

Quantifying evenness and linking it to diversity, beta diversity, and similarity

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Abstract. An enormous number of measures based on different criteria have been proposed to quantify evenness or unevenness among species relative abundances in an assemblage. However, a unified approach that can encompass most of the widely used indices is still lacking. Here, we first present some basic requirements for an evenness measure. We then propose that unevenness among species relative abundances in an assemblage can be measured by a normalized divergence between the vector of species relative abundances and the mean vector, where the mean vector represents the species relative abundances of a completely even assemblage. Thus, evenness among species relative abundances is measured by the corresponding normalized extent of closeness between these two vectors. We consider five divergence measures, leading to five classes of evenness indices. All our evenness measures are in terms of diversity (Hill number) of order $q > 0$ (here q controls the weighting of species relative abundances) and species richness (diversity of order $q = 0$). We propose quantifying evenness through a continuous profile that depicts evenness as a function of diversity order $q > 0$. The profiles can be easily and visually compared across multiple assemblages. Our evenness indices satisfy all the requirements presented in this paper and encompass many widely used evenness measures as special cases. When there are multiple assemblages, the abundance-based Jaccard- and Sørensen-type dissimilarity measures (which are monotonic functions of beta diversity) can be expressed as weighted averages of the individual species' compositional unevenness values; here, each individual species' compositional unevenness is calculated based on that species' abundances among assemblages. The contribution of a species to each dissimilarity measure can be clearly disentangled and quantified in terms of this single species' compositional unevenness among assemblages. Thus, our framework links the concepts of evenness, diversity, beta diversity, and similarity. Moreover, the framework can be readily extended to a phylogenetic version. A real data example is used to illustrate our approach. We also discuss some criteria and other measures that were previously proposed in the literature.

Key words: beta diversity; dissimilarity; divergence; diversity; evenness; Hill numbers; phylogenetic diversity; principle of transfer; similarity; unevenness.

INTRODUCTION

Until fairly recently, how to quantify biodiversity was one of the most controversial issues in ecology (Magurran and McGill 2011). Surprisingly, since an *Ecology* forum (Ellison 2010 and the papers following it), a consensus seems to have emerged about the use of Hill numbers, that is, the effective number of species (Hill 1973), as the diversity measure of choice for quantifying species diversity and decomposition. Hill numbers, parameterized by a diversity order q (where q controls the weights of species relative abundances), encompass the three most useful diversity measures: species richness (diversity of order $q = 0$), Shannon diversity ($q = 1$, i.e., the

exponent of Shannon entropy), and Simpson diversity ($q = 2$, i.e., the inverse of the Simpson concentration index); see Hill (1973) and Chao et al. (2014) for reviews.

Compared to diversity, quantifying evenness or unevenness among species relative abundances is an even more complicated and extensively discussed issue (Pielou 1966, Alatalo 1981, Routledge 1983, Smith and Wilson 1996, Gosselin 2001, 2006, Ricotta 2003, Olszewski 2004, Jost 2010, Tuomisto 2012, Kvålseth 2015, among others). A number of authors (Routledge 1983, Smith and Wilson 1996, Kvålseth 2015) discussed necessary properties for an evenness measure. Researchers from different perspectives and under different criteria have developed a wider range of (un)evenness measures than diversity indices. The list of evenness measures seems endless, reflecting that our concept of evenness is not very clear and also that disagreements exist about the

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requirements an evenness measure should satisfy. Indeed, before the possibility of similarly reaching a consensus can be considered to be more than a distant goal, it is necessary to formulate a unified methodology/approach that can encompass most useful evenness measures.

In this paper, we propose an intuitive and unified mathematical framework to obtain evenness measures. In our framework, unevenness among species relative abundances is measured by a normalized divergence between the vector of species relative abundances and the mean vector, where the mean vector represents the species relative abundances of a completely even assemblage with the same number of species. Thus, evenness among species relative abundances is measured by the corresponding normalized extent of closeness between these two vectors.

Here, we first present our perspective on some basic requirements for an evenness measure. Then we consider five divergence measures, leading to five classes of evenness indices. All divergence and evenness measures are in terms of (relative) abundance-based Hill numbers (i.e., $q > 0$) and species richness ($q = 0$), revealing explicitly the relation between evenness and diversity. Our measures possess all of the basic requirements presented later in this paper and encompass many previous evenness indices as special cases. When multiple assemblages are considered, we apply our measures to evaluate each *species' compositional evenness*, that is, evenness in this single species' relative abundances, among assemblages, calculated for each species, individually. Then the abundance-based Jaccard- and Sørensen-type dissimilarity measures (which are monotonic functions of beta diversity) can be expressed as weighted averages of the individual species' compositional unevenness values. Thus, our framework links among the concepts of diversity, evenness, beta diversity and similarity. The contribution of a species to the Jaccard- and Sørensen-type dissimilarity measures can be explicitly disentangled and quantified in terms of this single species' compositional unevenness among multiple assemblage.

In traditional taxonomic diversity analysis, all species are considered to be equally distinct from one another. However, in an evolutionary context, species differences can be based directly on their evolutionary relationships in the form of phylogenetic trees. Species that are closely related are generally less distinct in important ecological characteristics than are distantly related species. A vast number of phylogenetic diversity metrics and related (dis)similarity measures have been proposed; see Chao et al. (2014) for a review. When all species (as tip nodes) in a focal assemblage are connected by a rooted ultrametric phylogenetic tree, our framework can be extended to a phylogenetic version. Thus, the contribution of each species/node of the phylogenetic tree to a phylogenetic dissimilarity measure can also be assessed. A real data example is used for illustrating the proposed evenness

profiles and assessing the contribution of each species/node to taxonomic and phylogenetic dissimilarity measures.

BASIC REQUIREMENTS FOR AN EVENNESS MEASURE

The main reason for the development of the broad spectrum of evenness measures seen today is that different researchers require different criteria. Our proposed requirements for an evenness measure are systematically given separately for three cases: (1) Species richness is fixed but abundance-based diversity varies. (2) Species richness varies but abundance-based diversity is almost fixed. (3) Species richness and/or abundance-based diversity are varying.

