognized the problem and rectified their interpretation (Hardy and Jost 2008). To fix this problem, the upper bound in Eq. 13b can be used to construct a normalized measure in the range [0, 1]. As shown in Table 2 and Eq. 11b, the normalized measure $Q_b/[1 - 1/N(T-Q_a)]$ is exactly our differentiation measure $1-C_{\bar{z}_a}(T)$.

2. $q = 1$.—It follows from the inequality Eq. 13c that additive “beta” phylogenetic entropy is bounded by $T \log N$, if $N$ and $T$ are both fixed. Thus, additive “beta” is not constrained by alpha, and additive “beta” and alpha are independent (not confounded), as in the non-phylogenetic case. This can be also seen from Eq. 10a for the equal-weight case. However, since additive “beta” is bounded by $T \log N$, it follows that the differentiation measure $J_{\bar{z}_a}(T)$ (“beta”/gamma) is always close to 0 if the denominator gamma tends to be large, regardless of the true differentiation. In this case, the similarity measure $1 - J_{\bar{z}_a}(T)$ (i.e., alpha/gamma) is always close to unity. Thus, even though for $q = 1$, additive decomposition based on phylogenetic entropy is justified (as in the non-phylogenetic Shannon entropy), the normalized measure $J_{\bar{z}_a}(T)$ still cannot quantitatively differentiate, and its complement still does not reflect similarity. This happens because Shannon entropy does
not obey the replication principle. The upper bound in Eq. 13c reveals that phylogenetic entropy additive “beta” should be normalized not by gamma, but by $T \log N$ instead. This is clearly seen from Table 2 (for $q = 1$), and when this “beta” is normalized by this constant, our differentiation measure $1 - \hat{C}_{IN}(T)$ is obtained.

3. $q = 0$.—It follows from the inequality Eq. 13b that additive “beta” based on Faith's total branch length $L(T)$ is bounded by $(N - 1)/(T + 0\bar{I}_\beta(T)) = (N - 1)L_\alpha(T)$, so that the additive “beta” is positively constrained by alpha. The normalized differentiation measure using (lineage excess)/gamma is $[L_a(T) - L_\alpha(T)]/L_a(T) = (1 - 1/N)(1 - \bar{U}_{\alpha N}(T))$, where $\bar{U}_{\alpha N}(T)$ is the “phylo-Jaccard” similarity measure (Table 2). This resulting measure is a legitimate differentiation measure, but it ranges from 0 (when all assemblages are identical) to $1 - 1/N$ (when all assemblages have no shared lineages). We propose dividing the additive “beta” by its maximum value to obtain a normalized measure $[L_a(T) - L_\alpha(T)]/[N - 1 - L_\alpha(T)]$, which is identical to our differentiation measure $1 - \hat{C}_{\alpha N}(T)$ with range [0, 1].

As shown in Eq. 13b, the traditional “beta” phylogenetic generalized entropy for $q > 1$ is negatively constrained by the value of alpha, and for $q < 1$ it is positively constrained by the value of alpha. Thus, the anomalous behavior is also present for all other values of $q$. These anomalous behaviors can be easily fixed by using proper normalizations. For all orders $q \neq 1$, the dependence of the phylogenetic “beta” on its alpha can be removed by dividing the additive “beta” $\bar{I}_\beta(T)$ by its maximum possible value in Eq. 13b. In Appendix E, we prove for all $T$ that this “beta” $\bar{I}_\beta(T)$, when properly normalized so as to remove its dependence on alpha, yields the same normalized differentiation measure $1 - \hat{C}_{\alpha N}(T)$ (and normalized similarity measure $\hat{C}_{\alpha N}(T)$) as the multiplicative partitioning scheme applied to mean phylogenetic diversity.

The dependence relationship in Eq. 13b is equivalent to the following constraint which shows how the additive “beta” phylogenetic generalized entropy $\bar{I}_\beta(T)$ depends on gamma phylogenetic generalized entropy

$$0 \leq \bar{I}_\beta(T) \leq \frac{(1/N^{1-q} - 1)[T - (q - 1)^{\bar{I}_\beta(T)}]}{q - 1} \quad q \neq 1.$$

(13d)

For $q = 1$, a similar upper bound $T \log N$ is also obtained as in Eq. 13c. Similar conclusions and implications as those for Eq. 13b can be obtained. We omit the details. For all orders $q \neq 1$, if we normalize the “beta” phylogenetic generalized entropy $\bar{I}_\beta(T)$ by its maximum in Eq. 13d, then the normalized measure yields the normalized differentiation measure $1 - \bar{U}_{\alpha N}(T)$, a “true complementarity” measure from a regional view. The extension of Eqs. 13b, 13c, and 13d to the general non-ultrametric cases is provided in Appendix E.

The three measures (phylogenetic beta diversity, lineage excess, and phylogenetic generalized entropies) all lead to the two classes of normalized phylogenetic similarity measures $\hat{C}_{\alpha N}(T)$ (true local lineage overlap) and $\hat{U}_{\alpha N}(T)$ (true regional lineage overlap), as well as their corresponding differentiation measures. Thus, we finally achieve a consensus on the issue of normalized phylogenetic similarity and differentiation measures; see Table 2. We suggest using two types of profiles to characterize the proposed differentiation measures $1 - \hat{C}_{\alpha N}(T)$ and $1 - \bar{U}_{\alpha N}(T)$. (1) For a fixed order $q$ (including at least 0, 1, and 2), the first type of profile is obtained by plotting our differentiation measures as a function of time perspective $T$. (2) For any fixed time perspective $T$ (including at least $T = 0$ and $T$ = the age of the root of the pooled tree), the second type of profile is obtained by plotting our differentiation measures with respect to the order $q$. See Examples for illustrative plots and Discussion for the choices of $T$ and $q$.

**Examples**

In all examples, we consider three phylogenetic measures: $J_{\alpha N}(T) = 1 - \bar{I}_a(T)^{\alpha \bar{I}_a(T)}$ (based on phylogenetic generalized entropy, Eq. 13a), $1 - \hat{C}_{\alpha N}(T)$, and $1 - \bar{U}_{\alpha N}(T)$ (both are based on our mean phylogenetic diversity) to quantify the differentiation between two assemblages. For comparisons, we also consider the non-phylogenetic versions of these measures: $J_{\alpha N}$ (based on generalized entropy), $1 - \bar{C}_{\alpha N}$ and $1 - \bar{U}_{\alpha N}$ (based on Hill numbers); see Table 1 for all measures.

**Example 1: A simple hypothetical tree with completely distinct lineages**

To decide whether our proposed similarity and differentiation measures are more appropriate than the “similarity” and “differentiation” measures based on traditional additive partitioning of quadratic entropy and phylogenetic entropy, we will first apply all phylogenetic similarity and differentiation measures to very simple trees for which unequivocal answers exist. If a phylogenetic similarity or differentiation measures cannot yield logical and sensible results for simple trees, we would not expect it to work for complicated real trees.

Consider two assemblages of landlocked organisms that originated on a super-continent that broke into two parts. For simplicity, suppose all species in each assemblage began to diverge from their common ancestor very soon after separation of the continents $T$ years ago, and suppose each species is equally common so that the two assemblages are equally weighted. (Nothing important hinges on this latter assumption, which simplifies calculation.) The assemblages evolved in isolation for approximately $T$ years. See Appendix F for an illustrative figure and derivation details.

For this example ($N = 2$), our proposed normalized phylogenetic differentiation measures $1 - \hat{C}_{\alpha N}(T)$ and $1 - \bar{U}_{\alpha N}(T)$ are always 1 for any $q$, any richnesses $S$, and any values of $T$; see Table 3. This value of unity correctly indicates that we have two maximally distinct
PHYLOGENETIC BETA DIVERSITY

In Appendix F, the general formula is

\[ J \]

there is almost no differentiation. The measure

phylogenetic generalized entropies, Eq. 13a) depends on

their dispersal abilities. Then, after separation, some

node). While the continents are still joined, their faunas

occurs at 200 Myr ago (i.e., \( t = 40 \) Myr after the first

node). That is, some taxa radiate independently on each of the new continents, while others continue to cross the gap and are shared between continents. Assume that in the two present-day assemblages, there are 23 species in Assemblage 1 and 19 species in Assemblage 2, with 5 of these shared between assemblages (Fig. 3). We focus on the differentiation measure with equal weights in order to compare our measures with the additive approach. In each assemblage, all species are assumed to be equally abundant at the present time, and the actual relative abundances of the ancestral species in the past are the sums of the relative abundances of their descendants in the present-day assemblages. If an approach fails in this simple case, it cannot be a mathematically valid approach for more realistic cases.

Table 3 compares the non-phylogenetic and phylogenetic differentiation measures when the temporal perspective \( T \) is chosen to be the age of the basal node, 240 Myr ago. The phylogenetic measure \( J_qN(T) \) hardly differs from its non-phylogenetic counterpart \( J_qN^* \). In contrast, the difference between our new phylogenetic measures and their non-phylogenetic counterparts depends on \( q \). The difference is limited for \( q = 0 \), but the difference for \( q > 0 \) can be substantial.

Now imagine that we have been monitoring these assemblages since \( T = 240 \) Myr, and we watch how the assemblages diverge over time. If we are using sensible measures of evolutionary differentiation, we should witness the divergence increasing monotonically with time. We test this by plotting the temporal evolution of various differentiation measures beginning at the first node, as a function of time \( t \) after the first node. That is,

<table>
<thead>
<tr>
<th>Example qN</th>
<th>( 1 - C_{qN} )</th>
<th>( 1 - U_{qN} )</th>
<th>( J_{qN} )</th>
<th>( 1 - \tilde{C}_{qN}(T) )</th>
<th>( 1 - \tilde{U}_{qN}(T) )</th>
<th>( J_{qN}(T) )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Example 1</td>
<td>( q = 0 )</td>
<td>1</td>
<td>1</td>
<td>0.53</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>( q = 1 )</td>
<td>1</td>
<td>1</td>
<td>0.23</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>( q = 2 )</td>
<td>1</td>
<td>1</td>
<td>0.05</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Example 2</td>
<td>( q = 0 )</td>
<td>0.76</td>
<td>0.86</td>
<td>0.44</td>
<td>0.66</td>
<td>0.79</td>
</tr>
<tr>
<td></td>
<td>( q = 1 )</td>
<td>0.76</td>
<td>0.76</td>
<td>0.15</td>
<td>0.63</td>
<td>0.63</td>
</tr>
<tr>
<td></td>
<td>( q = 2 )</td>
<td>0.76</td>
<td>0.62</td>
<td>0.02</td>
<td>0.49</td>
<td>0.33</td>
</tr>
<tr>
<td>Example 3</td>
<td>( q = 0 )</td>
<td>0.26</td>
<td>0.41</td>
<td>0.21</td>
<td>0.27</td>
<td>0.42</td>
</tr>
<tr>
<td></td>
<td>( q = 1 )</td>
<td>0.52</td>
<td>0.52</td>
<td>0.14</td>
<td>0.36</td>
<td>0.36</td>
</tr>
<tr>
<td></td>
<td>( q = 2 )</td>
<td>0.80</td>
<td>0.67</td>
<td>0.08</td>
<td>0.33</td>
<td>0.20</td>
</tr>
</tbody>
</table>

Notes: Example 1 represents completely distinct lineages, with 10 species in each assemblage and no shared species. Example 2 has 23 species in Assemblage 1, 19 species in Assemblage 2, and 5 shared species. Example 3 contains rockfish data, with 38 species in Assemblage 1, 24 species in Assemblage 2, and 5 shared species. See Tables 1 and 2 and Eq. 13a for formulas. Note the small

Example 2: A more complex hypothetical tree

We now consider a more complicated hypothetical tree in order to examine the performance of differentiation measures as a function of evolutionary time. Consider a homogeneous super-continent that splits into two continents or assemblages. Fig. 3 shows the time-calibrated phylogenetic tree of the fauna of these continents. We assume that the age of the basal node is 240 million years (Myr) ago. The continental split occurs at 200 Myr ago (i.e., \( t = 40 \) Myr after the first node). While the continents are still joined, their faunas are identical with five taxa. Suppose the taxa vary in their dispersal abilities. Then, after separation, some

assemblages over this time interval. In contrast, the traditional differentiation measure \( J_{qN}(T) \) (based on phylogenetic generalized entropies, Eq. 13a) depends on the richesses \( S \) of the assemblages. Table 3 shows the \( J_{qN}(T) \) measures for the special case of \( S = 10 \). As derived in Appendix F, the general formula is \( J_{2N}(T) = 1/(2S - 1) \), while \( J_{1N}(T) = (\log 2)/\log (2S) \), and \( J_{0N}(T) = S/(2S - 1) \). This means that when the alpha diversity is large (equivalently \( S \) is large for this example), both \( J_{2N} \) and \( J_{1N} \) always approach zero, wrongly indicating that there is almost no differentiation. The measure \( J_{0N} \) approaches 1/2, indicating a normalization is needed. For this example, the correct answer is unequivocal: The two completely phylogenetically distinct assemblages should attain the maximum differentiation of unity. The traditional measures cannot measure differentiation properly even for a simple tree, so they cannot do it for a more complicated tree either.
we graph the differentiation measure between the two assemblages for the interval $[-T, -T + t]$, as a function of $t$, with $t$ ranging from zero (the basal node) to 240 Myr. A measure of normalized phylogenetic differentiation should be low (and zero for $q = 0$) when applied to the assemblages for $t < 40$ Myr, because this is the period when the species are all shared by the two assemblages prior to the continental break-up. Phylogenetic differentiation should increase monotonically beginning immediately after the break-up at $t = 40$ Myr, since the assemblages evolve independently after this time, diverging due to genetic drift and the action of different selective forces. After a very long time, the normalized differentiation should eventually approach unity.

In this example, all measures are computed for the interval $[-T, -T + t]$ as a function of $t$ instead of the time perspective $T$, so we drop the variable $T$ in all notations of measures. The graphs in Fig. 4 demonstrate the behavior of the traditional differentiation measure $J_{qN}$ and our two phylogenetic differentiation measure $1 - \bar{C}_{qN}$ and $1 - \bar{U}_{qN}$ for $q = 0, 1, 2$. When $q = 1$, the two measures $1 - \bar{C}_{1N}$ and $1 - \bar{U}_{1N}$ are identical; for $q = 0$, the measure $1 - \bar{U}_{0N}$ is higher than $1 - \bar{C}_{0N}$ while the ordering is reversed for $q = 2$. From Fig. 4, it is clear that our phylogenetic differentiation measures behave as expected and generally exhibit a consistent trend. They are both low (and zero for $q = 0$) prior to the break-up of the continents, and increase monotonically afterwards. The asymptotic values of our two normalized differentiation measures approach unity, although for $q = 2$, the rates of increase are slow.
For $q = 0$, the measure $J_{q N}$ displays a pattern similar to that of our measures; after the split, it steadily increases to a stable value, but it stabilizes at a different value than our measures. In sharp contrast, the traditional differentiation measures based on phylogenetic entropy ($q = 1$) and quadratic entropy ($q = 2$) in Fig. 4 begin to decrease after an initial rise following the continental break-up. For both, the asymptotic value is very low rather than unity. These measures will therefore mis-rank assemblages according to their phylogenetic differentiation. For example, the assemblages 200 Myr after the split are unambiguously more differentiated than the assemblages just 20 Myr after the split, but the traditional differentiation measures for $q = 1$ and $q = 2$ give the opposite ranking. These misbehaviors are consequences of their dependence on alpha, as predicted by our Eqs. 13b, 13c, and 13d. All these behaviors are analogous to the corresponding behaviors of non-phylogenetic “similarity” and “differentiation” measures based on classical indices like Shannon entropy and the Gini-Simpson index, as shown in Figs. 1 and 2 of Jost et al. (2010).

In this example, all the differentiation measures are computed for the interval $[-T, -T + t]$, where $T$ is fixed value of 240 Myr (the age of the root). This is because the plot as a function of $t$ (time after the age of the root) should unequivocally exhibit a non-decreasing trend so we can examine whether a measure behaves as expected. As discussed, we recommend in most applications to present two types of profiles to see how our proposed differentiation measures $1 - \bar{C}_q(N)(T)$ and $1 - \bar{U}_q(N)(T)$ behave when the temporal perspective $T$ varies (for a fixed $q$) or when order $q$ varies (for a fixed $T$). These two types of profiles for the hypothetical tree are shown in Appendix G. These two types of profiles are illustrated for a real phylogenetic tree in Example 3 with discussion.

**Example 3: A real phylogenetic tree for rockfish**

We now apply our methods to a real example discussed by Pavoine et al. (2009). The full data set contains a total of 52 rockfish species of the genus *Sebastes* collected over 20 years (1980–1986, 1993–1994, 1996, 1998–2007) from the Southern California Bight, USA. Love et al. (1998) found that the species richness declined at a constant rate due to heavy fishing in recent decades. Considering phylogeny, Magnuson-Ford et al. (2009) concluded that the large, evolutionarily isolated and morphologically distinctive species generally are more vulnerable to overfishing. Pavoine et al. (2009) applied their phylogenetic generalized entropy, given in our Eq. 2c, to examine whether the decline in species richness was associated with the change in the phylogenetic structure of the assemblage.

For illustrative purposes, we focus on measuring the phylogenetic differentiation between two contrasting assemblages. (Some additional analyses are provided in Appendix G.) The 1981 and 2003 assemblages are referred to as Assemblage 1 and 2, respectively. The phylogenetic tree of the 52 species (from Hyde and Vetter 2007) and the species relative abundances for these two assemblages, taken from Pavoine et al. (2009), are shown in Fig. 5a. Our purpose is to quantify the phylogenetic differentiation among the two sets of relative abundances, the weights for the two assemblages are thus equal in our analysis. A sub-tree containing only the three most abundant species in each assemblage is shown in Fig. 5b.

Consider a fixed time perspective at $T = 7.9$ Myr, the age of the root of the pooled tree. All the phylogenetic and non-phylogenetic differentiation measures for the interval $[-7.9, 0]$ are presented in Table 3. As we found for Example 2, the traditional abundance-sensitive differentiation measures $J_{q N}(T) (q > 0)$ are very low and close to their non-phylogenetic value $J_{q N}^*$, as shown by our measures should also be the more intuitive answer. In this real example, the increasing trend and high differentiation shown by our measures should also be the more intuitive and sensible answer after 1.6 Myr. Consider first the non-phylogenetic differentiation measure for $q = 2$. The two measures $1 - C_{2 N}$ and $1 - U_{2 N}$ both are dominated by the relatively common species shown in Fig. 5b. The most common species in Assemblage 1 correspond to a very rare species in Assemblage 2, and vice versa; see Fig. 5b. Therefore, when phylogeny is not considered,
the differentiation should be relatively high, as reflected by the high value of $1 - C_{2N} = 80\%$ and $1 - U_{2N} = 67\%$ at the tips (present day) in Table 3. The former is the effective average percentage of dominant species that are unique to each assemblage (and thus shared species constitute only about 20\% of the dominant species in each assemblage). The latter is the effective percentage of dominant species that are unique to the pooled assemblage (and thus, shared species constitute about 33\% of the dominant species in the pooled assemblage).

Our phylogenetic differentiation measures $1 - \bar{C}_{2N}$ and $1 - \bar{U}_{2N}$ are dominated by the “very important lineages” (those with high node abundances) and “evolutionarily deep” species (long branch lengths).

The most dominant species of Assemblage 2 ($S. miniatus$) diverged from the lineage of the three dominant species in Assemblage 1 around 1.6 Myr after the root; see Fig. 5b. The divergence time for the three most dominant species of Assemblage 1 occurred between 1.6 Myr and 2.2 Myr after the root. Around 2.2 Myr after the root, all five dominant species in Fig. 5b are in isolated lineages, and the sharp importance difference between the dominant ancestral lineages remains after that. Thus, the phylogenetic differentiation
between these two assemblages should begin increasing at 1.6 Myr after the root and should continue to increase with time $t$.