Basic requirements for an evenness measure when species richness is fixed

Our proposed criteria when species richness is fixed are the same as those for the concept of diversity because diversity is based on the evenness principle. That is, when species richness is fixed, the more even the species abundances, the higher the diversity. Here, we first present the mathematical formulas of species diversity, which are based on species relative abundances. Assuming there are S species in an assemblage with species relative abundance vector $\mathbf{p} = (p_1, p_2, \dots, p_S)$, taxonomic/species diversity (Hill number) of order q is defined as

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

For $q = 1$, we have

$${}^1D = \lim_{q \rightarrow 1} {}^qD = \exp \left(- \sum_{i=1}^S p_i \log p_i \right). \quad (1b)$$

When species richness S is fixed, evenness of \mathbf{p} , $E(\mathbf{p})$, should possess the same properties as an abundance-based diversity measure (Taillie 1979). We require two unequivocal shared properties:

Requirement 1a—When species richness is fixed, the fundamental and most essential property required for an evenness measure is the *principle of transfer*, which states that when an amount of abundance is transferred from a relatively more abundant species to a relatively less abundant species, evenness should increase. Specifically, assume that species i is more abundant than species j (i.e., $p_i > p_j > 0$). If an amount h , $0 < h < p_i - p_j$, is transferred from species i to species j , then evenness increases.

Requirement 1b— $E(\mathbf{p})$ should be continuous and symmetric with respect to $\mathbf{p} = (p_1, p_2, \dots, p_S)$. Here, symmetric means permutation-invariant.

The principle of transfer is equivalent to strict *Schur-concavity* of $E(\mathbf{p})$ with respect to \mathbf{p} (Marshall et al. 2011). Intuitively, Schur-concavity of evenness means that evenness increases as dispersion of abundances decreases, whereby “dispersion” of abundances is defined by the concept of majorization; see Appendix S1: Section S1 for mathematical details on majorization, Schur-concavity, and the related notion of the Lorenz curve/ordering.

Given there are S species, Requirement 1a also implies that any evenness measure attains a maximum value for a completely even assemblage with species relative abundance vector $\mathbf{p} = \bar{\mathbf{p}} = (1/S, 1/S, \dots, 1/S)$ (i.e., the mean vector); the most uneven assemblage should consist of one superdominant species (i.e., a species whose relative abundance is tending unity), and $(S - 1)$ species of vanishingly small abundances. For notational and derivational convenience, we simply regard a vanishingly small abundance as “zero” abundance (or the abundance of a present but undetected species) and denote the most uneven vector with S elements as $\mathbf{p}^0 = (1, 0+, \dots, 0+)$.

Basic requirement for an evenness measure when species richness is varying but diversity of order $q > 0$ is almost fixed

Requirement 2—When a vanishingly rare species is added to an assemblage so that the diversity of order $q > 0$ barely changes, evenness should not increase.

This property corresponds to Routledge’s (1983) second requirement (R2). Like Smith and Wilson (1996), Jost (2010), and Kvålseth (2015), here we do not require that $E(\mathbf{p})$ is continuous with respect to species richness.

Basic requirements for an evenness measure when richness and/or abundance-based diversity are varying

Requirement 3a—“Independence” or unrelatedness criterion: The range of values that an evenness measure can take should be a fixed interval, regardless of the values of species richness ($q = 0$) and abundance-based diversity ($q > 0$).

Requirement 3b—Scale invariance: Any evenness measure should not be affected by the units used. In particular, evenness for species raw abundances and relative abundances should be the same.

Although the criterion of “independence” on species richness has been adopted by several researchers, varying interpretations have been applied to it (Smith and Wilson 1996, Gosselin 2006, Kvålseth 2015); see *Discussion* for details. The meaning of the independence of two measures was the subject of a contentious debate in an *Ecology* Forum; see Ellison (2010) and papers following it. Chao et al. (2012) suggested the

adoption of the term “unrelatedness” to replace “independence” as a way to avoid confusion. Chao and Chiu (2016) gave two intuitive criteria to assure the “independence” or unrelatedness of two measures. These two criteria are: (1) The *minimum value* that one measure can take should be a *fixed* constant, and (2) the *maximum value* that a measure can take should also be a *fixed* constant, regardless of the values of the other measure. Based on their criteria, Requirement 3a means that both the minimum and maximum values that an evenness measure can take should be fixed constants, regardless of the values of diversity of any order $q \geq 0$. By convention, we set the minimum value = 0 and maximum value = 1. Then it follows from Requirement 1a that when $\mathbf{p} = \bar{\mathbf{p}}$, $E(\mathbf{p})$ attains the maximum value of 1, and when $\mathbf{p} = \mathbf{p}^0$, $E(\mathbf{p})$ approaches the minimum value of 0. The unrelatedness requirement assures that the same magnitude of evenness quantifies the same degree of equitability, even when the assemblages differ in richness or diversity. See *Discussion* for examples.

OUR FRAMEWORK LEADS TO FIVE CLASSES OF EVENNESS INDICES

Kvålseth (2015) introduced the value-validity property, allowing an evenness measure to be applied not only to rank different assemblages but also to rank the difference and proportional difference between any two pairs of assemblages; see Eqs. 7a–c of Kvålseth (2015). This property entails that an evenness measure must satisfy the following two requirements:

1. For an assemblage with S species, an evenness measure is expressed as the one-complement of a normalized distance for some distance metric d between the vector of species relative abundances \mathbf{p} and the mean vector $\bar{\mathbf{p}}$, as shown in the following form:
2. If a vector is expressed as a convex combination of $\bar{\mathbf{p}}$ and \mathbf{p}^0 , that is, $\mathbf{p} = \lambda\bar{\mathbf{p}} + (1 - \lambda)\mathbf{p}^0$, then the evenness of this vector \mathbf{p} must be λ .

$$E(\mathbf{p}) = 1 - \frac{d(\mathbf{p}, \bar{\mathbf{p}})}{d(\mathbf{p}^0, \bar{\mathbf{p}})}. \quad (2)$$

Kvålseth (2015) applied the Minkowski family of distances of order $\alpha > 0$; that is, $d_\alpha(\mathbf{p}, \bar{\mathbf{p}}) = (\sum_{i=1}^S |p_i - (1/S)|^\alpha)^{1/\alpha}$. When $\alpha = 1$, the resulting evenness measure reduces to the Bulla (1994) measure; when $\alpha = 2$ (Euclidean distance), it reduces to the measure proposed by F. M. Williams (unpublished data; see Kvålseth 2015), which is a transformation of the coefficient of variation among species relative abundances. Kvålseth (2015) indicated that Bulla’s evenness measure does not satisfy the principle of transfer, and hence advocated the use of Williams’ measure. However, Williams’ measure is based on the Euclidean distance; it thus

disproportionally favors dominant species and mainly quantifies the evenness among dominant species. In Kvålseth's approach, nearly all of the widely used evenness measures are excluded, mainly because there are no proper distances that can be used in Eq. 2 to obtain those measures. For Kvålseth's second requirement, most previous evenness measures for $\mathbf{p} = \lambda \bar{\mathbf{p}} + (1 - \lambda) \mathbf{p}^0$ are not equal to λ , but to an increasing function of λ .