Our phylogenetic differentiation measure $1 - \bar{C}_{2N}$ increases to 33% by the present time (Table 3 and the right panel of Fig. 6 as $t$ approaches 7.9 Myr). Similarly, the measure $1 - \bar{U}_{2N}$ increases to 20%. These are substantially lower than their corresponding non-phylogenetic differentiation measure because the node abundances near roots (where the differentiation values are near zero) are relatively high and dominant in the whole tree. But these values are much higher than the traditional additive phylogenetic “differentiation” values; our value for $q = 2$ is triple the value of 10% based on Rao’s quadratic entropy. In the past 7.9 Myr, if we focus on the abundant lineages (as appropriate for $q = 2$), the average percentage of non-shared lineages per assemblage is about 33% (and 20% in the pooled assemblage), showing that the values of our measures (33% and 20%) reflect reality, while the traditional additive measure may underestimate the phylogenetic effects of overfishing. Similarly for $q = 1$, the differentiation for our measure ($1 - \bar{C}_{1N} = 1 - \bar{O}_{1N}$) increases from zero to 36%, whereas the corresponding curve for phylogenetic entropy rises briefly and then counterintuitively drops to a low value of around 15% (Table 3, Fig. 6).

To see how our differentiation measures vary with the time perspective $T$ and with the order $q$, we suggest making two types of profiles for our proposed differentiation measures. The first type of profile plots the differentiation measure as a function of the temporal perspective $T$, with $q$ fixed. The second type plots the same measure as a function of $q$, with $T$ fixed. To illustrate the first type of profile, we evaluate the two proposed differentiation measures, $1 - \bar{C}_{qN}(T)$ and $1 - \bar{U}_{qN}(T)$, over the interval $[-T, 0]$ with $0 < T < 10$, for $q$ fixed; in Fig. 7a we choose to plot the profiles for $q = 0, 1$, and 2. For comparison, we also plot the profiles of the traditional measure $J_{qN}(T)$ for the same fixed values of $q$. In Fig. 7b, we show the other type of profiles, which plot the three measures as a function of $q$, $0 \leq q \leq 5$, separately for $T = 0$ (non-phylogenetic case) and $T = 7.9$ Myr.

The profiles in Fig. 7a show that the additive differentiation measure $J_{qN}(T)$ hardly varies with $T$, and all values for $q = 1$ and $q = 2$ are very low, as predicted by our theory for the case of high alpha (and thus high gamma) phylogenetic entropies. In such cases, the measure $J_{qN}(T)$ is nearly insensitive to the phylogenetic structure. This can also be seen by comparing the two profiles in Fig. 7b for the specific values of $T = 0$ (non-phylogenetic cases) and $T = 7.9$ Myr for $0 \leq q \leq 5$. All values of the measure $J_{qN}(T)$ for $T = 7.9$ Myr are close to their corresponding non-phylogenetic values for $T = 0$ (i.e., the measure $J_{qN}^*$); see also Table 3. The two measures $J_{qN}(T)$ and $J_{qN}^*$ vary slowly with the order $q$ as shown in Fig. 7b, and their values are very low (for $q \geq 1$) as predicted by our theory. Therefore, the two types of profiles in Figs. 7a and 7b confirm by example our theoretical proof that the measure $J_{qN}(T)$ often will not reflect either tree structure or differences in species abundances.

We next examine the behavior of our two proposed differentiation measures. Since the dominant species in the two assemblages began to diverge from each other between 1.6 Myr and 2.2 Myr after the root (i.e., between 5.7 Myr ago and 6.3 Myr ago; see Fig. 5b), those dominant species were in the same lineage 6.3 Myr ago or anytime earlier. As a result, the two proposed abundance-sensitive measures ($q = 1$ and 2) in Fig. 7a remain at relatively high levels when $T < 6.3$ Myr and start to decline around $T = 6.3$ Myr. Generally, as $T$ becomes larger, more dominant shared lineages are added to the two assemblages, implying the abundance-sensitive differentiation measures should generally exhibit a nonincreasing trend. The profiles of our differentiation measures for $q = 1$ and 2 clearly show the expected decreasing trend when $T$ is increased, and the decline rates differ for the two different orders of $q$. Also, comparing the two figures ($T = 0$ and $T = 7.9$ Myr) in Fig. 7b, we see that all values of the phylogenetic
differentiation measure \(1 - \bar{C}_{qN}(T)\) are much lower than the corresponding non-phylogenetic measure. Similar behavior is also found for the measure \(1 - \bar{U}_{qN}(T)\). The two types of profiles (in Fig. 7a and b) show that our measures can incorporate the differences in both tree structure and lineage abundances.

These hypothetical and real examples have confirmed empirically our theoretical findings in earlier sections. If our goal is to provide measures to quantify the similarity or differentiation, and compare the measures across regions with different alpha or gamma diversities, the traditional additive “differentiation” measures based on \((1 - \text{alpha/gamma})\) for phylogenetic entropy and quadratic entropy may lead to counterintuitive results, and for \(q > 0\), they are insensitive to tree structure when alpha diversity is high. For all orders of \(q\), these traditional measures can be fixed by normalizing them, again yielding our differentiation measures \(1 - \bar{C}_{qN}\) and \(1 - \bar{U}_{qN}\), whose ranges are always the interval \([0, 1]\) regardless of alpha or gamma diversity. Our measures behave as expected and conform to intuition, as shown by all examples.

**DISCUSSION**

In the past, a traditional additive approach has been applied to partitioning phylogenetic measures such as Rao’s quadratic entropy \(Q\), phylogenetic entropy \(H_P\), and phylogenetic generalized entropy. The difference between gamma and alpha phylogenetic generalized entropies (which include quadratic entropy and phylogenetic entropy as special cases) was then divided by gamma to obtain measures of phylogenetic differentiation. While these measures do have valid interpretations (Hardy and Jost 2008), their magnitudes do not reflect the degree of phylogenetic differentiation between assemblages. Our examples and mathematical analyses show that when within-group diversity is high, these abundance-sensitive differentiation measures approach a fixed value (zero) that has no relation to the phylogenies of the species or to the differences in their abundances across assemblages. Measures that become completely insensitive to the properties they are supposed to measure are not useful tools for biologists, and they will inevitably mislead in typical conservation and applications.
This behavior, caused by the measures' dependence on alpha diversity, has other disturbing consequences. The additive differentiation measure based on Rao's quadratic entropy can show that every single subfamily of plants exhibits very high differentiation (no shared lineages) between two assemblages, but when the same measure is applied to the pooled subfamilies, it would show that differentiation between the two assemblages was near zero. This can happen even if all subfamilies shared the same root node and had the same tree structure and same abundance distributions. The mere act of pooling necessarily lowers this differentiation measure, because pooling equally diverse subfamilies makes alpha increase, and this measure is confounded with alpha. These problems have clear mathematical causes. First, the additive framework was imposed on measures that are not additive (except when \( q = 1 \)), resulting in a between-group component that is confounded with the within-group component. Second, the measures do not obey the replication principle, so their alpha/gamma ratio does not reflect similarity between groups.

These are familiar problems that also arise when the additive framework is applied to non-phylogenetic generalized entropies. In the non-phylogenetic case, these problems were resolved by partitioning Hill numbers, which obey the replication principle (Jost 2007). In this paper we show how to extend this solution to the phylogenetic case, by partitioning the phylogenetic Hill numbers of Chao et al. (2010). Phylogenetic Hill numbers are multiplicatively partitioned into independent within- and between-group components, which are the phylogenetic alpha and beta diversities. The between-group or beta component is normalized in various ways to make phylogenetic similarity and differentiation measures. The normalizations yield weighted and phylogenetic generalizations of the Jaccard, Sørensen, Horn, and Morisita-Horn similarity measures. The proposed normalized similarity measures have the flexibility to reflect the resemblance or difference not only in relative abundances, but also in absolute abundances.

As in the non-phylogenetic case, the lineage excess (gamma – alpha phylogenetic Hill numbers) and the phylogenetic generalized entropy excess (gamma – alpha phylogenetic generalized entropies), when normalized properly, lead to some of these same similarity measures. The convergence of all these approaches demonstrates the underlying unity of this field and highlights the special character of our similarity measures \( \tilde{C}_{\alpha N}(T) \) and \( \tilde{U}_{\alpha N}(T) \); see Table 2. The similarity measure \( \tilde{C}_{\alpha N}(T) \) quantifies the effective average proportion of shared lineages per assemblage. The differentiation measure \( 1 - \tilde{C}_{\alpha N}(T) \) thus quantifies the effective average proportion of non-shared lineages per assemblage. The measure \( \tilde{C}_{\alpha N}(T) \) satisfies a phylogenetic generalization of the concept of a “true local overlap” measure (Wolda 1981, 1983). This quality “calibrates” the similarity measure in terms of an easily-visualizable set of reference assemblages. A similar interpretation can be made for the regional-overlap similarity measure \( \tilde{U}_{\alpha N}(T) \), which refers to the effective percentage of shared lineages in the pooled assemblage.

All similarity and differentiation measures that are monotonic transformations of our phylogenetic beta diversity (see Table 2) are replication invariant. For non-phylogenetic measures, this principle states that if \( N \) assemblages each consist of \( K \) identical subsets of abundances, and no species are shared between subsets within an assemblage, then the \( N \) assemblages as a whole should have the same degree of similarity or differentiation as the individual subsets. Jost et al. (2011) showed that this property is a necessary property for classical non-phylogenetic similarity and differentiation measures. Our proposed phylogenetic beta, similarity, and differentiation measures all satisfy this property of replication invariance; see Appendix C for a proof. This means our measures, unlike previous ones, are self-consistent when disjoint sub-trees are pooled.

Choice of temporal perspective \( T \) and order \( q \)

A conspicuous change from previous treatments of phylogenetic differentiation measures is our introduction of an explicit parameter \( T \) for the temporal perspective of the investigator. We introduced this in Chao et al. (2010), but it is even more important here. The broader our temporal perspective, the greater is the proportion of shared ancestry in the assemblages. Measures of normalized phylogenetic similarity have always concealed an implicit temporal perspective, most often the age of the root node of the tree under consideration. However, this choice is not always the most appropriate one for the question under investigation. One problem with this choice is that it is sample dependent, because the root will be determined by the species actually observed. Since nearly every study will use a different root, it will be difficult to compare results across studies. By making the perspective explicit, we give the investigator the freedom to think about this choice and, if necessary, to change it. The most natural and least arbitrary choice of temporal perspective \( T \) for many purposes will be the divergence time between the group of interest and its nearest outgroup. This is independent of the composition of the actual sample and depends only on the sampling protocol (the decision to sample members of one taxonomic group, birds for example, and reject others such as moths or bats). Another natural choice would be \( T \) near the time of the most recent common ancestor of all taxa alive today. Other choices may be useful depending on the purpose of an investigation. Because different investigations will require different temporal perspectives, we recommend reporting results in a form that facilitates changes of this perspective. Reporting \( \tilde{D}(T) \), with \( T \) equal to the age of the root node for the organisms under study, allows easy transformation to any time interval larger than \( T \).
If \( T \) is the new temporal perspective, then

\[
qD(T) = \left\{ \frac{T - T_r}{T} + \frac{T_r}{T} \left[ qD(T_r) \right]^{\frac{1}{1-q}} \right\}^{1/(1-q)}.
\]

This formula can be used to translate both phylogenetic alpha and gamma diversity to the new temporal perspective. The new alpha and gamma diversities can then be used to calculate beta and our similarity (or differentiation) measures for the new \( T \). See Fig. G1 (in Appendix G) and Fig. 7a for examples of profiles for our proposed phylogenetic differentiation between two assemblages as a function of the time perspective \( T \).

Our measures also contain the free parameter \( q \), which determines the sensitivity to present-day species abundances. When trying to identify past episodes of determining the sensitivity to present-day species abundances, \( q = 0 \) is recommended, since abundance information is not necessarily relevant to this question. In ecological studies such as those examining the phylogenetic relationships of the dominant species in a set of assemblages, or those examining functional diversity, we recommend reporting the results in the form of a similarity or differentiation profile, a graph of the chosen measure(s) as \( q \) varies from zero to about four or five (beyond which there is usually little change). This gives complete information about the system for the chosen time perspective \( T \), just as in the non-phylogenetic case; see Jost et al. (2011) for a non-phylogenetic similarity profile, and Fig. G1 (in Appendix G) and Fig. 7b for phylogenetic differentiation profiles of our proposed measures, as functions of \( q \).

**Functional beta diversity**

Functional diversity (FD) has been defined by Tilman (2001) as “the value and range of those species and organismal traits that influence ecosystem functioning.” Many measures have been proposed to assess FD of an assemblage. Among them, the dendrogram constructed from a trait-based distance matrix using a clustering scheme (Petchey and Gaston 2002) is widely used. Chao et al. (2010) suggested that the phylogenetic mean diversity approach given in Eqs. 4a and 4b can be applied to quantify functional diversity and interpreted as “the effective mean number of functional groups.” The approach proposed in the present paper can be used to quantify functional beta diversity among assemblages, and to generate intuitive and well-behaved measures of functional similarity and differentiation among assemblages. The partitioning method can also provide a unified framework for genetic, species, and ecosystem diversity partitioning. A critical requirement in our approach is that a tree structure can be constructed. We are currently developing Hill number types of functional diversity based on distance matrix directly.

**Applications to other disciplines**

The concept of diversity and its partitioning are useful in many disciplines. Our proposed decomposition can be applied in these disciplines, especially genetics. For example, a widely used genetic “differentiation” measure is Nei’s \( G_{ST} \) based on heterozygosity, the Gini-Simpson index of ecologists (Nei 1973, Jost 2008). \( (G_{ST} = 1 - H_{GS,T}/H_{GS,T}) \), where \( H_{GS,T} \) and \( H_{GS,T} \) denote, respectively, gamma and alpha Gini-Simpson index. It is often used to measure the differentiation of allele frequencies among subpopulations. Jost (2008) showed that \( G_{ST} \) and their relatives do not actually measure differentiation and proposed a new differentiation measure \( D \), which is our \( 1 - C_{2X} \) measure (Table 1). Our new phylogenetic differentiation measure \( 1 - C_{2X}(T) \) (Eqs. 11b and 11c) generalizes Jost’s \( D \) to take into account genetic distances and assembly weights. For this purpose, geneticists have often used the differentiation measure \( N_{ST} \) (Nei and Li 1979), which is based on nucleotide diversity (the average number of nucleotide differences between any two DNA sequences chosen randomly from a population). \( (N_{ST} = 1 - Q_{a}/Q_{T}) \), where \( Q_{a} \) and \( Q_{T} \) denote, respectively, gamma and alpha quadratic entropy. The nucleotide diversity is equivalent to Rao’s quadratic entropy, and \( N_{ST} \) is identical to the traditional differentiation measure \( J_{ST}(T) \). We have shown here by hypothetical and real examples that the measure \( J_{ST}(T) \) based on additive partitioning of Rao’s quadratic entropy does not measure differentiation. Thus, \( N_{ST} \) suffers the same drawback as \( G_{ST} \) and the measure \( J_{ST}(T) \). However, like additive beta quadratic entropy, it can be easily corrected, and the corrected measure is exactly our proposed phylogenetic differentiation measure \( 1 - C_{2X}(T) \), the phylogenetic generalization of Jost’s \( D \) measure; see Eq. 11b. This generalized measure is valid for both ultrametric and non-ultrametric trees. Hence, it also extends de Bello et al. (2010) to the general non-ultrametric weighted case. This provides a unified and rigorous framework for quantifying pure phylogenetic differentiation in both ecology and genetics, without confounding differentiation with within-group phylogenetic diversity. The new differentiation measure \( 1 - C_{2X}(T) \) merits investigation of its applications to genetics.

Leinster and Cobbold (2012) wrote “non-specialists are amazed to learn that a community of six dramatically different species is said to be no more diverse than a community of six species of barnacle.” Now that phylogenetic versions of the full range of diversity, similarity, and differentiation measures are available, it makes sense to incorporate phylogeny in all future diversity analyses. We hope that these new tools will encourage ecologists, geneticists, and conservation biologists to ask and answer new kinds of questions about the evolutionary forces that cause divergence of species assemblages or gene pools.

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Supplemental Material

Appendix A

An illustrative ultrametric tree (Ecological Archives M084-002-A1).

Appendix B

Diversity profile and strong replication principle for Hill numbers and phylogenetic Hill numbers (Ecological Archives M084-002-A2).

Appendix C

Diversity decomposition and related properties (Ecological Archives M084-002-A3).

Appendix D

Derivation of four classes of similarity measures and related properties (Ecological Archives M084-002-A4).

Appendix E

Mathematical flaws in the traditional additive approach based on generalized entropy excess or phylogenetic generalized entropy excess (Ecological Archives M084-002-A5).

Appendix F

A simple hypothetical tree with completely distinct lineages (Ecological Archives M084-002-A6).

Appendix G

Additional analysis of Examples 2 and 3 (Ecological Archives M084-002-A7).

Data Availability

Data associated with this paper have been deposited in Dryad: http://dx.doi.org/10.5061/dryad.vr4k2

**APPENDIX A. An illustrative ultrametric tree**

We first use a simple ultrametric tree in Fig. A1 to illustrate the original formulation of phylogenetic generalized entropy (Pavoine et al. 2009). This formulation is only valid for ultrametric trees. First, an ultrametric tree is subdivided into $M$ intervals, with each node defining an interval boundary, so that there are no internal nodes in each interval. The interval boundaries, which are the node ages, can be labeled $\{t_0, \ldots, t_k, \ldots, t_M\}$, starting at the most basal interval (so that $t_0 = -T$, and $t_M = 0$). The phylogenetic generalized entropy (Pavoine et al. 2009) is formulated as

$$qI(T) = \sum_{k=1}^{M} (t_k - t_{k-1}) q H_k,$$  \hspace{1cm} (A.1)

where the measure $qH_k$ is the generalized entropy of order $q$ in the $k$th evolutionary period,

$$qH_k = (1 - \sum \alpha_k^q)/(q - 1),$$

and $\{\alpha_{1k}, \alpha_{2k}, \ldots\}$ denote lineage “abundances” (i.e., the sum of the relative “abundances” descended from each branch) in that period (Fig. A1). These abundances are not estimates of their actual abundances of these ancestral species in the $k$th evolutionary period. They are interpreted as the measures of the importance of the branch’s descendents in the present-day assemblage. See the main text for details of this interpretation.

The mean phylogenetic diversity (Chao et al. 2010) defined in Eq. 4a of the main text for the divided tree structure in the interval $[-T, 0]$ becomes

$$q\bar{D}(T) = \left\{\frac{1}{T} \sum_{k=1}^{M} (t_k - t_{k-1}) \sum \alpha_k^q \right\}^{1/(1-q)} = \frac{1}{T} \left\{ \sum_{k=1}^{M} (t_k - t_{k-1}) \sum \left(\frac{\alpha_k}{T}\right)^q \right\}^{1/(1-q)}.$$

The branch diversity is thus

$$PD(T) = T \times \left\{ \sum_{k=1}^{M} (t_k - t_{k-1}) \sum \frac{\alpha_k^q}{T} \right\}^{1/(1-q)} = \left\{ \sum_{k=1}^{M} (t_k - t_{k-1}) \sum \left(\frac{\alpha_k}{T}\right)^q \right\}^{1/(1-q)}.$$

If we only consider an individual interval, say the $k$th interval, then the mean phylogenetic diversity becomes Hill numbers based on the importance values $\{\alpha_{1k}, \alpha_{2k}, \ldots\}$, and $PD$ in this interval is the product of this Hill number and the interval length.
Fig. A1. An ultrametric tree divided into non-overlapped evolutionary time periods. There are three internal speciation events between the root and tips. These three events divide the tree into four ($M = 4$) time periods. There are five species in the current assemblage with “abundances” $\{p_1, p_2, p_3, p_4, p_5\}$. Time period 1: there are two lineages with lineage “abundances” $\alpha_{11} = p_1 + p_2 + p_3$ and $\alpha_{23} = p_4 + p_5$; Time period 2: there are three lineages with lineage “abundances” $\alpha_{12} = p_1$, $\alpha_{22} = p_2 + p_3$, and $\alpha_{33} = p_4 + p_5$; Time period 3: there are four lineages with lineage “abundances” $\alpha_{13} = p_1$, $\alpha_{23} = p_2 + p_3$, $\alpha_{33} = p_4$, and $\alpha_{43} = p_5$; Time period 4: there are five lineages with lineage “abundances” $\alpha_{14} = p_1$, $\alpha_{24} = p_2$, $\alpha_{34} = p_3$, $\alpha_{44} = p_4$, and $\alpha_{54} = p_5$. Here “abundance of a lineage” is interpreted as the importance of the lineage’s contribution to the present assemblage.

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**APPENDIX B. Diversity profile and strong Replication Principle for Hill numbers and phylogenetic Hill numbers**

**Diversity (Hill number) profile**

A “diversity profile” is a single graph that plots the Hill number $D_q$ as a continuous function of the parameter $q$. This diversity profile completely characterizes the diversity of an assemblage with $S$ species and relative abundances $(p_1, p_2, ..., p_S)$. The diversity profile curve is a non-increasing function of $q$ (Hill 1973). The mathematical proof of this monotonicity is given in Beck and Schlögl (1993, p. 53).

Consider the following four assemblage structures (50 species in each) with different degrees of evenness. The species relative abundances $(p_1, p_2, ..., p_{50})$ are given below, $\sum_{i=1}^{50} p_i = 1$. In each case, we also give the CV (coefficient of variation), which is the ratio of standard deviation and mean of $(p_1, p_2, ..., p_{50})$. The magnitude of CV quantifies the degree of heterogeneity (or unevenness) of the probabilities $(p_1, p_2, ..., p_{50})$. When all probabilities are equal, CV = 0. A larger value of CV signifies higher degree of heterogeneity (or unevenness) among probabilities.

1. **Completely even assemblage:** $p_1 = p_2 = \ldots = p_{50} = 0.02$ (CV = 0).
2. **Slightly uneven assemblage:** $p_1 = p_2 = \ldots = p_{25} = 0.027, p_{26} = p_{27} = \ldots = p_{50} = 0.013$ (CV = 0.34).
3. **Moderately uneven assemblage:** $p_1 = p_2 = \ldots = p_{25} = 0.0364, p_{26} = p_{27} = \ldots = p_{50} = 0.00363$ (CV = 0.83).
4. **Highly uneven assemblage:** $p_1 = 0.225, p_2 = 0.202, p_3 = 0.180, p_4 = 0.157, p_5 = 0.134, p_6 = p_7 = \ldots = p_{50} = 0.0022$ (CV = 2.74).

The diversity profile for the four assemblages with different degree of unevenness are shown in Fig. B1. This profile is sensitive to the species abundance distribution. 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 information of species richness and relative abundances $(p_1, p_2, ..., p_3)$ is completely characterized by a diversity profile which depicts Hill numbers as a function of order $q$. 
Phylogenetic diversity profiles

We consider four hypothetical rooted phylogenetic trees, each with four species. The four trees vary in structure from simple to highly subdivided; Tree (a) presents the simplest case of maximally distinct lineages. The branch length is shown along each branch. See Fig. B2.

For each tree, we consider two species abundance distributions:
(1) Species are equally common: \((p_1, p_2, p_3, p_4) = (0.25, 0.25, 0.25, 0.25)\).
(2) Species abundances are uneven: \((p_1, p_2, p_3, p_4) = (0.1, 0.2, 0.3, 0.4)\).

As discussed in the main text, the following two types of profiles completely characterize phylogenetic diversity:
(1) The first type of diversity profile is obtained by plotting \(qPD(T)\) or \(qD(T)\) as functions of \(T\) separately for \(q = 0, 1,\) and \(2\); see Fig. B2.
(2) The other type of diversity profile is obtained by plotting \(qPD(T)\) or \(qD(T)\) as a function of order \(q\), for a selected value of temporal perspective \(T\). See Fig. B3 for the profiles for \(T = 1, 2, 3\).

Both tree structure and species abundances have effects on the patterns of the two types of profiles.
(1) Phylogenetic diversity profiles as a function of time for species abundances $(p_1, p_2, p_3, p_4) = (0.25, 0.25, 0.25, 0.25)$

(2) Phylogenetic diversity profiles as a function of time for species abundances $(p_1, p_2, p_3, p_4) = (0.1, 0.2, 0.3, 0.4)$

Fig. B2. Phylogenetic diversity profile as a function of time based on the mean diversity $\bar{D}(T)$ for $q = 0, 1$ and 2 and $0 < T < 5$ for the four phylogenetic trees and two species abundance distributions. The plots show that the effect of tree structures and the diversity ordering follows (a) $\geq$ (b) $\geq$ (c) $\geq$ (d) for the two species abundance distributions.
(1) Phylogenetic diversity profiles as a function of the order $q$ for species abundances $(p_1, p_2, p_3, p_4) = (0.25, 0.25, 0.25, 0.25)$

(2) Phylogenetic diversity profiles as a function of the order $q$ for species abundances $(p_1, p_2, p_3, p_4) = (0.1, 0.2, 0.3, 0.4)$

Fig. B3. Phylogenetic diversity profile as a function of order of $q$ for a fixed perspective time $T = 1, 2, \text{ and } 3$ based on the mean diversity $\overline{D}(T)$ for $0 \leq q \leq 5$ for four phylogenetic trees and two species abundance distributions.

**Strong Replication Principle for Hill numbers**

Suppose there are $S_k$ species in the $k$th assemblage, $k = 1, 2, \ldots, N$. Let the relative abundance of the $i$th species in the $k$th assemblage be $p_{ik}$. Assume that for a given value of $q$, each of the $N$ assemblages have the same Hill number $X$, implying $\sum_{i=1}^{S_k} p_{ik}^q = X^{1-q}$ for each $k = 1, 2, \ldots, N$. When the $N$ completely distinct assemblages are pooled with equal weight for each assemblage, each species relative abundance in the pooled tree becomes $p_{ik}/N$. Then the Hill number for the pooled assemblage becomes

$$\left\{ \sum_{k=1}^{N} \sum_{i=1}^{S_k} (p_{ik}/N)^q \right\}^{1/(1-q)} = \left( \sum_{k=1}^{N} X_k^{1-q} \right)^{1/(1-q)} = \frac{N}{X}.$$
Therefore, the strong Replication Principle holds for Hill numbers.

**Strong Replication Principle for phylogenetic Hill numbers (mean phylogenetic diversity)**

Suppose we have $N$ completely distinct assemblages (no lineages shared between assemblages in the interval $[-T, 0]$, though lineages within an assemblage may be shared; see Fig. 1 of the main text), all with the same mean diversity $\overline{D}(T) = X$ in the time interval $[-T, 0]$, based on an ultrametric tree. Then we can prove the following strong replication principle: If these assemblages are pooled in equal proportions, the mean diversity of the pooled assemblages is $N \times X$. Suppose that in the tree for the $k$th assemblage, the branch set is $B_k$ (we omit $T$ in the subscript and just use $B_k$ in the following proof for notational simplicity) with branch lengths $\{L_{ik} \mid i \in B_k\}$ and corresponding node abundances $\{a_{ik} \mid i \in B_k\}$, $k=1, 2, \ldots, N$. The $N$ assemblages have the same mean diversity $X$ over the time interval $[-T, 0]$, implying $\sum_{i \in B_k} (L_{ik} / T) a_{ik}^q = X^{1-q}$ for all $k=1, 2, \ldots, N$. When the $N$ assemblages are pooled with equal weight for each tree, each node abundance $a_{ik}$ in the pooled tree becomes $a_{ik}/N$. Then the measure $\overline{D}(T)$ for the pooled tree becomes

$$\left\{ \sum_{k=1}^{N} \sum_{i \in B_k} L_{ik} \left( \frac{a_{ik}}{N} \right)^q \right\}^{1/(1-q)} = \left\{ N^{1-q} \times X^{1-q} \right\}^{1/(1-q)} = N \times X.$$

The above proof can be directly extended to non-ultrametric trees (Chao et al. 2010). In our proof of this replication principle, the $N$ assemblages must have the same time $T$ (or for non-ultrametric trees, the same mean quantity $\overline{T}$), but may have different numbers of species, and the tree structures of the $N$ assemblages can be totally different. See Fig. 1 of the main text for an example.

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Appendix C. Diversity decomposition and related properties.

Let $y_{ij}$ denote any quantitative measure of species importance of the $i$th species in the $j$th assemblage. As in the main text, we refer to $y_{ij}$ as “abundance” for simplicity, although it can be absolute abundance, relative abundance, presence/absence, biomass, coverage of plants, basal area or any quantitative variable. Based on Hill numbers, gamma diversity is the effective number of species in the region, alpha diversity is the effective number of species per assemblage and beta diversity measures the effective number of completely distinct assemblages. Thus we must have a multiplicative decomposition in diversity partitioning; see Jost (2006, 2007). However, our assumptions are different from those in Jost (2007), and the resulting alpha and beta formulas (and their interpretations) are thus different. We first derive our new alpha and beta formulas under the following three assumptions:

(Assumption 1)
Gamma diversity is the diversity of the combined assemblage where species abundances are pooled over assemblages. This entails that assemblage weights must be the relative assemblage sizes (or weights are any surrogates that are proportional to the assemblage sizes.)

(Assumption 2)
Alpha diversity and beta diversity are independent. When assemblages are completely distinct, beta diversity is a fixed constant.

(Assumption 3)
When assemblage sizes are equal and all assemblages have identical diversity, alpha diversity is equal to the diversity of the individual assemblages.

As shown in Eq. 5a of the main text, any measure of species importance $y_{ij}$ can be expressed as $y_{ij} = y_{+j}w_jp_{iy}$, where $p_{iy} = y_{iy}/y_{+j}$ is the relative abundance of the $i$th species in the $j$th assemblage, $w_j = y_{+j}/y_{++}$ (relative assemblage size or the weight of the $j$th assemblage), with $w_1 + w_2 + \ldots + w_N = 1$. For the gamma diversity, we simply pool species abundances over assemblages to obtain $y_{i+} = \sum_{j=1}^{N} y_{ij} = y_{++} \sum_{j=1}^{N} w_jp_{iy}$ (the total abundance of the $i$th species) in the pooled assemblage. The gamma diversity of order $q$ is the Hill number based on the relative abundance $\overline{p}_i = y_{i+}/y_{++} = \sum_{j=1}^{N} w_jp_{iy}$ in the pooled assemblage (Routledge 1979; Jost 2006, 2007):

$$qD_{\gamma} = \left\{ \frac{\sum_{i=1}^{S} \left( \frac{y_{ij}}{y_{++}} \right)^q}{\sum_{j=1}^{N} \left( \sum_{j=1}^{N} w_jp_{iy} \right)^q} \right\}^{1/(1-q)} = \left\{ \frac{\sum_{i=1}^{S} \left( \sum_{j=1}^{N} w_jp_{iy} \right)^q}{\sum_{j=1}^{N} \left( \sum_{j=1}^{N} w_jp_{iy} \right)^q} \right\}^{1/(1-q)}, \quad q \neq 1. \quad \text{(C.1)}$$

When $q$ tends to 1, we have

$$1D_{\gamma} = \lim_{q \rightarrow 1} qD_{\gamma} = \exp \left\{ -\sum_{i=1}^{S} \left( \sum_{j=1}^{N} w_jp_{iy} \right) \log \left( \sum_{j=1}^{N} w_jp_{iy} \right) \right\}. \quad \text{When all assemblages are completely distinct (i.e. no shared species), the gamma diversity in Eq.}$$
(C.1) reduces to

\[ qD_{\gamma \text{ distinct}} = \left[ \sum_{j=1}^{N} w_j^q \sum_{i=1}^{S} p_{ij}^q \right]^{1/(1-q)}. \]

In this special case, the multiplicative partitioning gives

\[ qD_{\gamma \text{ distinct}} = \left[ \sum_{j=1}^{N} w_j^q \sum_{i=1}^{S} p_{ij}^q \right]^{1/(1-q)} = (qD_{\alpha \text{ distinct}}) \times (qD_{\beta \text{ distinct}}). \]  

(C.2)

For completely distinct assemblages, as long as there are no shared species among assemblages, the species abundance distributions in each assemblage can be arbitrary. So there are many different combinations of weights and individual diversities that yield the gamma diversity in Eq. (C.2). We first consider the specific case in Assumption 3 that all assemblages have identical diversity and assemblage sizes are also equal, i.e., \( \left( \sum_{i=1}^{S} p_{ij}^q \right)^{1/(1-q)} = K \) for \( j = 1, 2, \ldots, N \), and \( w_j = 1/N \), then Assumption 3 implies that we must have \( qD_{\alpha \text{ distinct}} = K \) in this special case. Meanwhile, Eq. (C.2) becomes

\[ qD_{\gamma \text{ distinct}} = \left\{ K \sum_{j=1}^{N} \left( \frac{1}{N} \right)^q \right\}^{1/(1-q)} = N \times K. \]

Thus we obtain \( qD_{\beta \text{ distinct}} = N \). From the second part of Assumption 2, we obtain that the fixed beta diversity for the completely distinct case must be \( N \), regardless of weights and the diversities of individual assemblages. Consequently, as long as assemblages are completely distinct, the formula (C.2) gives the following alpha diversity even weights are not equal and/or individual assemblages have different diversities:

\[ qD_{\alpha \text{ distinct}} = \frac{1}{N} \left\{ \sum_{i=1}^{S} \sum_{j=1}^{N} (w_j p_{ij})^q \right\}^{1/(1-q)}, \quad q \neq 1. \]  

(C.3)

Again, the independence of alpha and beta implies that beta diversity (based on shared information) is not relevant to the alpha formula. Therefore, Eq. (C.3) is also the alpha diversity for the general case, in which the assemblages are not necessarily completely distinct. That is, our proposed new alpha formula is (Eq. 6a in the main text)

\[ qD_{\alpha} = \frac{1}{N} \left\{ \sum_{i=1}^{S} \sum_{j=1}^{N} (w_j p_{ij})^q \right\}^{1/(1-q)}, \quad q \neq 1. \]

This alpha formula when \( q \) tends to 1 is

\[ \lim_{q \to 1} qD_{\alpha} = \exp \left\{ -\sum_{i=1}^{S} \sum_{j=1}^{N} w_j p_{ij} \log(w_j p_{ij}) - \log N \right\}. \]

Based on a multiplicative partitioning, we thus obtain the beta diversity for a general case:
The new beta diversity takes the minimum value of unity if and only if all assemblages are identical in species identities and species abundances, i.e., \( N \) sets of abundances \((y_{1j}, y_{2j}, \ldots, y_{Nj}), j = 1, 2, \ldots, N \) are identical. This ensures that beta diversity measures the differentiation of the \( N \) sets of abundances.

NOTES:

(1) If the target is to compare species relative abundances among assemblages, we can simply let \( y_{ij} \) represent the relative abundance of the \( i \)th species in the \( j \)th assemblage, i.e., let \( y_{ij} = p_{ij} \) in the above derivation. Then we have \( y_{i1} = y_{i2} = \ldots = y_{iN} = 1 \) and \( y_{+} = N \). It implies that all assemblage “sizes” are unity and \( w_{j} = y_{i,j} / y_{+} = 1/N \) for all \( j = 1, 2, \ldots, N \). Consequently, it reduces to a special equal-weight case. The gamma diversity in this special equal-weight case is to pool species relative abundances over assemblages and becomes Hill numbers based on the average of relative abundances \( \bar{p}_j = \sum_{i=1}^{N} (1/N)p_{ij} \) in the pooled assemblage.

(2) Assumption 3 in the above derivation for the special case that \( y_{ij} \) represents species relative abundances can thus be relaxed to Jost (2007) assumption: “when all assemblages have identical diversity, alpha diversity is equal to the diversity of the individual assemblages.” However, Assumption 3 is required if the target is extended to compare species absolute abundances among assemblages. see Point (3) below for further explanation.

(3) Jost (2007) required alpha to be some type of mean of the local diversities. This conventional definition of alpha led to a beta that can only be used to produce differentiation measures to compare species relative abundances, but not absolute abundances. In our proposed approach, we expand the conventional concept of alpha so that beta can quantify the differentiation among \( N \) sets of vectors \((y_{1j}, y_{2j}, \ldots, y_{Nj}), j = 1, 2, \ldots, N \) for any measure of species importance \( y_{ij} \). As explained above, if \( y_{ij} \) represents species relative abundance, then it reduces to the equal-weight case and our alpha is a function of species relative abundances only and thus satisfies the conventional alpha definition. It implies that if all individual diversities are identically \( X \), then the alpha diversity is \( X \). If \( y_{ij} \) represents species absolute abundance, then our alpha is a function of both species relative abundances and assemblage sizes. In this case, the conventional implication becomes the following generalized sense: only if all individual diversities are identically \( X \) and assemblage sizes (i.e., weights) are equal, then the alpha diversity is \( X \). This is Assumption 3 in our derivation.

(4) As shown in Theorem C1 below, an advantage of our approach is that for any arbitrary weights, our gamma is always greater than or equal to the alpha for all orders \( q \geq 0 \), and the beta component is always between unity (when all assemblages are identical in species absolute abundances) and \( N \) (when the \( N \) assemblages have no species in common).
**Theorem C1:** For any weights and any order \( q \geq 0 \), the gamma diversity and the new alpha diversity satisfy the following inequality:

\[
{\gamma}^q D_n \leq {\gamma}^q D_r \leq N({\gamma}^q D_n),
\]

or equivalently,

\[
(\overline{D_r}) / N \leq {\gamma}^q D_n \leq {\gamma}^q D_r.
\]

This implies that the beta diversity is always between 1 and \( N \), i.e., \( 1 \leq \overline{D_n} \leq N \).

**Proof:** This is a special case of the phylogenetic diversities. See a general proof later in Theorem C3.

From this theorem, we can conclude that for any arbitrary weights, our gamma is always greater than or equal to the new proposed alpha for all orders \( q \geq 0 \). The beta component using the new alpha formula is always between unity (when all assemblages are identical in species absolute abundances) and \( N \) (when the \( N \) assemblages have no species in common).

**Theorem C2:** Monotonicity in the sense of Hajdu (1981) and Gower and Legendre (1986) for a differentiation measure. When a new species with absolute abundance \( b \) is added to any assemblage, beta diversity should not be less than the beta diversity if the absolute abundance of the new species is \( a \), where \( b \geq a \geq 0 \). The special case of \( a = 0 \) implies that beta diversity does not decrease when a new species is added to any assemblage.

**Proof:** Let \( y_{ij} \) be any measure of species importance of the \( i \)th species in the \( j \)th assemblage. Define \( y_{ij} = \sum_{i=1}^{S} \sum_{j=1}^{N} y_{ij} \) as in the main text. If a new species with abundance \( a \) is added to the \( j \)th assemblage, then the beta diversity becomes

\[
{\gamma}^q D_\beta = {\gamma}^q D_\gamma = N \left[ \frac{\sum_{i=1}^{S} \sum_{j=1}^{N} \frac{y_{ij}}{y_{ij} + a}^q}{\sum_{i=1}^{S} \sum_{j=1}^{N} \left( \frac{y_{ij}}{y_{ij} + a} \right)^q} + \frac{a}{y_{ij} + a} \right]^{1/(1-q)}
\]

We prove the theorem by showing that \( \frac{\partial ({\gamma}^q D_\beta)}{\partial a} \geq 0 \), for any \( a \geq 0 \). For notational simplicity, let \( \sum_{i=1}^{S} \sum_{j=1}^{N} y_{ij} = A \) and \( \sum_{i=1}^{S} \sum_{j=1}^{N} y_{ij}^q = B \). Then

\[
\frac{\partial ({\gamma}^q D_\beta)}{\partial a} = \frac{q}{1-q} \left( \frac{qa^{q-1} - qA^{q-1}}{A+a^q} \right) \left( \frac{B}{A+a^q} \right) \left( \frac{B-A}{(A+a^q)(B+a^q)} \right).
\]
Since \((A+a^q)(B+a^q)\) is always positive, we have that if \(q > 1\), then \(A \geq B\), implying \(\frac{\partial (qD_\beta)}{\partial a} \geq 0\);

if \(q < 1\), then \(A \leq B\) implying \(\frac{\partial (qD_\beta)}{\partial a} \geq 0\). For \(q = 1\), the result follows from the concavity of the function \(f(x) = -x \log x\). The proof is thus completed.