Because most ecological applications require only ranking/comparing evenness across assemblages, we were thus motivated to develop a unified approach that can (1) encompass most useful evenness measures, (2) consider any diversity order $q > 0$ to obtain evenness profiles, and (3) always lead to measures that satisfy the essential principle of transfers, which then implies the evenness of the vector $\mathbf{p} = \lambda \bar{\mathbf{p}} + (1 - \lambda) \mathbf{p}^0$ to be an increasing function of λ .

Our unified approach is to replace the distance in Eq. 2 by a divergence measure in terms of species richness and abundance-based diversity ($q > 0$). Unlike a distance metric, a divergence measure does not require symmetry nor the triangle inequality. Here, we consider the q th-power of each species' relative abundance and define the q th-power vector $\mathbf{p}^q = (p_1^q, p_2^q, \dots, p_S^q)$. Let $\bar{\mathbf{p}}^q = ((1/S)^q, \dots, (1/S)^q)$ be the corresponding q th-power mean vector. We define the q th order divergence, $q > 0$, between the two vectors \mathbf{p}^q and $\bar{\mathbf{p}}^q$ for a proper function h as

$$\Delta_h(\mathbf{p}^q, \bar{\mathbf{p}}^q) = h(p_1^q, p_2^q, \dots, p_S^q) - h((1/S)^q, (1/S)^q, \dots, (1/S)^q). \quad (3a)$$

Any legitimate divergence measure should satisfy two conditions: (1) the divergence must be strictly Schur-convex with respect to \mathbf{p} . This condition implies that the divergence attains a minimum of 0 if and only if $\mathbf{p} = \bar{\mathbf{p}}$, that is, if and only if all abundances are even; and (2) the divergence approaches a maximum of 1 if and only if $\mathbf{p} = \mathbf{p}^0$. Then for any $q > 0$ our unified class of unevenness measures is expressed as a normalized divergence measure; that is, $\Delta_h(\mathbf{p}^q, \bar{\mathbf{p}}^q) / \Delta_h(\mathbf{p}^0, \bar{\mathbf{p}}^q)$, where the denominator $\Delta_h(\mathbf{p}^0, \bar{\mathbf{p}}^q)$ is a normalizing constant such that all our (un)evenness values are between 0 and 1. The corresponding evenness measure is

$${}^q E_h(\mathbf{p}) = 1 - \frac{\Delta_h(\mathbf{p}^q, \bar{\mathbf{p}}^q)}{\Delta_h(\mathbf{p}^0, \bar{\mathbf{p}}^q)}, q > 0. \quad (3b)$$

We propose quantifying evenness by using a continuous profile that depicts ${}^q E_h(\mathbf{p})$ as a function of diversity order $q > 0$. This profile-based evenness ordering is a partial ordering. We mainly focus on the interval $0 < q \leq 2$ because for large values of q , dominant species are increasingly overweighted. Therefore, the calculation of parametric evenness with values of $q > 2$ is recommended only if we are interested in the evenness of the abundances of dominant species.

We consider five classes of divergence measures. Below we only present the first two divergences because the resulting evenness measures can be linked to beta diversity and (dis)similarity indices. We first consider the function $h_1(x_1^q, x_2^q, \dots, x_S^q) = \sum_{i=1}^S x_i^q / (q - 1)$ in Eq. 3a for $q > 0$, $q \neq 1$. Then the class of divergence measures becomes

$$\begin{aligned} \Delta_1(\mathbf{p}^q, \bar{\mathbf{p}}^q) &= \frac{1}{q-1} \left(\sum_{i=1}^S p_i^q - S^{1-q} \right) \\ &= \frac{1}{q-1} \left[({}^q D)^{1-q} - S^{1-q} \right] \geq 0. \end{aligned} \quad (4a)$$

When q tends to 1, this divergence tends to the Kullback–Leibler divergence between $\mathbf{p} = (p_1, p_2, \dots, p_S)$ and the mean vector $\bar{\mathbf{p}} = (1/S, 1/S, \dots, 1/S)$; see Appendix S1: Section S2. It follows from Eq. 3b that the evenness measure of a general order q is

$${}^q E_1(\mathbf{p}) = \frac{1 - \sum_{i=1}^S p_i^q}{1 - S^{1-q}} = \frac{1 - ({}^q D)^{1-q}}{1 - S^{1-q}}, q > 0. \quad (4b)$$

This class of evenness measures of order q was proposed by Mendes et al. (2008). For q tending to 1, it reduces to Pielou's J' (Pielou 1966). For $q = 2$, it reduces to the Smith and Wilson (1996) measure, which is a normalized form of the steepest slope of a species accumulation curve (Olszewski 2004). In Appendix S1: Section S2, we prove that our first class of unevenness measures of any order q represents the magnitude or absolute value of the normalized slope connecting two points with diversity orders 0 and q in the Tsallis entropy profile.

Consider another function $h_2(x_1^q, x_2^q, \dots, x_S^q) = 1 / [(1 - q) \sum_{i=1}^S x_i^q]$, $q > 0$, $q \neq 1$ in Eq. 3a. Then the divergence measure becomes

$$\begin{aligned} \Delta_2(\mathbf{p}^q, \bar{\mathbf{p}}^q) &= \frac{1}{1-q} \left(\frac{1}{\sum_{i=1}^S p_i^q} - S^{q-1} \right) \\ &= \frac{1}{1-q} \left[({}^q D)^{q-1} - S^{q-1} \right] \geq 0. \end{aligned} \quad (5a)$$

When q tends to 1, this divergence tends to the Kullback–Leibler divergence between $\mathbf{p} = (p_1, p_2, \dots, p_S)$ and the mean vector $\bar{\mathbf{p}} = (1/S, 1/S, \dots, 1/S)$. It follows from Eq. 3b that the evenness measure of a general order q is

$${}^q E_2(\mathbf{p}) = \frac{1 - 1 / \sum_{i=1}^S p_i^q}{1 - S^{q-1}} = \frac{1 - ({}^q D)^{q-1}}{1 - S^{q-1}}, q > 0. \quad (5b)$$

To our knowledge, this evenness measure of general order q is new. For q tending to 1, it reduces to Pielou's J' ; for $q = 2$, it reduces to the measure proposed by Kvålseth (1991).

The other three classes of divergence measures and their corresponding evenness measures are listed in

Table 1, where the Minkowski family of distances of order $\alpha > 0$ considered by Kvålseth (2015) is also included. The resulting evenness measures include many commonly used evenness metrics. We can also demonstrate that the third and fifth classes of evenness measures are, respectively, the normalized absolute slopes of Hill-number and Rényi-entropy profiles.