**Decomposition of phylogenetic Hill numbers**

Using a decomposition similar to that for Hill numbers, we here derive the relationship between phylogenetic alpha, beta, and gamma diversities for ultrametric cases. For a fixed time perspective \(T\), we consider the diversity partitioning in the time interval \([-T, 0]\). Based on the mean phylogenetic Hill numbers developed by Chao et al. (2010) (see Eqs. 4a, 4b of the main text), gamma phylogenetic diversity is the effective number of completely distinct lineages with branch length \(T\) in the region, alpha phylogenetic diversity is the effective number of completely distinct lineages with branch length \(T\) per assemblage, and beta diversity measures the effective number of phylogenetically completely distinct assemblages. Thus, we must have a multiplicative decomposition in phylogenetic diversity partitioning. We derive below our phylogenetic formulas under the following assumptions for a fixed time perspective \(T\):

(Assumption 1)
Gamma phylogenetic diversity is the phylogenetic diversity of the combined assemblage, where species abundances are pooled over assemblages. This entails that assemblage weights are the relative assemblage sizes, (or weights are any surrogates that are proportional to the assemblage sizes.)

(Assumption 2)
Phylogenetic alpha diversity and phylogenetic beta diversity are independent. When assemblages are completely phylogenetically distinct, beta diversity is a fixed constant.

(Assumption 3)
When assemblage sizes are equal and all assemblages have identical phylogenetic diversity, alpha phylogenetic diversity is equal to the phylogenetic diversity of the individual assemblages.

In order for this demonstration to be self-contained, we repeat some definitions described in the main text. In the following derivation, \(B_T\) denotes the set of all branches in the time interval \([-T, 0]\), \(L_i\) denotes the length of Branch \(i\), \(a_{ij}\) denotes the total relative abundance descended from Branch \(i\) in the \(j\)th assemblage, \(w_j\) denotes the relative assemblage size, and \(a_{ij} = \sum_{j=1}^N w_j a_{ij}\).

Based on Eq. 4a of the main text and Assumption 1, the phylogenetic gamma diversity of order \(q\) in the time interval \([-T, 0]\) is obtained from the pooled ultrametric tree as expressed by:

\[
qD_j(T) = \frac{1}{T} \left\{ \sum_{i \in B_T} L_i \left( \frac{w_1 a_{i1} + w_2 a_{i2} + \ldots + w_N a_{iN}}{T} \right)^q \right\}^{1/(1-q)} \text{ for } q \geq 0 \text{ and } q \neq 1. \quad \text{(C.4)}
\]
When the \( N \) assemblages are completely phylogenetically distinct (no lineages shared between assemblages in the interval \([-T, 0]\), though lineages within an assemblage may be shared, see Fig. 1 of the main text), the above gamma diversity reduces to

\[
\alpha^q(T)_{\text{distinct}} = \frac{1}{T} \left\{ \sum_{i \in B_T} L_i \left( \frac{w_i a_{i1}}{T} \right)^q + \sum_{i \in B_T} L_i \left( \frac{w_i a_{i2}}{T} \right)^q + \ldots + \sum_{i \in B_T} L_i \left( \frac{w_i a_{iN}}{T} \right)^q \right\}^{1/(1-q)} ,
\]

where

\[
\left\{ \sum_{i \in B_T} L_i \left( \frac{a_{ij}}{T} \right)^q \right\}^{1/(1-q)}
\]

is the mean phylogenetic diversity of the \( j \)th assemblage. If all assemblages have identical diversity \( K \), then we have

\[
\left\{ \sum_{i \in B_T} L_i \left( \frac{a_{ij}}{T} \right)^q \right\}^{1/(1-q)} = K,
\]

or equivalently, for all \( j = 1, 2, \ldots, N \),

\[
\left\{ \sum_{i \in B_T} L_i \left( \frac{a_{ij}}{T} \right)^q \right\} = (T \times K)^{1-q}.
\]

Additionally, if weights are all identical to \( 1/N \), Eq. (C.5) becomes

\[
\alpha^q(T)_{\text{distinct}} = \frac{1}{T} \left( \frac{1}{N^q} \sum_{i \in B_T} L_i \left( \frac{a_{11}}{T} \right)^q + \sum_{i \in B_T} L_i \left( \frac{a_{i2}}{T} \right)^q + \ldots + \sum_{i \in B_T} L_i \left( \frac{a_{iN}}{T} \right)^q \right)^{1/(1-q)}
\]

\[
= \frac{1}{T} \left( \frac{1}{N^q} N(T \times K)^{1-q} \right)^{1/(1-q)} = K \times N .
\]

Assumption 3 assumes in this special case that the alpha diversity for the completely distinct case, \( \alpha^q(T)_{\text{distinct}} \), must equal to \( K \). The above equation then implies that the phylogenetic beta diversity \( \beta^q(T)_{\text{distinct}} \) in this special case must be \( N \). From the second part of Assumption 2, we obtain that the fixed beta diversity for the completely phylogenetically distinct case must be \( N \), regardless of weights and the diversities of individual assemblages. Then as long as the assemblages are completely distinct, the above formula gives the following phylogenetic alpha diversity of order \( q \):

\[
\alpha^q(T)_{\text{distinct}} = \frac{1}{T N^q} \sum_{i \in B_T} L_i \left( \frac{a_{i1}}{T} \right)^q + \frac{1}{T} \sum_{i \in B_T} L_i \left( \frac{a_{i2}}{T} \right)^q + \ldots + \frac{1}{T} \sum_{i \in B_T} L_i \left( \frac{a_{iN}}{T} \right)^q \right\}^{1/(1-q)} .
\]

Since alpha diversity is independent of shared information, this is also the alpha diversity for the general case, in which the assemblages are not necessarily completely phylogenetically distinct. That is, we obtain the proposed phylogenetic alpha formula (Eq. 8a of the main text):
\begin{align*}
q \bar{D}_\alpha(T) &= \frac{1}{TN} \sum_{i \in B_T} L_i \sum_{j=1}^N \left( \frac{w_j a_{ij}}{T} \right)^q \frac{1}{1-q}.
\end{align*}

Then the phylogenetic beta diversity for the general case is obtained by
\begin{align*}
q \bar{D}_\beta(T) &= \frac{q}{q} \bar{D}_\gamma(T) / q \bar{D}_\alpha(T).
\end{align*}

Letting \( q \) tend to one in Eqs. (C.4) and (C.6), we obtain the phylogenetic gamma and alpha diversities of order 1, given as (in Eqs. 7b and 8b in the main text)
\begin{align*}
\lim_{q \to 1} \frac{q}{q} \bar{D}_\gamma(T) &= \exp \left[ - \sum_{i \in B_T} \frac{L_i}{T} \left( \sum_{j=1}^N w_j a_{ij} \right) \log \left( \sum_{j=1}^N w_j a_{ij} \right) \right].
\end{align*}

The phylogenetic beta diversity of order 1 is obtained as the ratio of the above gamma to alpha.

When all weights are equal to each other, the phylogenetic gamma diversity reduces to
\begin{align*}
\lim_{q \to 1} \frac{q}{q} \bar{D}_\gamma(T) &= \exp \left[ - \frac{1}{N} \sum_{j=1}^N \sum_{i \in B_T} \frac{L_i}{T} \log \left( \frac{1}{N} \sum_{j=1}^N a_{ij} \right) \right].
\end{align*}

The phylogenetic alpha diversity becomes
\begin{align*}
\lim_{q \to 1} q \bar{D}_\alpha(T) &= \frac{1}{T} \left( \sum_{i \in B_T} L_i \left( \frac{a_{11} + a_{12} + \ldots + a_{1N}}{T} \right)^q \right) \frac{1}{1-q}, \quad q \geq 0 \quad \text{and} \quad q \neq 1.
\end{align*}

For the non-ultrametric cases, the phylogenetic alpha, beta and gamma have exactly the same form as those in the ultrametric cases except that \( T \) is replaced by \( T = \sum_{i \in B_T} a_{ij} \) in all formulas (here \( T_j \) denotes the mean base change in the \( j \)th assemblage) and replacing the branch set \( B_T \) by \( B_T \) (the set of branches connecting all focal species, with mean base change \( T_j \)).
Fundamental properties for phylogenetic diversity components

**Theorem C3**: For any arbitrary weights and all orders of \( q \), when the number of assemblages, \( N \), is fixed, the proposed phylogenetic alpha and gamma diversities for ultrametric trees satisfy the following inequality:

\[
^{q}\mathcal{D}_a(T) \leq ^{q}\mathcal{D}_y(T) \leq N[^{q}\mathcal{D}_a(T)], \tag{C.7}
\]

or equivalently,

\[
[^{q}\mathcal{D}_y(T)]/N \leq ^{q}\mathcal{D}_a(T) \leq ^{q}\mathcal{D}_y(T). \tag{C.8}
\]

This ensures that the phylogenetic beta is always in the range \( 1 \leq ^{q}\mathcal{D}_y(T) \leq N \). The above two inequalities are also valid for the non-ultrametric cases except that \( T \) should be replaced by \( \bar{T} \).

When all lineages are completely distinct, all diversity components reduce to those obtained in the partitioning of ordinary Hill numbers. Thus the conclusion is also valid for alpha, beta and gamma Hill numbers (see Theorem C1).

Proof: We prove this theorem only for the ultrametric cases; for the non-ultrametric cases, all steps are parallel. From Eq. (C.4) and (C.6), for \( q \neq 1 \), the phylogenetic gamma diversity and alpha diversity respectively are

\[
^{q}\mathcal{D}_y(T) = \frac{1}{T} \left\{ \sum_{i \in B_T} L_i \left( \sum_{j=1}^{N} \frac{w_j a_{ij}}{T} \right)^{q}\right\}^{1/(1-q)}
\]

and

\[
^{q}\mathcal{D}_a(T) = \frac{1}{TN} \left\{ \sum_{i \in B_T} L_i \sum_{j=1}^{N} \left( \frac{w_j a_{ij}}{T} \right)^{q}\right\}^{1/(1-q)}.
\]

(1) We first prove \( ^{q}\mathcal{D}_y(T) \leq N \times ^{q}\mathcal{D}_a(T). \) For \( q > 1 \), this conclusion follows directly from the following inequality:

\[
[^{q}\mathcal{D}_y(T)]^{-q} = \frac{1}{T^{1-q}} \left\{ \sum_{i \in B_T} L_i \left( \sum_{j=1}^{N} \frac{w_j a_{ij}}{T} \right)^{q}\right\} \geq \frac{1}{T^{1-q}} \left\{ \sum_{i \in B_T} L_i \sum_{j=1}^{N} \left( \frac{w_j a_{ij}}{T} \right)^{q}\right\} = [N \times ^{q}\mathcal{D}_a(T)]^{-q}.
\]

Similarly, for \( 0 \leq q < 1 \), the same conclusion follows from the following inequality:

\[
[^{q}\mathcal{D}_y(T)]^{-q} = \frac{1}{T^{1-q}} \left\{ \sum_{i \in B_T} L_i \left( \sum_{j=1}^{N} \frac{w_j a_{ij}}{T} \right)^{q}\right\} \leq \frac{1}{T^{1-q}} \left\{ \sum_{i \in B_T} L_i \sum_{j=1}^{N} \left( \frac{w_j a_{ij}}{T} \right)^{q}\right\} = [N \times ^{q}\mathcal{D}_a(T)]^{-q}.
\]

For \( q = 1 \), note that

\[
\log ^{q}\mathcal{D}_y(T) = - \sum_{i \in B_T} L_i \left( \sum_{j=1}^{N} w_j a_{ij} \right) \log \left( \sum_{j=1}^{N} w_j a_{ij} \right)
\]

and
\[
\log[N \times \mathcal{D}_a(T)] = - \sum_{i \in B_T} \frac{L_i}{T} \sum_{j=1}^N (w_j a_{ij}) \log(w_j a_{ij}).
\]

Since \( \log(\sum_{j=1}^N w_j a_{ij}) \geq \log(w_j a_{ij}) \), the proof is readily seen for \( q = 1 \).

(2) To prove \( \mathcal{D}_T(T) \geq \mathcal{D}_a(T) \), note that for \( q > 1 \), \( f(x) = x^q \) is a convex function, the Jensen inequality implies that for any Branch \( i \), we have

\[
\left( \frac{1}{N} \sum_{j=1}^N \frac{w_j a_{ij}}{T} \right)^q \leq \frac{1}{N} \sum_{j=1}^N \left( \frac{w_j a_{ij}}{T} \right)^q,
\]

and thus

\[
\sum_{i \in B_T} \frac{L_i}{T} \left( \frac{1}{N} \sum_{j=1}^N \frac{w_j a_{ij}}{T} \right)^q \leq \frac{1}{N} \sum_{i \in B_T} \sum_{j=1}^N \left( \frac{w_j a_{ij}}{T} \right)^q.
\]

which is equivalent to

\[
T^{1-q} \times N^{-q} \times [\mathcal{D}_{T}(T)]^{1-q} \leq T^{1-q} \times N^{-q} \times [\mathcal{D}_{a}(T)]^{1-q}.
\]

This yields \( \mathcal{D}_T(T) \leq \mathcal{D}_a(T) \) for \( q > 1 \).

For \( 0 \leq q < 1 \), \( f(x) = x^q \) is a concave function, then the Jensen inequality shows that for any Branch \( i \),

\[
\left( \frac{1}{N} \sum_{j=1}^N \frac{w_j a_{ij}}{T} \right)^q \geq \frac{1}{N} \sum_{j=1}^N \left( \frac{w_j a_{ij}}{T} \right)^q,
\]

and thus

\[
\sum_{i \in B_T} \frac{L_i}{T} \left( \frac{1}{N} \sum_{j=1}^N \frac{w_j a_{ij}}{T} \right)^q \geq \frac{1}{N} \sum_{i \in B_T} \sum_{j=1}^N \left( \frac{w_j a_{ij}}{T} \right)^q.
\]

The above inequality is equivalent to

\[
T^{1-q} \times N^{-q} \times [\mathcal{D}_{T}(T)]^{1-q} \geq T^{1-q} \times N^{-q} \times [\mathcal{D}_{a}(T)]^{1-q},
\]

which implies \( \mathcal{D}_T(T) \leq \mathcal{D}_a(T) \) for \( 0 \leq q < 1 \).

When \( q = 1 \), since \( f(x) = -x \log x \) is a concave function, the Jensen inequality leads to

\[
-(\frac{1}{N} \sum_{j=1}^N w_j a_{ij}) \log(\frac{1}{N} \sum_{j=1}^N w_j a_{ij}) \geq \frac{1}{N} \sum_{j=1}^N w_j a_{ij} \log(w_j a_{ij}).
\]

Then

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\[- \sum_{i \in B_T} \left( \frac{1}{N} \sum_{j=1}^{N_i} \frac{w_i d_{ij}}{T} \right) \log \left( \frac{1}{N} \sum_{j=1}^{N_i} \frac{w_i d_{ij}}{T} \right) \geq - \frac{1}{N} \sum_{i \in B_T} \sum_{j=1}^{N_i} \frac{w_i d_{ij}}{T} \log \left( \frac{w_i d_{ij}}{T} \right), \]

which is equivalent to
\[
\frac{1}{N} \log TN + \frac{1}{N} \log D_j(T) \geq \frac{1}{N} \log TN + \frac{1}{N} \log D_\alpha(T).
\]

Then the inequality \( D_j(T) \geq D_\alpha(T) \) is obtained.

**Theorem C4:** When assemblages are equally weighted, we have the following relationship for non-ultrametric trees between the phylogenetic beta component and quadratic entropy:
\[
2 \overline{D}_\beta(T) = (1 - Q_j / T)^{-1} / (1 - Q_\alpha / T)^{-1},
\]
where \( T = (T_1 + T_2 + \ldots + T_N) / N \) and \( T_j \) denotes the mean base change in the \( j \)th assemblage.

Proof: Allen et al. (2009) proved the following identity for both ultrametric and non-ultrametric trees:
\[
\sum_{i \in B_T} L_i a_i (1 - a_i) = \sum_{i \in B_T} d_{ij} p_j = Q.
\]

From the formula of \( 2 \overline{D}(\overline{T}) \) (e.g., Eq. 4a of the main text with \( T \) replaced by \( \overline{T} \)), we have
\[
\sum_{i \in B_T} L_i a_i (1 - a_i) = \overline{T} - \sum_{i \in B_T} L_i a_i^2 = \overline{T} - \overline{T}/2 \overline{D}(\overline{T}).
\]

We thus obtain for any tree
\[
2 \overline{D}(\overline{T}) = (1 - Q / \overline{T})^{-1}.
\]

Applying the above to the pooled tree gives
\[
2 \overline{D}_s(\overline{T}) = (1 - Q_j / \overline{T})^{-1}.
\]

Also, for the alpha quadratic entropy, we have
\[
Q_\alpha = \frac{1}{N} \sum_{i=1}^{N} Q_i = \frac{1}{N} (\overline{T}_1 - \sum L_i a_i^2 + \overline{T}_2 - \sum L_i a_i^2 + \ldots + \overline{T}_N - \sum L_i a_i^2) = T - \sum L_i a_i^2 / N = T - \overline{T} / 2 \overline{D}_\alpha(\overline{T}),
\]
which leads to
\[
2 \overline{D}_\alpha(\overline{T}) = (1 - Q_\alpha / \overline{T})^{-1}.
\]

Then we obtain
\[
2 \overline{D}_\beta(T) = 2 \overline{D}_\gamma(T) / \overline{D}_\alpha(T) = (1 - Q_j / T)^{-1} / (1 - Q_\alpha / T)^{-1}.
\]
Theorem C5: Phylogenetic beta diversity satisfies the property of replication invariance. Assume that there are $K$ subsets of abundances (taxonomic clades, for example) in each of $N$ assemblages, and no species are shared between subsets within an assemblage. If these $N$ assemblages are pooled and the phylogenetic beta diversity of the $N$ assemblages are identical for all individual subsets, then the assemblage as a whole should have the same phylogenetic beta as the individual subsets.

Proof: Without loss of generality, we prove this theorem for $K = 2$. Let $L_i$ denote the length of the $i$th branch in the pooled tree. For the first subset, let $a_{ij}$ be the relative abundance of the $i$th branch of the $j$th assemblage. Then the relative abundance of the $i$th branch in the pooled assemblage is

$$
q \bar{D}_p(\bar{T}_1) = N \left( \frac{\sum_{i \in B} L_i a_{i \ast}^q}{\sum_{j=1}^N \sum_{i \in B} \frac{L_i}{\bar{T}_1} w_{ij}^q a_{ij}^q} \right)^{1/(1-q)} = N \left( \frac{\sum_{i \in B} L_i a_{i \ast}^q}{\sum_{j=1}^N \sum_{i \in B} L_i w_{ij}^q a_{ij}^q} \right)^{1/(1-q)}
$$

where $\bar{T}_1 = \sum_{i \in B} L_i a_{i \ast}$, and $B$ is the branch set in the pooled tree. Note that the mean base change $\bar{T}_1$ in the denominator and the same base change in the numerator are cancelled out.

For the second subset, let $b_{ij}$ be the relative abundance of the $i$th branch of the $j$th assemblage. Then the relative abundance of the $i$th branch in the pooled assemblage is $b_{i \ast} = \sum_{j=1}^N w_j b_{ij}$. The phylogenetic beta diversity of these $N$ assemblages of the second subset is:

$$
q \bar{D}_p(\bar{T}_2) = N \left( \frac{\sum_{i \in B} L_i b_{i \ast}^q}{\sum_{j=1}^N \sum_{i \in B} \frac{L_i}{\bar{T}_2} w_{ij}^q b_{ij}^q} \right)^{1/(1-q)} = N \left( \frac{\sum_{i \in B} L_i b_{i \ast}^q}{\sum_{j=1}^N \sum_{i \in B} L_i w_{ij}^q b_{ij}^q} \right)^{1/(1-q)},
$$

where $\bar{T}_2 = \sum_{i \in B} L_i b_{i \ast}$. Here the mean base change $\bar{T}_2$ in the denominator is also cancelled out with the same base change in the numerator. When we pool the two subsets by the weights $\lambda$ and $1 - \lambda$, the phylogenetic beta diversity of the $N$ assemblages becomes

$$
q \bar{D}_p(\bar{T}) = N \left( \frac{\sum_{i \in B} L_i \lambda a_{i \ast}^q + \sum_{i \in B} L_i (1 - \lambda) b_{i \ast}^q}{\sum_{j=1}^N \sum_{i \in B} \frac{L_i}{\bar{T}} (\lambda w_j a_{ij}^q) + \sum_{i \in B} L_i (1 - \lambda) w_j b_{ij}^q} \right)^{1/(1-q)}
$$

$$
= N \left( \frac{\sum_{i \in B} L_i \lambda a_{i \ast}^q + \sum_{i \in B} L_i (1 - \lambda) b_{i \ast}^q}{\sum_{j=1}^N \sum_{i \in B} L_i \lambda w_j a_{ij}^q + \frac{1}{N} \sum_{j=1}^N (1 - \lambda) w_j b_{ij}^q} \right)^{1/(1-q)},
$$

(C.9)
where $\bar{T} = \sum_{i} L_i [\lambda a_i + (1 - \lambda) b_i]$ is the mean base change of the pooled tree. Again, $\bar{T}$ is cancelled out in the phylogenetic beta diversity.

If $qD_{\beta}(T_1) = qD_{\beta}(T_2) = X$, then it is readily seen from Eq. (C.9) that the phylogenetic beta for the pooled two subsets for the $N$ assemblages is $qD_{\beta}(T) = X$. Hence, the property of replication invariance is satisfied. The above proof shows that the replication invariance is still valid even if $T_1$ and $T_2$ are different. Since the ultrametric case is a special case of the non-ultrametric case, the property of replication invariance is also satisfied for ultrametric trees.

**Taxonomic alpha, beta and gamma diversities**

Sometimes a detailed phylogenetic tree is unavailable. In that case, all our formulas can be applied to a phylogenetic tree based on classical Linnaean taxonomic categories. Consider a taxonomic tree of $L$ levels. In general, each hierarchical level can be given unit length, though this might need to be adjusted depending on special knowledge of the group in question. The continuous time parameter $T$ in Eqs. 7a, 7b, 8a, 8b and 9 of the main text is replaced by a parameter $L$ (level) to distinguish taxonomic levels rather than calibrated times. It is straightforward to obtain the taxonomic alpha, beta, and gamma diversities by setting all branch lengths $L_i$ to unity in Eqs. 7a, 7b, 8a, 8b and 9 of the main text. Then we obtain the following formula for taxonomic gamma diversity of order $q$ for $L$ levels:

$$LD_{\gamma} q = \frac{1}{L^q} \sum_{i} \left( \sum_{i} \left( \frac{a_{i1}}{L} + \frac{a_{i2}}{L} + \ldots + \frac{a_{iN}}{L} \right) \right)^q.$$

The taxonomic alpha diversity becomes:

$$LD_{\alpha} q = \frac{1}{LN} \sum_{i} \left( \sum_{i} \left( \frac{a_{i1}}{L} \right)^q + \frac{a_{i2}}{L} \right)^q + \ldots + \frac{a_{iN}}{L} \right)^q \frac{1}{L^{1-q}}.$$

where $i$ ranges over all nodes in the $L$ levels taxonomy tree. The multiplicative taxonomic beta diversity is

$$LD_{\beta} q = \frac{LD_{\alpha} q}{LD_{\gamma} q}.$$

Just as we defined lineage excess for a phylogenetic tree, we can also define the clade excess as $LD_{\gamma} q - LD_{\alpha} q$ for a Linnaean taxonomic tree. The gamma diversity can be interpreted as the “mean effective number of taxonomic nodes per level for the pooled taxonomic tree”. The alpha diversity can be interpreted as the “mean effective number of taxonomic nodes per level for an individual taxonomic tree”. The beta diversity is interpreted as “the effective number of assemblages that are completely distinct to $L$ taxonomy levels” (i.e., no shared clades in all $L$ levels). The clade excess in a taxonomic tree can be interpreted as the effective number of regional clades not contained in a typical local assemblage.
LITERATURE CITED


APPENDIX D: Derivation of four classes of similarity measures and related properties

Four classes of non-phylogenetic similarity measures (Table 1 of the main text)

As noted in the main text, we propose for the first time a new alpha formula (Eq. 6a). Our beta diversity as a ratio of gamma and alpha is independent of the new alpha. An advantage of adopting the new alpha is that the resulting gamma is not less than alpha for any arbitrary weights and \( q \geq 0 \) and beta always lies in the range \([1, N]\) (see Appendix C). Therefore, we can transform the beta diversity onto \([0, 1]\) so that the normalized measure can be compared across multiple regions with different numbers of assemblages. We consider the following four transformations, as summarized in Table 1 of the main text. The three diversity components are valid for general weights (assemblage sizes) if \( q > 0 \), thus our measures are weighted generalizations of the equal-weight similarity and differentiations proposed in the literature.

Although our derivation and presentation in this Appendix are focused on ultrametric trees, our proposed measures are also valid for non-ultrametric trees if \( T \) is substituted for \( T \) in the derivation. In some cases, we will specifically give formulas for non-ultrametric trees.

(1) A class of species overlap measures from a local perspective:

\[
C_{qN} = \frac{(1/ND_q)^{q-1} - (1/N)^{q-1}}{1 - (1/N)^{q-1}} \quad \text{(local-overlap).}
\]

This measure quantifies the effective average proportion of an assemblage’s species that are shared across all assemblages. When assemblage weights are equal, it reduces to the overlap measure derived in Chao et al. (2008). This weighted measure is a “true local overlap” in the following sense: If \( N \) assemblages each have \( S \) equally common species, with exactly \( A \) species shared by all of them, and the remaining species in each assemblage not being shared with any other assemblages, then this measure gives \( A/S \) for all \( q \geq 0 \) and any weights. Its complement \( 1 - C_{qN} \) is the effective average proportion of unique species in a \( n \).

For \( q = 0 \), this measure is the \( N \)-assemblage Sørensen similarity, \( C_{aN} = (N - S/S)/(N-1) \). For \( q = 1 \), this measure is

\[
C_{1N} = \frac{H_a - H_T - \sum_{j=1}^N w_j \log w_j}{\log N}, \quad \text{(D.1)}
\]

where \( H_T = -\sum_{i=1}^N (\sum_{j=1}^N w_j p_{ij}) \log(\sum_{j=1}^N w_j p_{ij}) \) is the Shannon entropy of the pooled assemblage and \( H_a = -\sum_{j=1}^N w_j (\sum_{i=1}^N p_{ij} \log p_{ij}) \) is the weighted Shannon entropy of individual assemblages. This is a weighted generalization of the \( N \)-assemblage Horn (1966) similarity measure. When assemblage weights are equal, then the measure in Eq. (D.1) reduces to the \( N \)-assemblage Horn
similarity measure, \( 1-(H_f - H_a)/\log N \) (Chao et al. 2012). For \( q = 2 \), this measure is
\[
C_{2N} = 1 - \frac{\sum_{j,k=1}^{N} \sum_{i=1}^{S} (w_j p_{ij} - w_i p_{ik})^2}{(N-1) \sum_{j=1}^{N} \sum_{i=1}^{S} w_j p_{ij}^2} .
\] (D.2)

This is a weighted generalization of the \( N \)-assemblage Morisita-Horn similarity measure. The denominator (proportional to alpha diversity) in the above formula plays a normalization role. The index is unity if and only if \( w_j p_{ij} = w_i p_{ik} \) for any two assemblages \( j \) and \( k \) and any species \( i \).

This reveals that the index compares \textit{absolute} abundances species-by-species and is normalized by the alpha diversity (a local perspective). If our target is to compare relative abundances species-by-species, then assemblage weights are equal, Eq. (D.2) reduces to the \( N \)-assemblage Morisita-Horn similarity index: (Jost 2007, Chao et al. 2012):
\[
C_{2N} = 1 - \frac{\sum_{j,k=1}^{N} \sum_{i=1}^{S} (p_{ij} - p_{ik})^2}{(N-1) \sum_{i=1}^{S} \sum_{j=1}^{N} p_{ij}^2} .
\]

The index is unity if and only if \( p_{ij} = p_{ik} \) for any two assemblages \( j \) and \( k \) and any species \( i \), i.e., the two assemblages have identical species-by-species relative abundances.

(2) A class of species overlap measures from a regional perspective:
\[
U_{qN} = \frac{(1/D_q)^{1-q} - (1/N)^{1-q}}{1-(1/N)^{1-q}} \text{(regional-overlap)}.
\]

This class of measures quantifies the effective proportion of shared species in the pooled assemblage. This weighted measure is a “true regional overlap” in the following sense: Assume that the sets of abundances for \( N \) assemblages are identical. If there are \( S \) completely distinct, equally abundant species in the region, with exactly \( R \) species shared by all \( N \) assemblages, and with the remaining \( S-R \) species evenly distributed in \( N \) assemblages, then for all orders of \( q \geq 0 \) and any weights this measure equals the species overlap \( R/S \) in the region. Thus, the measure \( 1-U_{qN} \) is a “true complementarity” measure.

For \( q = 0 \), this measure is the \( N \)-assemblage Jaccard measure, \( U_{0N} = (S/S-1/N)/(1-1/N) \). For \( q = 1 \), this measure is identical to the measure in Eq. (D.1). For \( q = 2 \), we refer to the measure as the “regional overlap” and it can be expressed as
\[
U_{2N} = 1 - \frac{\sum_{j=1}^{N} \sum_{k=1}^{N} (w_j p_{ij} - w_k p_{ik})^2}{(N-1) \sum_{i=1}^{S} \overline{p}_i^2} ,
\] (D.3)

where \( \overline{p}_i = \sum_{j=1}^{N} w_j p_{ij} \). The numerator in the above formula is the same as that in Eq. (D.2), but the denominator is proportional to the gamma diversity (a regional perspective). This reveals that the index compares \textit{absolute} abundances species-by-species and is normalized by the gamma diversity. For the equal weight case, it reduces to a measure that compares relative abundances species-by-species.

(3) A class of homogeneity measures:
This measure is linear in the proportion of regional diversity contained in the typical assemblage.

For \( q = 0 \), this measure is the \( N \)-assemblage Jaccard similarity index. For \( q = 2 \), this measure is identical to the weighted version of the \( N \)-assemblage Morisita-Horn similarity measure. However, for \( q=1 \), this measure does not reduce to the \( N \)-assemblage Horn similarity measure.

(4) A class of the complement of turnover rate measures:

\[
V_qN = \frac{N - sD_p}{N - 1} = 1 - \frac{sD_p - 1}{N - 1} \quad \text{(turnover-complement)}.
\]

The complement of this measure is linear in beta and measures the relative species turnover rate per assemblage. It represents the proportion of a typical assemblage that changes from one assemblage to another.

When \( q = 0 \), this similarity measure reduces to the \( N \)-assemblage Sørensen similarity measure. For \( q = 2 \), this measure is identical to the regional overlap given in Eq. (D.3). However, for \( q=1 \), this measure does not reduce to the \( N \)-assemblage Horn similarity measure.

We summarize the above four classes in Table 1 of the main text and their special cases for \( q = 0, 1, \) and 2.

Derivation of four classes of phylogenetic similarity measures (Table 2 of the main text)

(1) A class of true lineage overlap measures from a local perspective

\[
\overline{C}_qN(T) = \frac{[1/\sqrt[q]{D_p(T)}]^{q^{-1}} - (1/N)^{q^{-1}}}{1 - (1/N)^{q^{-1}}}.
\]  \hspace{1cm} \text{(D.4)}

This class is the phylogenetic generalization of the \( C_{qN} \) overlap measure given in Table 1. It can be derived by analogy with \( C_{qN} \) as follows. When \( q > 1 \), \( [1/\sqrt[q]{D_p(T)}]^{q^{-1}} \) is a strictly increasing function of \( 1/\sqrt[q]{D_p(T)} \) and thus can also be used to measure similarity. Its minimum is \( (1/N)^{q^{-1}} \) (when all assemblages are completely phylogenetically distinct) and its maximum is 1 (when all assemblages are identical). Our proposed overlap measure \( \overline{C}_qN(T) \) is the measure obtained by linearly standardizing \( [1/\sqrt[q]{D_p(T)}]^{q^{-1}} \) onto the range of \([0, 1]\). That is,

\[
\overline{C}_qN(T) = \frac{[1/\sqrt[q]{D_p(T)}]^{q^{-1}} - \min}{\max - \min} = \frac{[1/\sqrt[q]{D_p(T)}]^{q^{-1}} - (1/N)^{q^{-1}}}{1 - (1/N)^{q^{-1}}}.
\]  \hspace{1cm} \text{(D.5)}

For \( q < 1 \), \( [1/\sqrt[q]{D_p(T)}]^{q^{-1}} \) is a strictly decreasing function of \( 1/\sqrt[q]{D_p(T)} \) and thus can be used to measure dissimilarity. Its maximum is \( (1/N)^{q^{-1}} \) (when all assemblages are completely phylogenetically distinct) and its minimum is 1 (when all assemblages are identical). Thus it can be transformed to its corresponding similarity in the range of \([0, 1]\) by
\[
\frac{\max - [1/\bar{D}_\beta(T)]^{q-1}}{\max - \min} = \frac{(1/N)^{q-1} - [1/\bar{D}_\beta(T)]^{q-1}}{(1/N)^{q-1} - 1},
\]
which is exactly the same as \(C_{qN}(T)\) in Eq. (D.5). See Table 2 of the main text for the special cases of \(q = 0, 1,\) and 2. Here for \(q = 1\), we have the following expression for the general non-ultrametric case when assemblage weights are not equal:

\[
C_{1N}(T) = \lim_{q \to 1} C_{qN}(T) = \frac{H_{\alpha} - H_{\gamma} - T\sum_{j=1}^{N} w_j \log w_j}{T \log N},
\]

where \(H_{\alpha}\) and \(H_{\gamma}\) denote respectively the gamma and alpha phylogenetic entropies. For \(q = 2\), we give an alternative expression for the general non-ultrametric case:

\[
C_{2N}(T) = \frac{1/\bar{D}_\beta(T) - 1/N}{1 - 1/N} = \frac{2 \sum_{i \in \mathcal{B}_N} \sum_{j > k} L_i w_i a_{ij} w_k a_{ik}}{(N-1)[\sum_{i \in \mathcal{B}_N} L_i (w_i^2 a_{i1}^2 + w_i^2 a_{i2}^2 + \ldots + w_i^2 a_{iN}^2)]}. 
\]

\[
= 1 - \frac{\sum_{i \in \mathcal{B}_N} \sum_{j > k} (w_i a_{ij} - w_k a_{ik})^2}{(N-1) \sum_{i \in \mathcal{B}_N} \sum_{j=1}^{N} w_i^2 a_{ij}^2}. \quad (D.7)
\]

The index is unity if and only if \(w_i a_{ij} = w_k a_{ik}\) for all node \(i\) in the branch set and for any two assemblages \(j\) and \(k\). This reveals that the index compares absolute abundances node-by-node among the \(N\) sets of node abundance sets and is normalized by the phylogenetic alpha diversity. If assemblage weights are equal, then it reduces to

\[
\overline{U}_{qN}(T) = 1 - \frac{Q_{\gamma} - Q_{\alpha}}{(1 - 1/N)(T - Q_{\alpha})} = \frac{2 \sum_{i \in \mathcal{B}_N} \sum_{j > k} L_i a_{ij} a_{ik}}{(N-1) \sum_{i \in \mathcal{B}_N} \sum_{j=1}^{N} a_{ij}^2}
\]

\[
= \frac{\sum_{i \in \mathcal{B}_N} \sum_{j > k} (a_{ij} - a_{ik})^2}{(N-1) \sum_{i \in \mathcal{B}_N} \sum_{j=1}^{N} a_{ij}^2}. \quad (D.8)
\]

In the last expression, we see that this similarity measure attains the maximum value of unity if and only if \(a_{ij} = a_{ik}\) for all node \(i\) in the branch set and for any two assemblages \(j\) and \(k\). This reveals that the similarity quantifies the node-by-node resemblance among the \(N\) sets of node relative abundance sets.

(2) A class of true lineage overlap measures from a regional perspective

\[
\overline{U}_{qN}(T) = \frac{[1/\bar{D}_\beta(T)]^{1-q} - (1/N)^{1-q}}{1 - (1/N)^{1-q}}. \quad (D.8)
\]

The proof is generally parallel to those in the construction of \(C_{qN}(T)\). When \(q < 1\),
$[1/q\bar{D}_\beta(T)]^{1-q}$ is a strictly increasing function of $1/q\bar{D}_\beta(T)$ and thus can also be used to measure similarity. Its minimum is $(1/N)^{1-q}$ (when all assemblages are completely phylogenetically distinct) and its maximum is 1 (when all assemblages are identical). Thus the linearly standardized measure is

$$\frac{[1/q\bar{D}_\beta(T)]^{1-q} - \min}{\max - \min} = \overline{U}_{qN}(T).$$

For $q > 1$, $[1/q\bar{D}_\beta(T)]^{1-q}$ is a strictly decreasing function of $1/q\bar{D}_\beta(T)$ and thus can be used to measure dissimilarity. Its maximum is $(1/N)^{1-q}$ (when all assemblages are completely phylogenetically distinct) and its minimum is 1 (when all assemblages are identical). Thus it can be transformed to its corresponding similarity in the range of [0, 1] by

$$\frac{\max - [1/q\bar{D}_\beta(T)]^{1-q}}{\max - \min} = \frac{(1/N)^{1-q} - [1/q\bar{D}_\beta(T)]^{1-q}}{(1/N)^{1-q} - 1} = \overline{U}_{qN}(T).$$

See Table 1 of the main text for the special cases of $q = 0, 1,$ and 2. For $q = 1$, the measure $\overline{U}_{1N}(T)$ for a non-ultrametric tree is equivalent to $\overline{C}_{1N}(T)$ in Eq. (D.6). For $q = 2$, the measure $\overline{U}_{qN}(T)$ for a non-ultrametric tree can be expressed as

$$\overline{U}_{2N}(T) = \frac{2N \sum_{i \in B_T} \sum_{j > k} L_i w_i a_j w_k a_k}{(N-1)[\sum_{i \in B_T} L_i (\sum_{j=1}^N w_j a_j)^2]}$$

$$= 1 - \frac{\sum_{i \in B_T} \sum_{j > k} L_i (w_j a_j - w_k a_k)^2}{(N-1)[\sum_{i \in B_T} L_i (\sum_{j=1}^N w_j a_j)^2]}.$$  \hspace{1cm} (D.9)

The index is unity if and only if $w_j a_j = w_k a_k$ for all node $i$ in the branch set and for any two assemblages $j$ and $k$. This shows that the index compares the absolute abundances node-by-node among the $N$ sets of node abundance sets and is normalized by the phylogenetic gamma diversity. When assemblage weights are equal, we have

$$\overline{U}_{2N}(T) = 1 - \frac{Q_j - Q_a}{(N-1)(\overline{T} - Q_j)} = \frac{2N \sum_{i \in B_T} \sum_{j > k} L_i a_j a_k}{(N-1)[\sum_{i \in B_T} (\sum_{j=1}^N L_i a_j)^2]}$$

$$= 1 - \frac{\sum_{i \in B_T} \sum_{j > k} L_i (a_j - a_k)^2}{(N-1)[\sum_{i \in B_T} (\sum_{j=1}^N L_i a_j)^2]}.$$  \hspace{1cm} (D.10)

This shows that the similarity measure $\overline{U}_{qN}(T)$ quantifies the node-by-node resemblance among the $N$ sets of node relative abundance sets.

(3) A class of phylogenetic homogeneity measures which are linear in the inverse of phylogenetic beta:
This measure is obtained by considering the inverse beta \( 1/\sqrt{\beta} \). It attains its maximum value of unity when all assemblages are identical, and it attains its minimum value of \( 1/N \) when all assemblages are completely phylogenetically distinct. Then \( S_{qN}(T) \) is obtained by the linear normalization \( S_{qN}(T) = [1/\sqrt{\beta}(T) - \text{min}]/(\text{max} - \text{min}) \). When assemblage have equal weights, see Table 2 in the main text for the special cases of \( q = 0 \) and 2.

(4) A class of the complement of lineage turnover rate:

\[
\bar{V}_{qN}(T) = \frac{N - q\sqrt{\beta}(T)}{N - 1}.
\]

The phylogenetic beta \( q\sqrt{\beta}(T) \) attains the minimum value of unity (when all assemblages are identical), and it attains the maximum value of \( N \) (when all assemblages are completely phylogenetically distinct). Thus it can be linearly standardized to produce a similarity measure in the range of \([0, 1]\): \( \bar{V}_{qN}(T) = [\max - \sqrt{\beta}(T)]/(\max - \min) \). The corresponding differentiation measure is linear in beta and measures the lineage turnover rate per assemblage. It also represents the proportion of a typical assemblage that changes from one assemblage to another. See Table 2 in the main text for the special case of \( q = 0 \) and 2.