PROPERTIES

All our proposed five classes of evenness measures (Table 1) satisfy the basic required properties stated

previously. It is readily seen that our proposed measures satisfy Requirements 1a, 1b, and 3b (i.e., properties of Hill numbers) because our measures are functions of Hill numbers. All the proposed evenness measures attain the fixed maximum value of unity when $\mathbf{p} = \bar{\mathbf{p}}$; all measures approach the fixed minimum value of 0 when $\mathbf{p} = \mathbf{p}^0$, fulfilling Requirement 3a. Note that when diversity ${}^qD > 1$ and almost fixed as S increases, the five classes of evenness measures are monotonically decreasing function of S . Consequently, when an additional vanishingly rare species is added so that diversity remains almost the same, all the five measures decrease,

TABLE 1. Five proposed classes (Classes 1–5) of divergence measures of order $q > 0$ and the corresponding evenness measures in $[0, 1]$ and their special cases.

Class of divergence/distance	Evenness measure	References and remarks
(1) $\Delta_1(\mathbf{p}^q, \bar{\mathbf{p}}^q)$ $= \frac{1}{q-1} \left(\sum_{i=1}^S p_i^q - S^{1-q} \right)$ $= \frac{1}{q-1} \left[({}^qD)^{1-q} - S^{1-q} \right] \geq 0$	${}^qE_1(\mathbf{p}) = \frac{1 - \sum_{i=1}^S p_i^q}{1 - S^{1-q}}$ $= \frac{1 - ({}^qD)^{1-q}}{1 - S^{1-q}}$	General q : Mendes et al. (2008) $q = 1$: Pielou (1966) $q = 2$: Smith and Wilson (1996) Unevenness: normalized slope of Tsallis-entropy profile
(2) $\Delta_2(\mathbf{p}^q, \bar{\mathbf{p}}^q)$ $= \frac{1}{1-q} \left(\frac{1}{\sum_{i=1}^S p_i^q} - S^{q-1} \right)$ $= \frac{1}{1-q} \left[({}^qD)^{q-1} - S^{q-1} \right] \geq 0$	${}^qE_2(\mathbf{p}) = \frac{1 - 1/\sum_{i=1}^S p_i^q}{1 - S^{q-1}}$ $= \frac{1 - ({}^qD)^{q-1}}{1 - S^{q-1}}$	General q : New $q = 1$: Pielou (1966) $q = 2$: Kvålseth (1991)
(3) $\Delta_3(\mathbf{p}^q, \bar{\mathbf{p}}^q)$ $= S - \left(\sum_{i=1}^S p_i^q \right)^{1/(1-q)}$ $= S - {}^qD \geq 0$	${}^qE_3(\mathbf{p}) = \frac{\left(\sum_{i=1}^S p_i^q \right)^{1/(1-q)} - 1}{S - 1}$ $= \frac{{}^qD - 1}{S - 1}$	General q : Jost (2010) $q = 1$: Heip (1974) $q = 2$: Kvålseth (1991) Unevenness: normalized slope of Hill-number profile
(4) $\Delta_4(\mathbf{p}^q, \bar{\mathbf{p}}^q)$ $= \left(\sum_{i=1}^S p_i^q \right)^{1/(q-1)} - (1/S)$ $= (1/{}^qD) - (1/S) \geq 0$	${}^qE_4(\mathbf{p}) = \frac{1 - \left(\sum_{i=1}^S p_i^q \right)^{1/(q-1)}}{1 - (1/S)}$ $= \frac{1 - (1/{}^qD)}{1 - (1/S)}$	General q : New $q = 1$: new $q = 2$: Smith and Wilson (1996)
(5) $\Delta_5(\mathbf{p}^q, \bar{\mathbf{p}}^q)$ $= -\log \left(\sum_{i=1}^S p_i^q \right)^{1/(1-q)} + \log S$ $= \log \frac{S}{{}^qD} \geq 0$	${}^qE_5(\mathbf{p}) = \frac{\log \left(\sum_{i=1}^S p_i^q \right)^{1/(1-q)}}{\log S}$ $= \frac{\log {}^qD}{\log S}$	General q : Jost (2010) $q = 1$: Pielou (1966) $q = 2$: Smith and Wilson (1996) Unevenness: Normalized slope of Rényi-entropy profile
(6) Minkowski distances $d_\alpha(\mathbf{p}, \bar{\mathbf{p}})$ $= \left(\sum_{i=1}^S p_i - (1/S) ^\alpha \right)^{1/\alpha}$	${}^\alpha E_6(\mathbf{p}) = 1 - \left[\frac{\sum_{i=1}^S p_i - (1/S) ^\alpha}{[1 - (1/S)]^\alpha + (S-1)S^{-\alpha}} \right]^{1/\alpha}$	General q : Kvålseth (2015) $q = 1$: Bulla (1994) $q = 2$: F. M. Williams (unpublished data)

Notes: Class 6 represents the Minkowski family of distances $d_\alpha(\mathbf{p}, \bar{\mathbf{p}})$ of order α considered by Kvålseth (2015). All slopes refer to the magnitude or absolute value of the slope connecting two points with diversity orders 0 and q in a specified profile.

fulfilling Requirement 2. In the special case of ${}^qD = 1$ (i.e., $\mathbf{p} = \mathbf{p}^0$), all evenness measures approach the absolute minimum value of 0 for any value of S , meaning that evenness does not increase and thus that Requirement 2 is also fulfilled.

Requirement 1a implies that the proposed five classes of evenness measure also possess the following additional properties:

- P1: Evenness decreases when the abundance of the rarest species is slightly reduced. This corresponds to Routledge's (1983) first requirement (R1).
- P2: Lorenz ordering is preserved when *species richness is fixed* across assemblages. That is, when two assemblages have the same number of species, if the Lorenz curve of Assemblage I is nowhere below the curve of Assemblage II, then the evenness of Assemblage I based on our measures must not be lower than that of Assemblage II. See *Discussion* for comparison of our framework with the Lorenz-ordering approach.
- P3: If a relative abundance vector is expressed as a convex combination of $\bar{\mathbf{p}}$ and \mathbf{p}^0 , that is, $\mathbf{p}^\lambda = \lambda\bar{\mathbf{p}} + (1-\lambda)\mathbf{p}^0$, then the evenness of \mathbf{p}^λ is a monotonically increasing function of λ . In other words, Kvålseth's (2015) stringent requirement (i.e., evenness for \mathbf{p}^λ must be λ) is relaxed to be an increasing function of λ . For example, the evenness of \mathbf{p}^λ of the first class of measures in Table 1 turns out to be $\lambda(2-\lambda)$ for $q = 2$. See Appendix S1: Section S3 for derivation and the corresponding formula for Pielou's J' .

In addition, our proposed five classes of evenness measures satisfy the following property:

- P4: Replication monotonicity. Assume an assemblage consists of K replicates of the original assemblage (referred to as a K -replicated assemblage). Each replicate has the same number of species and the same set of species abundances as the original one, but with completely different, unique species in each replicate. Then the evenness of the K -replicated assemblage is an increasing function of K if the original assemblage is not completely even; replication invariance is only valid for a completely even case.

This monotonicity property represents a drastic difference between our theory and most previous approaches in which replication invariance is an essential requirement (Hill 1973, Taillie 1979, Smith and Wilson 1996, Gosselin 2001, 2006, Tuomisto 2012). For examples, our replication monotonicity implies that the evenness values for three hypothetical assemblages with abundances (1, 99), (1, 1, 99, 99) and (1, 1, 1, 99, 99, 99) has the following rank: (1, 99) < (1, 1, 99, 99) < (1, 1, 1, 99, 99, 99), whereas the replication invariance approach would

conclude that the three assemblages have the same degrees of evenness.

The mathematical proof of replication monotonicity for our measures is shown in Appendix S1: Section S3. Here, we provide an intuitive justification: Consider a maximally uneven two-species assemblage in which one species has a vanishingly low abundance, resulting in an evenness near the minimum value of 0. When the assemblage is replicated, if the replication invariance is required, then the evenness of the resulting four-species assemblage must also be near 0. However, note that there are two very abundant species in this four-species assemblage; its evenness should be greater than 0 to some extent because the species relative abundance vector of the four-species assemblage is more even than an assemblage with one super-dominant species and three vanishingly rare species. This example also reveals, under the requirement of replication invariance, that the minimum value an evenness measure can take is necessarily dependent on species richness, violating Requirement 3a, which requires an absolute fixed minimum value for any species richness.

LINKING UNEVENNESS AND BETA/DISSIMILARITY FOR MULTIPLE ASSEMBLAGES

Assume that there are $N \geq 2$ assemblages, with S species indexed by 1, 2, ..., S in the *pooled* assemblage. Let $\mathbf{Z} = [z_{ik}] \geq 0$ be an $S \times N$ abundance/composition matrix:

$$\mathbf{Z} = \begin{bmatrix} z_{11} & z_{12} & \cdots & z_{1N} \\ z_{21} & \cdot & \cdots & \cdot \\ \cdot & \cdot & \cdots & \cdot \\ z_{S1} & z_{S2} & \cdots & z_{SN} \end{bmatrix}. \quad (6a)$$

We refer to z_{ik} as the species abundance of the i th species in the k th assemblage. The abundance z_{ik} can be any measure of species importance such as a species-incidence (presence-absence) record, species absolute abundance (i.e., the number of individuals), within-assemblage relative abundance, density, biomass, spatial coverage of corals, or basal area of plants. Let $z_{i+} = \sum_{k=1}^N z_{ik}$ be the total abundance of the i th species in the pooled assemblage, and $\bar{z}_{i+} = z_{i+}/N$ be the average abundance of the i th species per assemblage. Also, define $z_{++} = \sum_{k=1}^N \sum_{i=1}^S z_{ik}$ as the total abundance/size of the matrix \mathbf{Z} .

The assessment of beta diversity and (dis)similarity in species abundance distributions among a set of assemblages in a geographical area, over a time period, or along an environmental gradient subject is an active research focus in ecology. Chao and Chiu (2016) defined beta diversity as a ratio of gamma and alpha; that is, ${}^qD_\beta = {}^qD_\gamma / {}^qD_\alpha$, where ${}^qD_\gamma = \{\sum_{i=1}^S (z_{i+}/z_{++})^q\}^{1/(1-q)}$ denotes the gamma diversity (i.e., the effective number of species in the pooled assemblage), and ${}^qD_\alpha = (1/N) \{\sum_{i=1}^S \sum_{k=1}^N (z_{ik}/z_{++})^q\}^{1/(1-q)}$ denotes the alpha diversity

(i.e., the effective number of species per assemblage); see their paper for interpretations and the sense of “effective.” They further proved for any diversity order $q \geq 0$, that two major approaches to beta diversity (variance framework and diversity decomposition) lead to the same classes of (dis)similarity measures including the abundance-based Jaccard- and Sørensen-type nonoverlap or dissimilarity measures.

Note that the conventional evenness measures, as discussed in previous sections, are evaluated among S species relative abundances in a single assemblage. For multiple assemblages, however, we compute each single species compositional (un)evenness among the N assemblages. That is, for species i , we evaluate evenness for the N -element vector $\mathbf{p}^{(i)} = \{z_{i1}/z_{i+}, z_{i2}/z_{i+}, \dots, z_{iN}/z_{i+}\}$, that is, the species relative abundances among the N assemblages. For example, the evenness measures derived in Eqs. 4b and 5b, respectively, become:

$$\begin{aligned} {}^q E_1(\mathbf{p}^{(i)}) &= \frac{1 - \sum_{k=1}^N (z_{ik}/z_{i+})^q}{1 - N^{1-q}}, \\ {}^q E_2(\mathbf{p}^{(i)}) &= \frac{1 - 1/(\sum_{k=1}^N (z_{ik}/z_{i+})^q)}{1 - N^{q-1}}. \end{aligned} \quad (6b)$$

In the following we show how to link the first class of unevenness measures to the Jaccard-type dissimilarity measures, thus allowing the contribution of each species to be explicitly evaluated. The derivations for the corresponding link between the second class of evenness measures and the Sørensen-type dissimilarity are parallel and given in Appendix S1: Section S4.

Linking species compositional unevenness to Jaccard-type dissimilarity measures

To establish the link, species are assumed to have different impacts or “weights” based on their abundances. Let the q th order weight of species i be ${}^q w_{1i} = z_{i+}^q / \sum_{j=1}^S z_{j+}^q$, $i = 1, 2, \dots, S$. Then the weighted average of individual species compositional unevenness values based on the first class of unevenness measure $1 - {}^q E_1(\mathbf{p}^{(i)})$ leads to the abundance-based Jaccard-type dissimilarity measure $1 - U_{qN}$ (Chao and Chiu 2016: Eq. 12a). That is, we have

$$\begin{aligned} \sum_{i=1}^S ({}^q w_{1i}) [1 - {}^q E_1(\mathbf{p}^{(i)})] \\ = \sum_{i=1}^S \frac{z_{i+}^q}{\sum_{j=1}^S z_{j+}^q} \frac{\left[\sum_{k=1}^N (z_{ik}/z_{i+})^q - N^{1-q} \right]}{1 - N^{1-q}} \end{aligned} \quad (7a)$$

$$= \frac{\sum_{i=1}^S \sum_{k=1}^N (z_{ik}^q - \bar{z}_{i+}^q)}{(N^q - N) \sum_{j=1}^S \bar{z}_{j+}^q} = 1 - U_{qN}. \quad (7b)$$