**Phylogenetic beta and lineage excess lead to the same similarity and differentiation measures**

As discussed in the main text, the lineage excess \( \sqrt{\alpha\gamma}(T) - \sqrt{\alpha}(T) \) cannot be directly applied to compare the similarity or differentiation across multiple regions because it depends on the number of assemblages and also on the mean phylogenetic alpha (equivalently, gamma) diversity. However, we show below that, after proper normalizations, the lineage excess also leads to the same four classes of normalized similarity and differentiation measures as those in Table 2 of the main text. For easy demonstration, we prove for the differentiation measures.

(1) A class of the lineage turnover rate \( 1 - \bar{V}_{qN}(T) \)

As proved in Eq. (C.7) of Appendix C, we have \( \sqrt{\alpha\gamma}(T) - \sqrt{\alpha}(T) \leq N[\sqrt{\alpha\gamma}(T)] \). This implies

\[
0 \leq \sqrt{\alpha\gamma}(T) - \sqrt{\alpha}(T) \leq (N - 1)[\sqrt{\alpha\gamma}(T)], \tag{D.13}
\]

which shows the lineage excess depends on alpha and \( N \). The dependence can be removed in this case by normalization and the resulting measure is \( 1 - \bar{V}_{qN}(T) \):

\[
[\sqrt{\alpha\gamma}(T) - \sqrt{\alpha}(T)]/[\text{max} - \sqrt{\alpha}(T)] = [\sqrt{\alpha\gamma}(T) - 1]/(N - 1) = 1 - \bar{V}_{qN}(T).
\]

(2) A class of phylogenetic differentiation measures \( 1 - S_{qN}(T) \)
As we proved in Eq. (C.8) of Appendix C, \( \frac{\hat{\mathcal{D}}_\gamma(T)}{N} \leq \frac{\hat{\mathcal{D}}_\alpha(T)}{N} \leq \hat{\mathcal{D}}_\gamma(T) \). We then have

\[
0 \leq \hat{\mathcal{D}}_\alpha(T) - \hat{\mathcal{D}}_\gamma(T) \leq (1 - 1/N)[\hat{\mathcal{D}}_\alpha(T)],
\]

which shows the lineage excess depends on gamma and \( N \). The normalized measure turns out to be \( 1 - \bar{S}_{\psi\psi}(T) \):

\[
[\hat{\mathcal{D}}_\psi(T) - \hat{\mathcal{D}}_\psi(T)] / \{(1 - 1/N)[\hat{\mathcal{D}}_\psi(T)]\} = [1 - 1/\phi(T)] / (1 - 1/N) = 1 - \bar{S}_{\psi\psi}(T).
\]

(3) A class of phylogenetic differentiation measures \( 1 - \bar{C}_{\psi\psi}(T) \)

We first prove the following two inequalities:

\[
0 \leq [\hat{\mathcal{D}}_\psi(T)]^{1-q} - [\hat{\mathcal{D}}_\psi(T)]^{1-q} \leq (1 - N^{1-q})[\hat{\mathcal{D}}_\psi(T)]^{1-q}, \quad q > 1,
\]

and

\[
0 \leq [\hat{\mathcal{D}}_\psi(T)]^{1-q} - [\hat{\mathcal{D}}_\psi(T)]^{1-q} \leq (N^{1-q} - 1)[\hat{\mathcal{D}}_\psi(T)]^{1-q}, \quad 0 < q < 1.
\]

The inequality in Eq. (C.7) of Appendix C, \( \hat{\mathcal{D}}_\gamma(T) \leq N[\hat{\mathcal{D}}_\alpha(T)] \), implies that for \( q > 1 \), we have \( [\hat{\mathcal{D}}_\psi(T)]^{1-q} \geq N^{1-q}[\hat{\mathcal{D}}_\psi(T)]^{1-q} \). Then the inequality in Eq. (D.15) follows. For \( 0 \leq q < 1 \), Eq. (D.16) also follows directly from the same inequality. Dividing \( [\hat{\mathcal{D}}_\psi(T)]^{1-q} - [\hat{\mathcal{D}}_\psi(T)]^{1-q} \) (for \( q > 1 \)) or \( [\hat{\mathcal{D}}_\psi(T)]^{1-q} - [\hat{\mathcal{D}}_\psi(T)]^{1-q} \) (for \( 0 \leq q < 1 \)) by its maximum possible value (given the actual value of alpha diversity) gives \( 1 - \bar{C}_{\psi\psi}(T) \). That is,

\[
\left[ [\hat{\mathcal{D}}_\psi(T)]^{1-q} - [\hat{\mathcal{D}}_\psi(T)]^{1-q} \right] / (N^{1-q} - 1)[\hat{\mathcal{D}}_\psi(T)]^{1-q} = \frac{[\hat{\mathcal{D}}_\psi(T)]^{1-q} - 1}{N^{1-q} - 1} = 1 - \bar{C}_{\psi\psi}(T).
\]

Moreover, let \( H_{\psi\psi} \) and \( H_{\alpha\alpha} \) denote respectively the gamma and alpha phylogenetic entropies. Then we have

\[
\lim_{q \to 1} \left[ [\hat{\mathcal{D}}_\psi(T)]^{1-q} - [\hat{\mathcal{D}}_\psi(T)]^{1-q} \right] / (N^{1-q} - 1)[\hat{\mathcal{D}}_\psi(T)]^{1-q} = \frac{H_{\psi\psi} - H_{\alpha\alpha} + T \log N + T \sum_{j=1}^N w_j \log w_j}{T \log N} = 1 - \bar{C}_{11}(T).
\]

In the special case of equal weight, the above reduces to

\[
\lim_{q \to 1} \left[ [\hat{\mathcal{D}}_\psi(T)]^{1-q} - [\hat{\mathcal{D}}_\psi(T)]^{1-q} \right] / (N^{1-q} - 1)[\hat{\mathcal{D}}_\psi(T)]^{1-q} = \frac{H_{\psi\psi} - H_{\alpha\alpha}}{T \log N}.
\]

(4) A class of phylogenetic complementarity measures \( 1 - \bar{U}_{q\psi}(T) \)

The inequality in Eq. (C.8) of Appendix C, \( \hat{\mathcal{D}}_\gamma(T) / N \leq \hat{\mathcal{D}}_\alpha(T) \leq \hat{\mathcal{D}}_\gamma(T) \), implies that for \( 0 < q < 1 \), we have \( (1/N^{1-q})[\hat{\mathcal{D}}_\gamma(T)]^{1-q} \leq \hat{\mathcal{D}}_\alpha(T) \leq [\hat{\mathcal{D}}_\gamma(T)]^{1-q} \). Thus, we obtain
$$0 \leq [q \overline{D}_j(T)]^{1-q} - [q \overline{D}_a(T)]^{1-q} \leq (1 - 1/N^{1-q})[q \overline{D}_j(T)]^{1-q}, \quad 0 \leq q < 1;$$

and

$$0 \leq [q \overline{D}_a(T)]^{1-q} - [q \overline{D}_j(T)]^{1-q} \leq (1 - 1/N^{1-q})^{-1}[q \overline{D}_r(T)]^{1-q}, \quad q > 1.$$

Dividing $$[q \overline{D}_a(T)]^{1-q} - [q \overline{D}_j(T)]^{1-q}$$ (for $$q > 1$$) or $$[q \overline{D}_a(T)]^{1-q} - [q \overline{D}_j(T)]^{1-q}$$ (for $$0 \leq q < 1$$) by its maximum possible value (given the actual value of gamma diversity) gives the “true complementarity” lineage measure, $$1 - \overline{U}_{qN}(T)$$. That is,

$$\frac{[q \overline{D}_a(T)]^{1-q} - [q \overline{D}_j(T)]^{1-q}}{(1 - 1/N^{1-q})[q \overline{D}_j(T)]^{1-q}} = \frac{1 - [q \overline{D}_a(T)]^{1-q} - [q \overline{D}_j(T)]^{1-q}}{1 - 1/N^{1-q}} = 1 - \overline{U}_{qN}(T).$$

Moreover, we have

$$\lim_{q \to 1} \frac{[q \overline{D}_a(T)]^{1-q} - [q \overline{D}_j(T)]^{1-q}}{(1 - 1/N^{1-q})[q \overline{D}_j(T)]^{1-q}} = \frac{H_{P,\gamma} - H_{P,\alpha} + T \log N + T \sum_{j=1}^N w_j \log w_j}{T \log N}$$

$$= 1 - \overline{U}_{1N}(T) = 1 - \overline{C}_{1N}(T).$$

In the special case of equal weight, the above reduces to

$$\lim_{q \to 1} \frac{[q \overline{D}_a(T)]^{1-q} - [q \overline{D}_j(T)]^{1-q}}{(1 - 1/N^{1-q})[q \overline{D}_j(T)]^{1-q}} = \frac{H_{P,\gamma} - H_{P,\alpha}}{T \log N} = 1 - \overline{U}_{1N}(T) = 1 - \overline{C}_{1N}(T).$$

Thus, our phylogenetic beta and the lineage excess both lead to the same four classes of normalized similarity measures ($$\overline{C}_{qN}(T)$$, $$\overline{U}_{qN}(T)$$, $$\overline{V}_{qN}(T)$$ and $$\overline{S}_{qN}(T)$$) and their corresponding differentiation measures. Although normalization is not a general cure for problems of dependence on alpha (or gamma), all the resulting normalized measures discussed above are functions of beta only. Thus, dependence on alpha or on gamma is removed in our cases as our beta is independent of alpha and gamma (Chao et al. 2012).

LITERATURE CITED


Non-phylogenetic approach based on the generalized entropies

When our goal is to measure similarity and differentiation among multiple assemblages, the traditional approach that incorporates species relative abundances has been based on additive partitioning of generalized entropy $qH$ (including Shannon entropy and the Gini-Simpson index) or phylogenetic generalized entropy $qI(T)$ (including phylogenetic entropy $H_P$ and quadratic entropy $Q$). We first review the non-phylogenetic version (Jost 2006, 2007 and Jost et al. 2010) so that readers can better understand what the mathematical flaws are in the additive approach. Since the generalized entropies $qH = (1 - \sum p_i^q)/(q - 1)$ include Shannon entropy and the Gini-Simpson index as special cases, our discussion is focused on the additive “beta” based on the generalized entropy excess. Since the “beta” diversity for the Gini-Simpson index is related to our measure only in the equal-weight case (see Table 1 of the main text), we focus on the equal-weight case and show how to fix and connect the additive measures to our measures.

Let $qH_\gamma$ and $qH_\alpha$ denote respectively the gamma and alpha generalized entropies. The additive “beta” (generalized entropy excess) is defined as $qH_\beta = qH_\gamma - qH_\alpha$. Jost et al. (2010, p. 73, their Eq. 8) proved the following relationships which show how the additive “beta” is constrained by alpha generalized entropy (equivalently by gamma generalized entropy, as will be shown later of this Appendix):

$$0 \leq qH_\beta = qH_\gamma - qH_\alpha \leq \frac{(1 - N^{1-q})(1 - (q - 1)(qH_\alpha))}{q - 1}, \quad q \neq 1. \quad (E.1)$$

$$0 \leq \lim_{q \to 1} qH_\beta = \lim_{q \to 1} qH_\gamma - \lim_{q \to 1} qH_\alpha \leq \frac{(1 - N^{1-q})(1 - (q - 1)(qH_\alpha))}{q - 1} = \log N. \quad (E.2)$$

We discuss the following three special cases in detail so that we can transparently see how the generalized entropy excess depends on alpha for each order $q = 0, 1$ and 2.

1. $q = 2$ case

For $q = 2$, Eq. (E.1) gives the inequality $H_{GS,\gamma} - H_{GS,\alpha} \leq (1 - 1/N)(1 - H_{GS,\alpha})$, where $H_{GS,\gamma}$ and $H_{GS,\alpha}$ denote respectively gamma and alpha Gini-Simpson measures. This shows that the “beta” Gini-Simpson is confounded with alpha, and is negatively constrained by alpha. When the alpha Gini-Simpson is high (i.e., when $H_{GS,\alpha}$ tends to 1), the maximum value of “beta”, $(1 - 1/N)(1 - H_{GS,\alpha})$, tends to 0. So the “beta” Gini-Simpson is necessarily to be small, regardless of the actual differentiation between groups. In this case, the differentiation measure
“beta”/gamma always approaches zero, and the similarity measure alpha/gamma always approaches unity (Jost 2006, 2007), supposedly indicating a high degree of similarity between groups, even when the groups are completely dissimilar (no shared species). Due to this dependence on alpha, the additive “beta”/gamma based on the Gini-Simpson index does not measure differentiation, and alpha/gamma does not measure compositional similarity. One way to fix this (Jost et al. 2010) is to normalize the additive “beta” by dividing it by its upper limit given the observed values of alpha and $N$, yielding \[ \frac{H_{GS,p} - H_{GS,a}}{[(1 - 1/N) (1 - H_{GS,a})]}, \] which is identical to our equal-weight differentiation measure $1-C_{2N}$ (see Table 1 of the main text).

(2) $q = 1$ case
For $q = 1$, Eq. (E.2) shows that the additive “beta” entropy is bounded by a constant $\log N$, not on alpha, as the additive partitioning for entropy really is a complete partitioning. So under an additive framework, traditional differentiation as measured by (“beta” entropy)/(gamma entropy) must tend to zero if the denominator (gamma entropy) is large. This partly explains why, even though additive “beta” entropy measures pure differentiation, additive “beta”/gamma based on entropy is not a proper differentiation measure. (Another reason is that entropies do not obey the Replication Principle). Also, when gamma Shannon entropy is high, the so-called similarity measure alpha/gamma approaches unity. Thus the additive alpha/gamma based on entropy does not measure compositional similarity (again, because entropies do not obey the Replication Principle). It is also readily seen from Eq. (E.2) that for entropy, instead of using beta/gamma, one should use the normalized measure “beta”/(log $N$) in the range [0, 1] as a proper differentiation measure. As shown in Chao et al. (2012), entropy “beta”/(log $N$) is identical to equal-weight $1-C_{1N}$ measure defined in Table 1 of the main text.

Thus, the additive approach applied to the two concave measures (entropy and Gini-Simpson index, which is a generalized entropy) may lead to inconsistent conclusions and biologically misleading interpretations (Jost 2006, 2007). All authors in a recent Forum on diversity partitioning (Ellison 2010 and papers following it) therefore agreed that diversity measures should be based on Hill numbers instead of Shannon entropy and the Gini-Simpson measure.

(3) $q = 0$ case
For $q = 0$, Eq. (E.1) is equivalent to the constraint \[ S - \bar{S} \leq (N - 1)\bar{S}, \] where $S$ denotes species richness in the pooled assemblage (gamma species richness) and $\bar{S}$ denotes the average species richness in an individual assemblage (alpha species richness). Eq. (E.1) implies that the “beta” species richness is confounded with alpha, and is positively constrained by alpha. The generalized entropy of order 0 is species richness minus one, but here we just use species richness instead because the latter is the measure that has been considered for diversity decomposition. Based on species richness, the differentiation measure “beta”/gamma = $(S - \bar{S})/S = (1 - 1/N)(1 - U_{0N})$ where $U_{0N}$ is the homogeneity measure defined in Table 1 of the main text. Thus, “beta”/gamma based on species richness can be used as a differentiation measure, but its range still depends on $N$ since it ranges from 0 (when all assemblages are identical) to $1 - 1/N$ (when all assemblages have no shared species). Our approach is to remove the dependence of the additive “beta” on alpha by using a normalized measure $(S - \bar{S})/[(N - 1)\bar{S}]$, which is identical to $1-C_{0N}$ (see Table 1 of the main text). The normalized measure is always in the range [0, 1] so it can be compared across regions with different number of assemblages.
For a general order $q > 1$, Eq. (E.1) shows that additive “beta” generalized entropy is strongly negatively constrained by the value of alpha. If alpha generalized entropy of order $q > 1$ tends to the maximum possible value $1/(q-1)$, then the “beta” is necessarily to be small. In contrast, for $q < 1$, Eq. (E.1) shows that the additive “beta” generalized entropy is positively constrained by the value of alpha. As shown for the orders $q = 0$ and 2 above, the dependence of the additive generalized entropy “beta” on its alpha can be removed by dividing the additive “beta” by its maximum possible value in Eqs. (E.1) and (E.2). Based on those maximum values and the relationship between Hill numbers and generalized entropy, $(^q D)^{-q} = 1-(q-1)(^q H)$, we can readily show that the normalized measure turns out to be $1-C_N^\alpha$. That is, for $q \neq 1$, we have

$$
\frac{^q H_\gamma - ^q H_\alpha}{\max( ^q H_\gamma - ^q H_\alpha )} = \frac{(q-1)(^q H_\gamma - ^q H_\alpha)}{(1-N^{1-q})[1-(q-1)(^q H_\alpha)]}
= \frac{1-(q-1)(^q H_\alpha) - [1-(q-1)(^q H_\alpha)]}{(1-N^{1-q})[1-(q-1)(^q H_\alpha)]}
= \frac{1-(^q D_\alpha)^{-q}}{1-N^{1-q}} = 1-C_N^\alpha.
$$

(E.3)

For $q = 1$, the entropy “beta” should be normalized by the upper bound $\log N$. The normalized measure becomes

$$
\frac{^1 H_\gamma - ^1 H_\alpha}{\max( ^1 H_\gamma - ^1 H_\alpha )} = \frac{(^1 H_\gamma - ^1 H_\alpha)}{\log N} = 1-C_N^\alpha.
$$

(E.4)

The dependence relationship in Eq. (E.1) is equivalent to the following constraint which shows how the additive “beta” generalized entropy depends on gamma generalized entropy:

$$
0 \leq ^q H_\beta = ^q H_\gamma - ^q H_\alpha \leq \frac{1/N^{1-q} - 1}{(q-1)(^q H_\gamma)} \cdot \frac{1-(q-1)(^q H_\alpha)}{q-1}, \quad q \neq 1;
$$

(E.5)

$$
0 \leq ^1 H_\beta = ^1 H_\gamma - ^1 H_\alpha \leq \lim_{q \rightarrow 1} \frac{1/N^{1-q} - 1}{(q-1)(^1 H_\gamma)} \cdot \frac{1-(q-1)(^1 H_\alpha)}{q-1} = \log N.
$$

(E.6)

Parallel discussion to those for the dependence on alpha can be made. Here we only single out the special case of $q = 2$. In this case, Eq. (E.5) gives the constraint $H_{G\alpha} - H_{G\gamma} \leq (N-1)(1-H_{G\alpha})$. This shows that the “beta” Gini-Simpson is also negatively confounded with gamma. When the gamma Gini-Simpson is high (i.e., $H_{G\alpha}$ tends to 1), the maximum value of “beta”, $(N-1)(1-H_{G\alpha})$, tends to 0. So the “beta” Gini-Simpson is necessarily to be small. We note that for the Gini-Simpson index, Eq. (C.7) in Appendix C implies that $(1-H_{G\alpha})^{-1} \leq N(1-H_{G\alpha})^{-1}$. Thus, for a fixed $N$, $H_{G\alpha}$ tends to 1 if and only if $H_{G\gamma}$ tends to 1. The condition “alpha Gini-Simpson is high” is equivalent to the condition “gamma Gini-Simpson is high”.

For a general order of $q$, we can remove the gamma-dependence by normalization. Dividing
by its maximum, the normalized measure turns out to be $1 - U_{qN}$. That is,

$$\frac{(q-1)(q_H - q_a)}{1/N^{1-q} - 1[(q-1)[(q_H - q_a)] = \frac{[1/qD_{\rho}]^{1-q} - 1}{1/N^{1-q} - 1} = 1 - U_{qN}.}$$  \hspace{1cm} (E.7)

For $q = 1$, the entropy “beta” should be normalized by the upper bound log $N$ in Eq. (E.6). The normalized measure becomes

$$\frac{1/q_H - 1/q_a}{\max(1/q_H - 1/q_a)} \log N = 1 - U_{1N} = 1 - C_{1N}. \hspace{1cm} (E.8)$$

Thus eliminating the gamma dependence, we get a class of complementarity measures.

The above discussion shows the generality of the two classes of overlap measures $C_{qN}$ and $U_{qN}$, because they are the normalized similarity measures that are common to both the additive approach based on generalized entropy and the approach based on Hill numbers.

**Traditional additive framework based on the phylogenetic generalized entropies**

We now extend the dependence relationships in Eqs. (E.1) and (E.2) to the phylogenetic generalizations in the following Theorem E1, and extend the dependence relationships in Eqs. (E.5) and (E.6) to the phylogenetic generalizations in the following Theorem E2.

**Theorem E1**: The phylogenetic generalized entropy excess (or the phylogenetic additive “beta” in the main text), $qI_{\beta}(T) = qI_{\gamma}(T) - qI_{\alpha}(T)$, depends on alpha generalized entropy through the following inequality (see Eq. 13b, 13c in the main text)

$$0 \leq qI_{\beta}(T) = qI_{\gamma}(T) - qI_{\alpha}(T) \leq \frac{(1 - N^{1-q})[T - (q-1)[qI_{\alpha}(T)]]}{q-1} \hspace{1cm} q \neq 1, \hspace{1cm} (E.9)$$

For $q = 1$, we have

$$0 \leq 1/q_H(T) - 1/q_a(T) \leq \lim_{q \to 1} \frac{(1 - N^{1-q})[T - (q-1)[qI_{\alpha}(T)]]}{q-1} = T \log N. \hspace{1cm} (E.10)$$

The normalized measures turn out to be:

$$\frac{[qI_{\gamma}(T) - qI_{\alpha}(T)]}{\max[qI_{\gamma}(T) - qI_{\alpha}(T)]} = \frac{(q-1)[qI_{\gamma}(T) - qI_{\alpha}(T)]}{(1 - N^{1-q})[T - (q-1)[qI_{\alpha}(T)]]} = 1 - C_{qN}(T), \hspace{1cm} q \neq 1; \hspace{1cm} (E.11)$$

$$\frac{[1/q_H(T) - 1/q_a(T)]}{\max[1/q_H(T) - 1/q_a(T)]} = \frac{1/q_H(T) - 1/q_a(T)}{T \log N} = 1 - C_{1N}(T). \hspace{1cm} (E.12)$$

**Proof**: From Eq. 2c of the main text, the phylogenetic generalized entropy can be expressed as
$$^qI(T) = (T - \sum_{i \in B_q} L_i a_i^q)/(q-1).$$

Then we can obtain the relationship between $^qI(T)$ and our mean phylogenetic diversity $\bar{D}(T)$:

$$^q\bar{D}(T) = \left\{ 1 - \frac{(q-1)[^qI(T)]}{T} \right\}^{1/(1-q)}.$$

(E.13)

In Eq. (C.7) of Appendix C, we have proved $^q\bar{D}_\gamma(T) \leq N[^q\bar{D}_\alpha(T)]$, which is equivalent to

$$\left\{ 1 - \frac{(q-1)[^qI_\gamma(T)]}{T} \right\}^{1/(1-q)} \leq N\left\{ 1 - \frac{(q-1)[^qI_\alpha(T)]}{T} \right\}.$$

If $q < 1$, the above implies

$$\left\{ 1 - \frac{(q-1)[^qI_\gamma(T)]}{T} \right\} \leq N^{1-q}\left\{ 1 - \frac{(q-1)[^qI_\alpha(T)]}{T} \right\},$$

which then implies

$$^qI_\gamma(T) - ^qI_\alpha(T) \leq \frac{(1-N^{1-q})\{T-(q-1)[^qI_\alpha(T)]\}}{q-1}.$$

For $q > 1$, we obtain exactly the same inequality. We thus finish the proof of (E.9). For the case of $q = 1$, Eq. (E.10) follows by direct computation. To obtain the normalized measure in Eq. (E.11), we note from Eq. (E.13),

$$^q\bar{D}_\beta(T) = \frac{^q\bar{D}_\gamma(T)}{^q\bar{D}_\alpha(T)} = \frac{(T-(q-1)[^qI_\alpha(T)])^{1/(1-q)}}{(T-(q-1)[^qI_\alpha(T)])^{1/(1-q)}}.$$

This leads to the following for $q \neq 1$

$$\frac{[^qI_\gamma(T)-^qI_\alpha(T)]}{\max[^qI_\gamma(T)-^qI_\alpha(T)]} = \frac{(q-1)[^qI_\gamma(T)-^qI_\alpha(T)]}{(1-N^{1-q})\{T-(q-1)[^qI_\alpha(T)]\}}$$

$$= \frac{T-(q-1)[^qI_\alpha(T)]\{T-(q-1)[^qI_\alpha(T)]\}}{(1-N^{1-q})\{T-(q-1)[^qI_\alpha(T)]\}}$$

$$= \frac{1-[^q\bar{D}_\beta(T)]^{1-q}}{1-N^{1-q}} = 1-C_{q\beta}(T).$$

The proof for the case of $q = 1$ is straightforward and thus omitted.

**Theorem E2:** The phylogenetic generalized entropy excess (or the phylogenetic additive “beta” in the main text), $^qI_\beta(T) = ^qI_\gamma(T) - ^qI_\alpha(T)$, depends on gamma generalized entropy through the following inequality (Eq. 13d in the main text)
0 ≤ \( qI_p(T) = qI_a(T) - I_a(T) \leq \frac{1/N^q - 1}{q-1} \{ T - (q-1)[qI_a(T)] \}, \quad q \neq 1. \quad (E.14) \)

For \( q = 1 \), we have

\[
0 \leq 1I_p(T) = 1I(T) - I_a(T) \leq \lim_{q \to 1} \frac{1/N^q - 1}{q-1} \{ T - (q-1)[qI_a(T)] \} = T \log N.
\]

The normalized measures turn out to be:

\[
\frac{[qI_a(T) - qI_a(T)]}{\max[qI_a(T) - qI_a(T)]} = \frac{1}{1/N^q - 1} \{ T - (q-1)[qI_a(T)] \} = 1 - \overline{U}_q(T), \quad q \neq 1;
\]

\[
\frac{[qI_a(T) - qI_a(T)]}{\max[qI_a(T) - qI_a(T)]} = \frac{1}{T \log N} = 1 - \overline{C}_1(T) = 1 - U_{1N}(T).
\]

Proof: In Eq. (C.8) of Appendix C, we have proved \( qD(T) / N \leq q\overline{D}_a(T) \). Then from Eq. (E.13), we have

\[
\frac{1}{N} \left\{ 1 - \frac{(q-1)[qI_a(T)]}{T} \right\} \leq \left\{ 1 - \frac{(q-1)[qI_a(T)]}{T} \right\}^{1/(1-q)}.
\]

The proof steps are then parallel to those in Theorem E1 and thus are omitted.

**Generalizing to non-ultrametric cases**

In Pavoine et al.’s (2009) original formulation (see Eq. 2d of the main text and Appendix A), phylogenetic generalized entropy can be defined only for ultrametric trees. We give a new formulation in Eq. 2c of the main text. We can readily extend Eq. 2c to non-ultrametric trees. That is, phylogenetic generalized entropy which is a function of mean base change \( T \) can be formulated as

\[
qI(T) = \left[ \overline{T} - \sum_{l \in B_T} L_\lambda a_\lambda^q \right] / (q-1).
\]

For the non-ultrametric cases we can extend Eq. (E.13) to the following relationship between our mean phylogenetic diversity and phylogenetic generalized entropy:

\[
qD(T) = \left\{ 1 - \frac{(q-1)[qI(T)]}{T} \right\}^{1/(1-q)}.
\]

Then all conclusions in Theorems E1 and E2 can be similarly extended to the non-ultrametric cases by substituting \( \overline{T} \) for \( T \). Therefore, all mathematical flaws associated with the ultrametric cases are also carried over to the non-ultrametric cases. However, normalization can be applied to fix the flaws and we obtain the same classes of similarity and differentiation measures as those in Table 1 of the main text.
LITERATURE CITED

Appendix F: A simple hypothetical tree with completely distinct lineages

In Example 1 of the main text, we considered two assemblages of landlocked organisms (Fig. F1) that originated on a super-continent that broke into two parts. Assume that the two assemblages evolved in isolation for approximately $T$ years. Although this example is simple, it provides an initial comparison so that the analyses for more complicated example and real data can be better understood.

![Fig. F1: A simple hypothetical tree. All $S$ species in each assemblage diverged from their common ancestor $T$ years ago, and all species are equally common in each assemblage.](image)

### (1) $q = 2$ case

Let us first apply Rao’s quadratic entropy $Q$, the most frequently used measure that incorporates both abundances and phylogeny, to this simple tree (Fig. F1). Usually the distance measure used is the branch length in years connecting any two individuals in the assemblage to their most recent common node. Then Rao’s quadratic entropy, in its non-normalized form, is the mean divergence time between two randomly chosen individuals of an assemblage. In this example, the divergence time between two individuals is zero if they belong to the same species, and $T$ otherwise (see Fig. F1). If there are $S$ species in each continental assemblage, the quadratic entropy $Q$ of each continent will be $0 \times (1/S) + T \times (1-1/S) = T(1-1/S)$. This would be the alpha quadratic entropy $Q_\alpha$ of the assemblages. For any fixed $T$, the alpha value will be high (i.e., tends to the maximum possible value of $T$) if and only if species richness $S$ is high. The gamma value is the quadratic entropy of the pooled assemblage, $Q_\gamma = T[1-1/(2S)]$. For traditional additive partitioning based on quadratic entropy, the quadratic entropy excess or “beta” diversity is defined as gamma minus alpha, in this case $Q_\beta - Q_\alpha = T/(2S)$. When $S$ is high, this “beta” diversity necessarily approaches zero, even though the lineages of the two assemblages are completely
distinct (no shared lineages) since the date of the root of the tree.

The “differentiation” measure \( J_{2N}(T) \) is obtained by dividing this “beta” by the gamma quadratic entropy (e.g. Hardy and Senterre 2007). A value near zero would be interpreted as indicating little or no differentiation, while a value near unity would be interpreted as indicating high differentiation. However, in this case the differentiation measure reduces to \( J_{2N}(T) = [T/(2S)]/[T - T/(2S)] = 1/(2S - 1) \), a number that approaches zero when \( S \) is high, even though the two assemblages are completely distinct and have been evolving independently since time \( T \). Our theoretical result in the main text implies that when the within-assemblage quadratic entropy is high, the additive “differentiation” measure based on quadratic entropy always tends to zero for any assemblages, not just for simple completely distinct trees. These behaviors of additive “beta” and differentiation “beta”/gamma are exactly like the well-known problems of its parent measure, the Gini-Simpson index (Jost 2006, 2007, Hardy and Jost 2008). Similar findings hold for more complicated trees and real data as shown in the main text. In Fig. F2 (left panel), we show the pattern of the differentiation \( J_{2N}(T) \) as a function of species richness. This function is decreasing to 0 as \( S \) is large. The measure \( J_{2N}(T) \) is independent of \( T \), as shown in Fig. F2 (right panel) specifically for \( S = 10 \).

Biologists using \( Q \) to make conservation decisions for this imaginary set of continents with large \( S \) will conclude that since the additive “differentiation” measure is near zero, the second continent is superfluous and need not be a conservation priority. Yet the assemblages are equally diverse and share no species, and have been evolving in isolation since time \( T \), so each may consist entirely of endemic genera or families.

Now turn to our proposed phylogenetic beta diversity (Eq. 10b in the main text) for \( q = 2 \), with our temporal perspective \( T \) as the age of the continental split (the age of the basal node).

\[
2D_\beta(T) = (1-Q_x/T)^{-1}/(1-Q_y/T)^{-1} = (T/S)^{-1}/(T/(2S))^{-1} = 2,
\]

implying that there are two distinct assemblages, as expected. All the differentiation measures (see Table 1 of the main text) take the maximum possible value of unity for all \( S \). For examples, the proposed differentiation measures \( 1-C_{2N}(T) \) and \( 1-U_{2N}(T) \) are

\[
1-C_{2N}(T) = 1 - [1/(2D_\beta(T))] = 1,
\]

\[
1-U_{2N}(T) = 2D_\beta(T) - 1/N - 1 = 1.
\]

This is consistent with our intuition, because the two assemblages are completely distinct after time \( T \), so the differentiation should attain the maximum value of unity.

(2) \( q = 1 \) case

For \( q = 1 \), traditional additive decomposition is based on the phylogenetic entropy \( H_p = -\sum L_i a_i \log a_i \). For the tree in Fig. F1, we have the alpha value \( H_{p,a} = T(\log S) \), and the gamma value \( H_{p,y} = T[\log(2S)] \). The additive “beta” (phylogenetic entropy excess) is \( H_{p,y} - H_{p,a} = T(\log 2) \), and the “differentiation” measure \( J_{1N}(T) = (\log 2)/[\log(2S)] \). When gamma is high
(equivalently, when \( S \) is large), this differentiation measure tends to zero (Fig. F2, left panel), supposedly indicating no differentiation, even though the two assemblages are completely distinct. This counter-intuitive behavior will arise for all trees, not just for simple completely distinct trees. As we have proved in Theorem E1 of Appendix E, traditional additive “beta” entropy for any tree is bounded by \( T \log N \), implying “beta”/gamma always tends to zero if gamma is large. Although in the case of \( q = 1 \), alpha and “beta” (\( H_P \) excess) are independent, “beta”/gamma is not a legitimate measure of differentiation (because the numerator and denominator do not obey the Replication Principle). As shown in Table 1 of the main text, dividing “beta” by \( T \log N \), we obtain the correct differentiation value of unity for this example.

When assemblage weights are equal, our proposed beta in terms of phylogenetic entropy is given in Eq. 10a for \( q = 1 \). For any temporal perspective \( T \), we have

\[
\overline{H_p}(T) = \exp[(H_{p,\gamma} - H_{p,\alpha})/T] = \exp(\log 2) = 2,
\]
indicating that there are two completely distinct assemblages. The proposed differentiation measures are

\[
1 - \overline{C}_{0N}(T) = 1 - \overline{C}_{0N}(T) = \log(\overline{H_p}(T) / \log N) = \log 2 / \log 2 = 1 \quad \text{(see Table 1 of the main text for \( N = 2 \)) for all \( S \) and all \( T \); see Fig. F2.}
\]

(3) \( q = 0 \) case

The phylogenetic generalized entropy for the case \( q = 0 \) is based on \( 0 I(T) = \) total branch length \( L(T) \) minus tree height \( T \). For the simple tree in Fig. F1, we have gamma branch length \( L_{\gamma}(T) = 2TS \) and alpha branch length \( L_{\alpha}(T) = TS \). Thus, the alpha value \( 0 I_{\alpha}(T) = L_{\alpha}(T) - T = (S - 1)T \) and the gamma value \( 0 I_{\gamma}(T) = L_{\gamma}(T) - T = (2S - 1)T \), implying the additive “beta” is \( ST \). Clearly, this beta is positively constrained by alpha for any fixed \( T \). The “differentiation” in this special case is \( J_{0N}(T) = S/(2S - 1) \). When \( S \) is large enough, this differentiation measure tends to the value of 1/2 (see Fig. F2) for this example and in general it tends to \( 1 - 1/N \) for \( N \) completely distinct assemblages. For small values of \( S \), this differentiation measure gives a value that is different from 1/2 (Fig. F2).

Our proposed beta for \( q = 0 \), for any temporal perspective \( T \), is

\[
\overline{H_p}(T) = L_{\gamma}(T) / L_{\alpha}(T) = 2,
\]
correctly indicating two completely distinct assemblages in the region. Our proposed differentiation measure is given in Table 1 in terms of tree length turns out again to correctly take its maximum possible value of unity. That is,

\[
1 - \overline{C}_{0N}(T) = \frac{L_{\gamma}(T) / L_{\alpha}(T) - 1}{N - 1} = 1;
\]

\[
1 - \overline{U}_{0N}(T) = \frac{1 - L_{\alpha}(T) / L_{\gamma}(T)}{1 - 1/N} = 1.
\]

The upper bound in Eq. 13b of the main text for the traditional additive “beta” in this case reduces to \( (N - 1)[T + 0 I_{\alpha}(T)] = ST \). Dividing the additive “beta” \( 0 I_{\alpha}(T) - 0 I_{\gamma}(T) = ST \) by this upper bound, we see the normalized value is equal to unity for all \( S \) and all \( T \); see Fig. F2. Similarly, the upper
bound in Eq. 13d for the traditional additive “beta” reduces to \((N^{-1} - 1)[T + 0 I (T)] = ST\). Again, the normalized value is equal to unity for all \(S\) and all \(T\).

In summary, for the simplest tree for a pair of assemblages with completely distinct lineages, defined in Fig. F1, our proposed normalized phylogenetic differentiation measures \(1 - \overline{C}_{qN}(T)\) and \(1 - \overline{U}_{qN}(T)\) (based on our mean phylogenetic diversity) are always 1 for all \(q = 0, 1, 2\), and all richnesses \(S\) and all temporal perspective \(T\), indicating that we have two completely distinct assemblages over this time interval; see Fig. F2. In contrast, the traditional differentiation measure \(J_{qN}(T)\) (based on phylogenetic generalized entropies) depends on \(S\). We have \(J_{2N}(T) = 1/(2S - 1)\), \(J_{1N}(T) = (\log 2) /[\log (2S)]\), and \(J_{0N}(T) = S/(2S - 1)\). As shown in Fig. F2 (right panel) for \(S = 10, J_{2N} = 0.053, J_{1N} = 0.23\) and \(J_{0N} = 0.53\). The left panel of Fig. F2 shows, as \(S\) tends to be large, that both \(J_{2N}\) and \(J_{1N}\) approach to zero and \(J_{0N}\) approaches 1/2. These erratic behaviors show that traditional approach based on phylogenetic generalized entropies does not work even for the simplest trees. However, as we have proved in Theorems E1 and E2 in Appendix E, traditional approach can be easily fixed by normalization. The normalized measures turn out to be the proposed differentiation measures \(1 - \overline{C}_{qN}\) and \(1 - \overline{U}_{qN}(T)\).

![Fig. F2: Comparison of the proposed differentiation measures, \(1 - \overline{C}_{qN}(T)\) and \(1 - \overline{U}_{qN}(T)\) (based on our mean phylogenetic diversity) and the traditional differentiation measure \(J_{qN}(T)\) (based on the traditional additive partitioning of phylogenetic generalized entropy).](image)

(Left panel) Plots of the differentiation measures as a function of species richness. All measures are independent of the value of \(T\). Both the proposed measures, \(1 - \overline{C}_{qN}(T)\) and \(1 - \overline{U}_{qN}(T)\), are unity for all \(q = 0, 1, 2\) and all richness \(S\). The measure \(J_{qN}(T)\) depends on \(q\): for \(q = 0\), measure tends to 1/2 when \(S\) is large; for \(q = 1\), measure tends to 0 when \(S\) is large; for \(q = 2\), measure tends to 0 when \(S\) is large.

(Right panel) Plots of the differentiation measures as a function of \(T\) given \(S = 10\) for \(q = 0, 1\) and 2.
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APPENDIX G. Additional analysis of Examples 2 and 3

Example 2. Two types of profiles of differentiation measures

In the main text, we suggest using two types of profiles to characterize the proposed differentiation measures \(1 - C_{q\psi}(T)\) and \(1 - U_{q\psi}(T)\). Here we illustrate these two types of profiles based on the hypothetical time-calibrated tree in Fig. 3 of the main text.

1) The first type of profile shows how our differentiation measures vary with the time perspective \(T\) by evaluating the proposed differentiation measures as a function of the temporal perspective \(T\) over the interval \([-T, 0]\), for a fixed order \(q\) (including at least \(q = 0, 1\) and \(2\)). Here the time perspective can vary from \(T = 0\) (the current time) to \(T = \infty\). For the tree in Fig. 3 of the main text, the splitting time between assemblages correspond to a specific value of \(T = 200\), and the root of the pooled tree corresponds to a specific value of \(T = 240\). In Fig. G1(a), we show profiles which plot the measures \(1 - C_{q\psi}(T)\) and \(1 - U_{q\psi}(T)\) as a function of time perspective \(T, 0 < T < 250\), for \(q = 0, 1\) and \(2\) separately. For comparison, we also include the profile for the traditional differentiation measure \(J_{qN}(T)\) based on the phylogenetic generalized entropies.