Eqs. 7a, b link the first class of unevenness measure to the Jaccard-type dissimilarity measures for any $q > 0$,

because the unevenness measures are only meaningful for $q > 0$. However, the Jaccard-type dissimilarity measure $1 - U_{qN}$ in Eq. 7b is actually also valid for $q = 0$ (i.e., only species presence/absence data are counted). Chao and Chiu (2016) showed that the zero-order measure $1 - U_{0N}$ reduces to the classic N -assemblage richness-based Jaccard dissimilarity index. Thus, this class of measures $1 - U_{qN}$ generalizes the classic Jaccard index to incorporate species abundances (if $q > 0$). When the data matrix $[z_{ik}]$ represents within-assemblage relative abundances, this measure for $q = 1$ and 2 reduces, respectively, to the traditional N -assemblage entropy-based heterogeneity (Horn 1966) and regional species-dissimilarity (Chiu et al. 2014) measures.

This class of dissimilarity measures for *all* $q \geq 0$ is a complementarity measure that quantifies the effective proportion of nonshared species in the pooled assemblage (Chao and Chiu 2016:922). They also showed that the Jaccard-type dissimilarity measure of order q is a monotonic transformation of multiplicative beta diversity ${}^q D_\beta$; that is, $1 - U_{qN} = [({}^q D_\beta)^{q-1} - 1]/(N^{q-1} - 1)$ for $q \neq 1$, and $1 - U_{1N} = \log({}^1 D_\beta)/\log N$. Therefore, our approach also links beta diversity and the first class of unevenness measures:

$${}^q D_\beta = \left(1 + (N^{q-1} - 1) \sum_{i=1}^S ({}^q w_{1i}) [1 - {}^q E_1(\mathbf{p}^{(i)})] \right)^{1/(q-1)}, \quad q > 0, q \neq 1.$$

Note that when q tends to 1, the weight becomes the proportion of a species' total abundance; that is, ${}^1 w_{1i} = z_{i+}/\sum_{j=1}^S z_{j+} = z_{i+}/z_{++}$; the unevenness measure $1 - {}^q E_1(\mathbf{p}^{(i)})$ tends to Pielou's (1966) unevenness measure based on $\mathbf{p}^{(i)} = \{z_{i1}/z_{i+}, z_{i2}/z_{i+}, \dots, z_{iN}/z_{i+}\}$. This special case was first discussed in Ricotta (2017), who established a bridge between Pielou's measure and the Horn (1966) heterogeneity index (i.e., $1 - U_{1N}$). Specifically, we have

$$\begin{aligned} \lim_{q \rightarrow 1} \sum_{i=1}^S ({}^q w_{1i}) [1 - {}^q E_1(\mathbf{p}^{(i)})] \\ = \sum_{i=1}^S \frac{z_{i+}}{z_{++}} \left[1 - \frac{\sum_{k=1}^N (-z_{ik}/z_{i+}) \log(z_{ik}/z_{i+})}{\log N} \right] \\ = \frac{1}{z_{++} \log N} \sum_{i=1}^S \sum_{k=1}^N z_{ik} \log \frac{z_{ik}}{z_{i+}} = 1 - U_{1N}. \end{aligned} \quad (7c)$$

This leads to

$${}^1 D_\beta = \exp \left((\log N) \sum_{i=1}^S ({}^1 w_{1i}) [1 - {}^1 E_1(\mathbf{p}^{(i)})] \right). \quad (7d)$$

Based on Eqs. 7a–c, the contribution of each species to the Jaccard-type dissimilarity measure can be disentangled and quantified. For $q > 0$, the contribution of

species i is simply $(^q w_{1i})[1 - ^q E_1(\mathbf{p}^{(i)})]$, that is, the product of the weight and the first class of unevenness measures for $\mathbf{p}^{(i)}$. Note the contribution of any species is 0 if $^q E_1(\mathbf{p}^{(i)}) = 1$; species i has an even abundance among the N assemblages, whereas the contribution is positive if $^q E_1(\mathbf{p}^{(i)}) < 1$; that is, the abundances of species i are not evenly distributed among the N assemblages. For $q = 1$, the contribution of species i reduces to the product of the species weight and Pielou's unevenness measure based on $\mathbf{p}^{(i)}$, and it can be simplified to $(z_{++} \log N)^{-1} \sum_{k=1}^N z_{ik} \log(z_{ik}/\bar{z}_{i+})$.

For $q = 0$, if we define $0^0 \equiv 0$ so that any absent species does not contribute to the computation and define Y_i as the number of assemblages in which species i is detected, then the contribution of species i can be obtained from Eq. 7b and expressed as

$$\frac{\sum_{k=1}^N (z_{ik}^0 - \bar{z}_{i+}^0)}{(N^q - N) \sum_{j=1}^S \bar{z}_{j+}^0} = \frac{1}{S} \frac{(N - Y_i)}{(N - 1)},$$

which is positive if species i is not detected in at least one of the N assemblages, and is 0 if species i is detected in all assemblages.

PHYLOGENETIC BETA/DISSIMILARITY VIA UNEVENNESS MEASURES

Our link between species compositional unevenness measures and taxonomic dissimilarity indices can be readily generalized to a phylogenetic version. Here, we only highlight the major extension for the framework. Assume that there are N assemblages and S species (as tip nodes) connected by a rooted ultrametric phylogenetic tree. We assume all phylogenetic diversity measures are computed from a given fixed time reference point that is ancestral to all taxa considered in the study. The age of the root is typically chosen as a reference point.

For a given reference point, assume that the tree depth is T and there are B branches/nodes in the pooled tree, $B \geq S$. The major difference between the taxonomic and phylogenetic approaches lies in the expansion of a set of S species to a set of B nodes/branches. Let L_i denote the length of the i th branch. We extend the definition of z_{ik} in the taxonomic case to include any node i by defining z_{ik} (node/branch abundance) for $i = 1, 2, \dots, B$ as the total abundance descending from node/branch i . See Appendix S2: Fig. S1 for a simple illustrative example ($N = 2$, $S = 5$, $B = 8$).

Chiu et al. (2014) extended the taxonomic Jaccard- and Sørensen-type dissimilarity measures to their phylogenetic versions. We can similarly link node compositional unevenness to the two types of phylogenetic dissimilarity indices. Here, a *node compositional unevenness* measure is calculated for single-node relative abundances among the N assemblages. That is, for the i th

node, $i = 1, 2, \dots, B$, the node compositional unevenness is quantified as a normalized divergence between the node relative abundance vector $\mathbf{a}^{(i)} = \{z_{i1}/z_{i+}, z_{i2}/z_{i+}, \dots, z_{iN}/z_{i+}\}$ and the mean vector $\bar{\mathbf{p}}(N) = (1/N, 1/N, \dots, 1/N)$, where z_{i+} denotes the total abundance of the i th node. Because the extension and derivation are generally parallel, all details are provided in Appendix S2.

A WORKED EXAMPLE

The data considered here were collected by Caccianiga et al. (2006) and analyzed in Ricotta et al. (2016, 2018). The original data set, which can be found in Ricotta et al. (2016: Appendix S2), contains abundances for a total of 45 Alpine species sampled in 59 vegetation plots each of approximately 25 m² along a primary succession on the Rutor glacier (northern Italy). Based on the age of the glacial deposits, plots were assigned to three successional stages: early succession (17 plots), midsuccession (32 plots), and late succession (10 plots); see the mentioned papers for details.

We first compute species relative abundances within each plot, and then average these relative abundances across the plots within each stage. This entails that all plots have equal weights in obtaining the species relative abundance data. Our analyses were based on the three sets of species relative abundances given in Fig. 1. The phylogenetic tree of the 45 species (Fig. 1) was taken from Ricotta et al. (2015, their Appendix A). The age of the root for these 45 species is approximately 147 million years (Myr).

In Fig. 2, we plot the evenness profiles as a function of order q ($0 < q \leq 2$) based on the six classes of measures in Table 1 (denoted as E_1 – E_6 in Fig. 2) for the three successional stages. Detailed numerical results are provided in Appendix S3: Table S1. In Fig. 3, we show the contribution of each species to the Jaccard-type taxonomic dissimilarity index for three diversity orders ($q = 0, 1$, and 2). The species contributions to the Sørensen-type index (shown in Appendix S3: Fig. S1) are nearly proportional to those of the Jaccard-type index (i.e., the pattern is the same notwithstanding some differences in magnitude). In Fig. 4, we present the contribution of each species/node in the phylogenetic tree to the Jaccard-type phylogenetic dissimilarity; here, the corresponding branch length is taken into account in the contribution. As with taxonomic dissimilarity, the species-contribution pattern for the Sørensen-type phylogenetic dissimilarity is nearly identical to that for the Jaccard-type phylogenetic index; see Appendix S3: Fig. S2. All data used in this example and the R code “Evenness” for computing our proposed evenness indices and making all relevant plots are provided (see Data Availability).

In good agreement with the results of Ricotta et al. (2016, 2018), a general tendency toward an increase in evenness values from the early successional stages to the

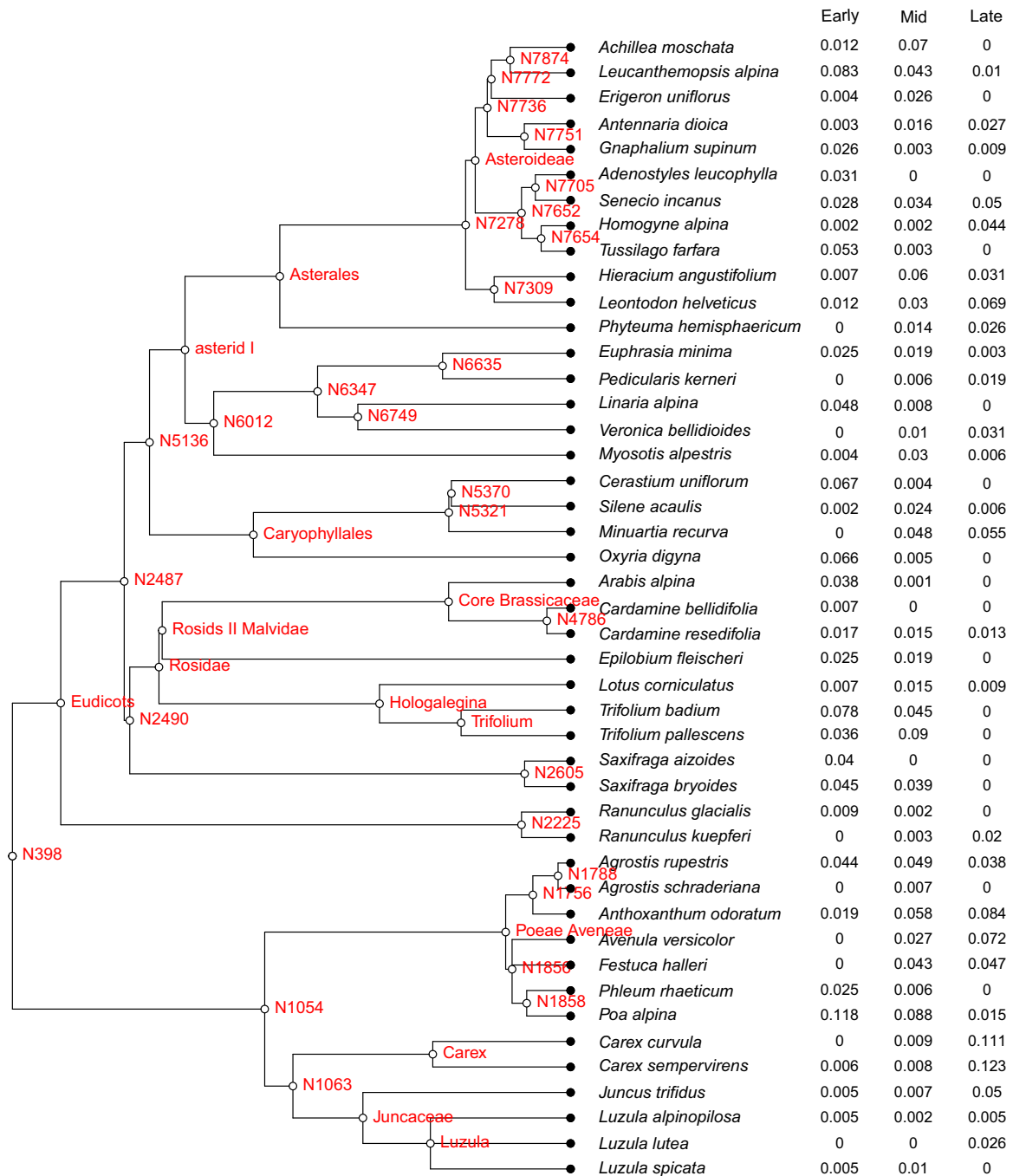


FIG. 1. The phylogenetic tree of 45 Alpine species and the species relative abundances in three succession stages: early, mid, and late (Caccianiga et al. 2006, Ricotta et al. 2016, 2018). A zero relative abundance means that the species was not recorded in that stage. The age of the root is approximately 147 Myr.