2) For any fixed time perspective \(T\) (including at least \(T = 0\) and \(T = \) the age of the root of the pooled tree), the other type of profile is obtained by plotting our differentiation measures with respect to the order \(q\). In Fig. G1(b), for \(T = 0\) (i.e., phylogeny is ignored), we plot the profiles for three non-phylogenetic measures \((1 - C_{qN}, 1 - U_{qN}\) and \(J^*_{qN}\)) as a function of order \(q, 0 \leq q \leq 5\). Then for \(T = 240\) My (the age of the root of the pooled phylogenetic tree), we also plot the corresponding profiles for three phylogenetic differentiation measures, \(1 - C_{qN}(T), 1 - U_{qN}(T)\) and \(J_{qN}(T)\).

The profile for each fixed value of \(q\) in Fig. G1(a) reveals that the additive differentiation measure \(J_{qN}(T)\) based on the phylogenetic generalized entropies is hardly sensitive to the tree structure, as it remains at a almost constant level for any \(T, 0 < T < 250\). This is also clearly seen from comparing the two panels \((T = 0\) and \(T = 240\) My) in Fig. G1(b); all values of the phylogenetic differentiation measures \(J_{qN}(T)\) at \(T = 240\) My are close to the values of their non-phylogenetic counterparts (i.e., the measure \(J^*_{qN}\)). In Fig. G1(b), for each fixed temporal perspective \(T\), although \(J^*_{qN}\) and \(J_{qN}(T)\) decrease gradually with the order of \(q\) as shown in each figure of G1(b), their values are very low (for \(q \geq 1\), as predicted by our theory for the case of high alpha (and thus high gamma) phylogenetic entropies. This can also be seen by examining the level of \(J_{qN}(T)\) for \(q = 1\) and \(2\) in Fig. G1(a). Thus, the two types of profiles in Fig. G1 confirm by example our theoretical proof that the measure \(J_{qN}(T)\) often will not reflect either tree structure or differences in species abundances.
The two proposed measures for $q = 1$ and 2 in Fig. G1(a) show high differentiation between the two assemblages when the perspective time $T$ is less than 200 (the splitting time of the continents). After that, both measures start to decrease, and the decrease is sharper for $q = 2$. For $q \geq 1$, as $T$ becomes larger so that more dominant shared lineages are added to the two assemblages, our two abundance-sensitive differentiation measures show the expected decreasing trend, especially for $q = 2$. Also, comparing the two panels ($T = 0$ and $T = 240$ My) in Fig. G1(b), we see that all values of the phylogenetic differentiation measure $1 - C_{qN}(T)$ at $T = 240$ My are much lower than the corresponding non-phylogenetic measure at $T = 0$. Similar behavior is also observed for the measure $1 - U_{qN}(T)$. These two types of profiles are very useful to characterize the behavior of the proposed differentiation measures as a function of the time perspective $T$ and the order $q$.

![Graphs showing differentiation measures](image)

Fig. G1. Profiles of differentiation measures. (a) Profiles of three phylogenetic differentiation measures, $1 - C_{qN}(T)$, $1 - U_{qN}(T)$, and the traditional differentiation measure $J_{qN}(T)$, as a function of the time perspective $T$, $0 \leq T \leq 250$, for $q = 0$ (left panel), $q = 1$ (middle panel), and $q = 2$ (right panel). All measures are computed for the interval for the interval $[-T, 0]$, and $T$ varies from 0 to 250. The vertical dotted line in all figures refers to the split time ($T = 200$ My, see Fig. 3 in the...
main text). (b) (Left panel) Profiles of three non-phylogenetic differentiation measures (i.e., $T = 0$), $1 - C_{qN}$, $1 - U_{qN}$ and $J_{qN}^*$, as a function of order $q$, $0 \leq q \leq 5$. (Right panel) Profiles of three phylogenetic differentiation measures, $1 - C_{qN}(T)$, $1 - U_{qN}(T)$ and the traditional differentiation measure $J_{qM}(T)$, for the specific time perspective $T = 240$ My, the age of the root of the pooled phylogenetic tree.

**Example 3. More analysis for two rockfish assemblages**

As discussed in the main text, the full data set in Pavoine et al. (2009) contains a total of 52 rockfish species of the genus *Sebastes* collected over 20 years (1980-1986, 1993-1994, 1996, 1998-2007) from the Southern California Bight. It is helpful to first examine the time series of the whole 20 years data. For each of the 20 years, we computed three types of diversity measures: (1) the non-phylogenetic diversity (Hill numbers $qD$), (2) The phylogenetic mean diversity $qD(T)$ of Chao et al. (2010); see Eqs. 4a and 4b of the main text. (3) The phylogenetic generalized entropy $qI(T)$ of Pavoine et al. (2009); see Eqs. 2c and 2d of the main text.

The plots of the two diversities $qD$ and $qD(T)$ for $q = 0, 1$ and 2 as a time series are shown in Fig. G2. A general decline trend is clearly seen for species richness $qD$ and the mean lineage length $qD(T)$, but the long-term decreasing trend for each of $q = 1$ and 2 for both diversities is not significant over the 20 years. Since the units for the measure $qI(T)$ for $q = 0, 1$ and 2 are different, it is meaningless to plot the three-order phylogenetic generalized entropies in a graph, thus the corresponding plots for the measure $qI(T)$ are omitted. It is noteworthy that the phylogenetic diversity measures are much less “noisy” across years than the ordinary diversity measures; they may measure a more stable and characteristic property of assemblages.

**Fig. G2: Hill numbers and mean phylogenetic diversity for 1980-2007 rockfish data (Pavoine et al. 2009).** (Left panel) Non-phylogenetic diversity (Hill numbers). (Right panel) Mean phylogenetic diversity. A regression line is fitted to each time series of diversities for each order of $q$.

As in the main text, we focus on comparing the 1981 assemblage and 2003 assemblage, and
these two assemblages are referred to as Assemblage 1 and 2 respectively. The species abundance and phylogenetic data are provided in Fig. 5a of the main text for the 1981 and 2003 assemblages. For these two contrasting assemblages, we show in Table G1 three types of diversity measures for each of the two assemblages. For each diversity measure, we calculated values for three orders \( q = 0, 1 \) and 2. The mean diversity \( qD(T) \) and the measure \( qI(T) \) are calculated for \( T = 7.9 \) My, which is the age of the root in the pooled phylogenetic tree. In the following analysis, unless otherwise stated, \( T \) always refers to this age.

Table G1: Three types of diversity measures for two rockfish assemblages.

\[ T = \text{age of the root node.} \]

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>( q = 0 )</td>
<td>( qD )</td>
<td>( qD(T) )</td>
</tr>
<tr>
<td>( q = 1 )</td>
<td>10.47</td>
<td>4.62</td>
</tr>
<tr>
<td>( q = 2 )</td>
<td>5.54</td>
<td>2.57</td>
</tr>
</tbody>
</table>

Table G1 shows that for each type of diversity measures and each order \( q = 0, 1 \) and 2, the non-phylogenetic diversity (Hill numbers), mean phylogenetic diversity, and phylogenetic generalized entropy of rockfish in Assemblage 2 is less than the corresponding value in Assemblage 1. For all measures based on Hill numbers, the values for \( q = 0, 1 \) and 2 are in the same units of “effective number of species”, so they can be compared directly. The decline in species richness \( (qD) \) is more pronounced than the decline in typical species \( (qD) \) and abundant species \( (qD) \). This implies the change in non-phylogenetic diversity is mainly due to fewer rare species in Assemblage 2. The units of our phylogenetic measure \( qD(T) \) are also the same, “effective number of lineages”, for all orders of \( q \). Table G1 therefore also implies that the decline in phylogenetic diversity over the past 7.9 My is mainly due to fewer rare lineages in Assemblage 2. Since the effective total branch lengths is \( T \times qD(T) \), we can also conclude that the total lineage length is significantly reduced due to fewer rare lineages in Assemblage 2. While the measure \( qI(T) \) also reveals a decline in phylogenetic generalized entropies, different orders of this measure have different units and thus are not comparable.

Table G2 presents the decomposition for the three types of diversity measures considered in Table G1. Since our target is to compare the relative abundances of the two assemblages, the weights for the two assemblages are equal in our following analysis. For both Hill numbers and the mean phylogenetic diversity, our beta is interpreted as “the effective number of completely distinct assemblages”, which ranges between 1 and 2 for \( N = 2 \) assemblages. The gamma, alpha and diversity/lineage excess for these two measures decreases with the order \( q \). For the three orders of \( q = 0, 1 \), and 2, the phylogenetic beta diversities are very stable in a narrow range of 1.20 and 1.28, whereas non-phylogenetic beta diversity varies in a range of 1.26 and 1.67. Again, the excess based on phylogenetic generalized entropy have different units for the three orders, and thus are not comparable.
Table G2: Decomposition of Hill numbers, mean phylogenetic diversity, or generalized entropy for two rockfish assemblages, $T = 7.9$ My, the age of the root node

<table>
<thead>
<tr>
<th>Order $q$</th>
<th>Diversity components</th>
<th>Measures</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$qD$</td>
<td>$qD(T)$</td>
</tr>
<tr>
<td>$q = 0$</td>
<td>Gamma</td>
<td>39</td>
</tr>
<tr>
<td></td>
<td>Alpha</td>
<td>31</td>
</tr>
<tr>
<td></td>
<td>Excess</td>
<td>8</td>
</tr>
<tr>
<td></td>
<td>Beta</td>
<td>1.26</td>
</tr>
<tr>
<td>$q = 1$</td>
<td>Gamma</td>
<td>13.82</td>
</tr>
<tr>
<td></td>
<td>Alpha</td>
<td>9.67</td>
</tr>
<tr>
<td></td>
<td>Excess</td>
<td>4.15</td>
</tr>
<tr>
<td></td>
<td>Beta</td>
<td>1.43</td>
</tr>
<tr>
<td>$q = 2$</td>
<td>Gamma</td>
<td>8.95</td>
</tr>
<tr>
<td></td>
<td>Alpha</td>
<td>5.35</td>
</tr>
<tr>
<td></td>
<td>Excess</td>
<td>3.60</td>
</tr>
<tr>
<td></td>
<td>Beta</td>
<td>1.67</td>
</tr>
</tbody>
</table>

For the two rockfish assemblages, we applied in the main text the traditional differentiation measure $J_{qN}$ (based on phylogenetic generalized entropies), and the two proposed differentiation measures $1 - C_{qN}$ and $1 - U_{qN}$ (based on our mean phylogenetic diversity) as well as their corresponding non-phylogenetic measures; see Tables 1 and 2 of the main text and related discussion. There we evaluated these differentiation measures for the interval $[-T, -T+t]$, an interval of time $t$ after the root of the phylogenetic tree (see Fig. 6 of the main text). Here we apply the three phylogenetic differentiation measures to compare the two assemblages in each evolutionary time period from the root to the tips. We follow Pavoine et al. (2009) in dividing the evolutionary tree by each speciation event, producing 50 periods indexed from root to tips by 1, 2, ..., 50. The starting time of the first period represents the age of the root whereas the end of the last period represent the current time. This is the reverse ordering of Pavoine et al. (2009) as they indexed periods from tips to root. We chose an index from root to tips in order to be consistent with our other graphs in the main text.

1. Within each evolutionary period, we calculated the proposed phylogenetic gamma diversity $qD_{\gamma}$, alpha diversity $qD_{\alpha}$, and lineage excess $qD_{\gamma} - qD_{\alpha}$. In the left panel of Fig. G3, we show the plots for the alpha, gamma and lineage excess in each time period for $q = 0$ (first row), 1 (second row) and 2 (third row). As we have shown in the main text, both the beta diversity and lineage excess lead to the same classes of normalized differentiation measures: $1 - C_{qN}$ and $1 - U_{qN}$. So in the right panels of the same figure, we show the corresponding
plots for the differentiation between the two assemblages based on the two convergent measures $1 - C_{qN}$ and $1 - U_{qN}$ for $q = 0, 1$ and $2$. All measures are calculated within a time period.

(2) Within each evolutionary period, we also calculated alpha and gamma phylogenetic generalized entropies ($\alpha_I$ and $\gamma_I$) and phylogenetic generalized entropy excess $\gamma_I - \alpha_I$. These measures are plotted in the middle panels of Fig. G3 for $q = 0$ (first row), 1 (second row) and 2 (third row). The differentiation measure $J_{qN} = 1 - \frac{\alpha_I}{\gamma_I}$ based on the phylogenetic generalized entropies is shown in the right panels of the same figure for $q = 0, 1$ and $2$. All measures are calculated within a time period.

From Appendix A our mean phylogenetic diversity measures, when applied to an evolutionary period without any internal nodes, reduce to Hill numbers of the importance values of lineages (the total abundance of the descendants of lineage in the present assemblage). The phylogenetic generalized entropies reduce to generalized entropies of the importance values of lineages; see Fig. A1 (Appendix A). So the diversities based on ordinary Hill numbers $qD$ in Table G2 represent the phylogenetic diversity at the tips (i.e., the 50th period or the present time). Also, within each period, our comparison is simply based on the non-phylogenetic differentiation measures. That is, the two measures $1 - C_{1N} = 1 - U_{1N}$ and $1 - C_{2N}$ respectively reduce to the complement of classical Horn and Morisita-Horn similarity measures within each period (see Table 1 of the main text). The two differentiation measures $J_{1N}$ and $J_{2N}$ reduce respectively to additive “beta”/gamma based on Shannon entropy and Gini-Simpson indices. Therefore, the differentiation measure $1 - C_{qN}$ based on Hill numbers in Table 3 of the main text is identical to the phylogenetic measure at the tips or the present time.

For both traditional and proposed approaches, the left and middle panels of Fig. G3 show that the gamma value (black bar plus white bar in each interval) and alpha value (white bar) are increasing from root to tips for all values of $q$. For $q = 0$, the distributional patterns for the alpha, gamma and lineage excess are similar for the two approaches; and the three differentiation measures exhibits similar behaviors (see the first row, right panel). However, for $q = 1$ and $2$, the patterns are drastically different. In our approach, the lineage excess (black bar in the left panels) in each interval tends to increase as time period moves from root to tips especially for $q = 2$. (For $N = 2$, the maximum possible percentage of lineage excess is 50% of gamma when the two assemblages are completely distinct). In the case of $q = 2$, the percentage tends to 40% (= excess/gamma = 3.6/8.95, see Table G2) at the tips. In the case of $q = 1$, the percentage tends to 30% (= 4.15/13.82, see Table G2) at the tips.

The two measures $1 - C_{2N}$ and $1 - C_{1N} = 1 - U_{1N}$ are very low in the first six periods. They then start to increase and reach a relatively high level, and increasing up to 80% for $q = 2$ and 52% for $q = 1$ in the present time. The measure $1 - U_{2N}$ behaves similarly and increases to 67% in the present time. See Table 3 of the main text. In contrast, the generalized entropy excess becomes a strikingly small portion of gamma for all intervals when time period moves from root to tips. The two differentiation measures $J_{1N}$ and $J_{2N}$ are low in the first six periods and exhibit a slightly increasing trend from the seventh to the eighth (for $q = 2$) or ninth (for $q = 1$) period. But after that,
the two differentiation measures steadily decrease, as shown in the second and third rows, right panel of Fig. G3. (Theoretically, these differentiation measures will tend to zero whenever gamma is high for $q = 1$, and whenever alpha is high for $q = 2$.)

As explained, the two measures $1 - C_{1N}^1 (= 1 - U_{1N})$ and $1 - C_{2N}^2$, when applied to each interval, respectively reduce to the complement of classical Horn and Morisita-Horn similarity measures, we can use the properties of these two classical measures to explain our results. It is known that the Morisita-Horn measure ($q = 2$) is dominated by the very abundant species. Thus our measure $1 - C_{2N}^2$ in each period is dominated by the “very important lineages” (those with high node abundances). As indicated in the main text, the most abundant species in Assemblage 1 are $S. paucispinis$ (36.45%), $S. mystinus$ (15.19%) and $S. goodei$ (12.72%), and the total relative abundances for these three species is around 64%, but they became quite rare in Assemblage 2 (the relative abundance are respectively 0.13%, 8.19% and 0); see Fig. 5b of the main text. In Assemblage 2, the three most abundant species are $S. miniatus$ (39.9%), $S. caurinus$ (9.17 %) and $S. mystinus$ (8.19 %), but the two most abundant species were quite rare in Assemblage 1 (3.82 % and 2.23 % respectively). As will be explained below, the split between these species is also evolutionarily deep; they have been in isolated lineages from the eleventh period to the present. Therefore, the measure for $q = 2$ from the eleventh period onward is mainly determined by those lineages.

For the initial six periods, all those abundant lineages in the assemblages had not diverged yet (see Fig. 5a in the main text), so that the two assemblages have the same dominant ancestral species. Thus the difference between the two assemblages in the first six periods is low for all measures, as shown by almost no differentiation for the time periods 1 to 6 in Fig. G3 for $q = 2$ case. At the beginning of the seventh period, $S. caurinus$ diverged from the lineage of the other four dominant species (see Fig. 5b). Then at the beginning of the eighth period (about 1.6 My after the root), the most dominant species of Assemblage 2 ($S. miniatus$) diverged from the lineage of the three dominant species in Assemblage 1 ($S. paucispinis$, $S. mystinus$, and $S. goodei$). At the beginning of ninth period, $S. mystinus$ diverged from the lineage of the two species ($S. paucispinis$, and $S. goodei$). Then the two species $S. paucispinis$, and $S. goodei$ diverged at the beginning of the eleventh period (about 2.2 My after the root). All the five dominant species evolved independently after that time.

Since those dominant species started to diverge between the seventh and eleventh evolutionary periods, all our measures $1 - C_{1N}^1 (= 1 - U_{1N})$, $1 - C_{2N}^2$ and $1 - U_{2N}$ sharply increases in these periods. From the eleventh period, the considerable discrepancy between our differentiation measure and the traditional one for $q = 1$ and 2 leads to totally opposite conclusions. Based on the phylogenetic entropy and especially quadratic entropy, the two assemblages have low differentiation in each time period after the eleventh period. However, our measure indicates high differentiation in each period after the eleventh. Note that the dominant species are in isolated lineages in time periods 11 to 50, implying that the sharp abundance difference for the dominant ancestral lineages remains unchanged in these periods. Thus the difference between the two assemblages from periods 11 to 50 should all be quite high (as shown in the third row, right panels of Fig. G3); the differentiation values of the measure $1 - C_{2N}^2$ from periods 11 to 50 are between 60% and 80% (period 50) as shown in Fig. G3 for $q = 2$; the differentiation values of the measure
$1 - \overline{U}_{2N}$ from period 11 to 50 are between 50% and 67% (period 50). However, the differentiation based on quadratic entropy counter-intuitively shows very low differentiation value of around 8% throughout the time periods 11 to 50.

Similarly for $q = 1$, the differentiation measure $1 - \overline{C}_{1N} (= 1 - \overline{U}_{1N})$ increases from zero to 52% from root to tips whereas the corresponding curve for phylogenetic entropy rises briefly and then counter-intuitively drops to a low value around 14% at the tips. As explained, we think an increasing trend and relatively high differentiation should be the more intuitive and sensible answer from periods 11 to 50 for this real tree. These observations also help explain the findings for our case study in the main text; see Fig. 6 of the main text and related discussion.
Fig. G3: Phylogenetic partitioning and differentiation within each evolutionary period (periods are ordered from the root to tips) for two rockfish assemblages (the 1981 assemblage and 2003 assemblage). \( q = 0 \) (the first row), \( q = 1 \) (the second row) and \( q = 2 \) (the third row).

(Left panels) Plots of our phylogenetic gamma diversity \( \gamma D^q \) (white plus black bar) and alpha diversity \( \alpha D^q \) (white bar), black bar denotes lineage excess \( \gamma D^q - \alpha D^q \). All measures are calculated within each period; see Eqs. 7a, 7b, 8a and 8b of the main text. (The maximum possible percentage of beta is 50% of gamma.)

(Middle panels) Plots of the gamma phylogenetic generalized entropy \( \gamma I^q \) (white plus black bar)
and alpha $^qI_\alpha$ (white bar), black bar denotes phylogenetic generalized entropy excess $^qI_y - ^qI_\alpha$. All measures are calculated within each period; see Eqs. 2c and 2d of the main text.

(Right panels) Plots of the proposed differentiation measure $1 - C_{qN}$ (solid circles) and $1 - \sum_{qN}$ (solid triangles) based on our mean phylogenetic diversity, and the traditional differentiation measure $J_{qN} = 1 - ^qI_\alpha / ^qI_y$ (open circles) based on the phylogenetic generalized entropy.

LITERATURE CITED