late-successional stages is observed. All evenness profiles in Fig. 2 show that the early-successional and mid-successional stages have approximately the same degree of evenness among species relative abundances. For $q = 1$, with the exception of E_4 , which shows the three stages have almost the same levels of evenness, each of the other five measures reveal that the species relative

abundances are more even in the late-successional stage than in any of the other two stages. For dominant species ($q = 2$), E_2 , E_3 , and E_5 also reveal that the late-successional stage is more even, whereas the other three measures show that the three stages have close evenness levels. The lower evenness values in the initial successional stages are most likely associated with the random

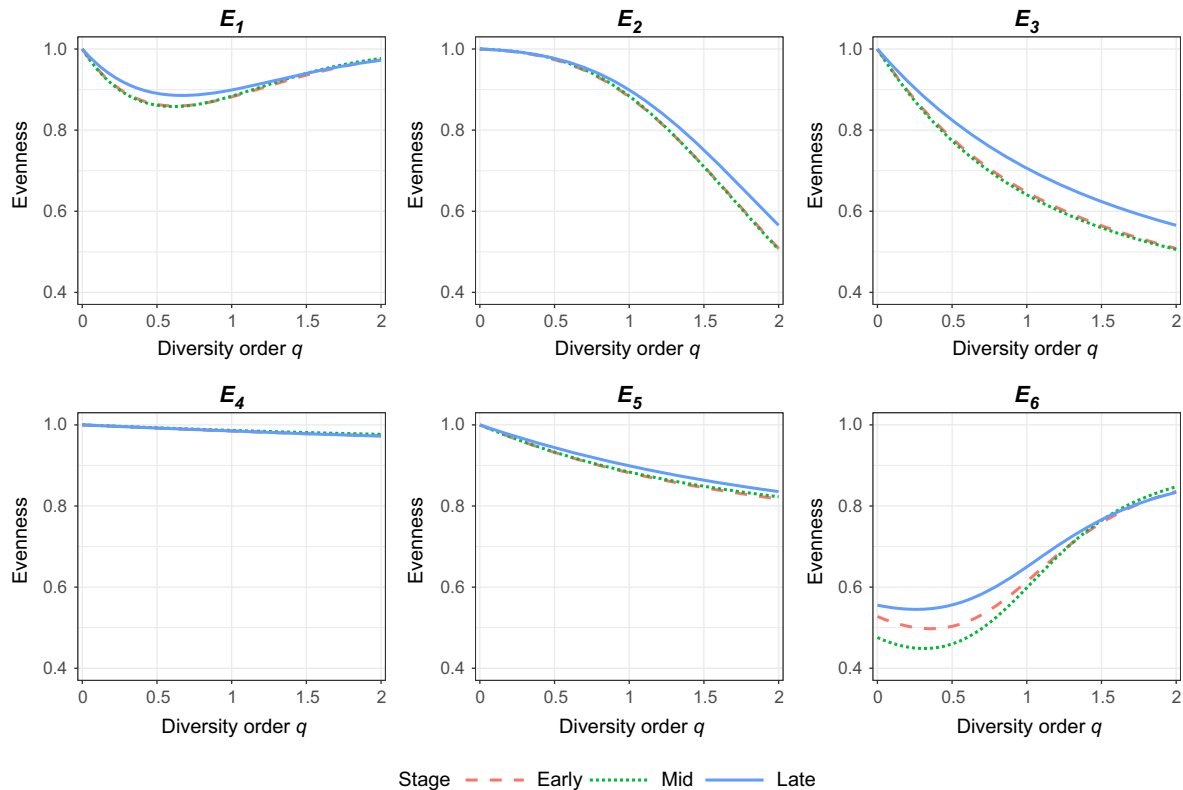


FIG. 2. Evenness profiles as a function of order q ($0 < q \leq 2$) based on the six classes of evenness measures in Table 1 (E_1 – E_6 in the six panels) for 45 Alpine species in three successional stages: early (red), mid (green), and late (blue).

dispersal mechanisms that drive the colonization of the glacial deposits by the first pioneer species. The increasing structural uniformity of vegetation over time (Caccianiga et al. 2006) will then lead to an increase in evenness, especially in the late-successional stage.

This trend is accompanied by a taxonomic and phylogenetic shift from early-successional ruderal forbs, such as *Cerastium uniflorum*, *Oxyria digyna*, or *Tussilago farfara*, to late-successional stress-tolerant graminoids, such as *Carex curvula*, *Carex sempervirens*, or *Festuca halleri*, which are among the species that contribute most to the taxonomic differences among successional stages in Fig. 3 (Caccianiga et al. 2006, Ricotta et al. 2018). The species contributions to the Jaccard-type taxonomic dissimilarity index vary significantly as a function of the parameter q . For $q = 0$, the highest contributions to taxonomic dissimilarity are provided by those species that are exclusive to a single successional stage, such as *Adenostyles leucophylla* or *Luzula lutea*, whereas for $q = 2$, attention is shifted towards the dominant species, such as *C. curvula*, *C. sempervirens*, or *Poa alpina* (Fig. 3). From our theory, the contribution of each species for $q > 0$ is the product of its weight (proportion of species total abundance for $q = 1$ or squared total abundance for $q = 2$) and the unevenness of its abundances among the three stages. For each node of a phylogenetic

tree, the contribution should be additionally multiplied by its branch length.

C. sempervirens and *C. curvula* are the two most abundant species in the late stage, but they are very rare in the early and midstages. Thus, the unevenness for each of the two species among the three stages is high and the weight (proportion of species total abundance) is also large, leading to a relatively large contribution of each species to the taxonomic dissimilarity for $q = 1$ and $q = 2$. Also, the ubiquitous stress-tolerant graminoid *P. alpina* is the most abundant species in the early stage and the second most abundant in the mid-stage, but is very rare in the late stage (Caccianiga et al. 2006). Similar arguments lead to its relatively large contribution especially for $q = 2$. For $q = 1$, several species with intermediate abundances also contribute to some extent because of the relatively high unevenness in abundances among the three stages.

Likewise, looking at Fig. 4, we observe that for $q = 0$, the highest contributions to phylogenetic dissimilarity are mainly associated with single species (i.e., the tip nodes of the phylogenetic tree) because most of the descendants of internal nodes were found in all three stages except for node N2605 (associated to the genus *Saxifraga*; see Fig. 1) which was only found in the early and midstages. This is also why for $q = 0$ only the

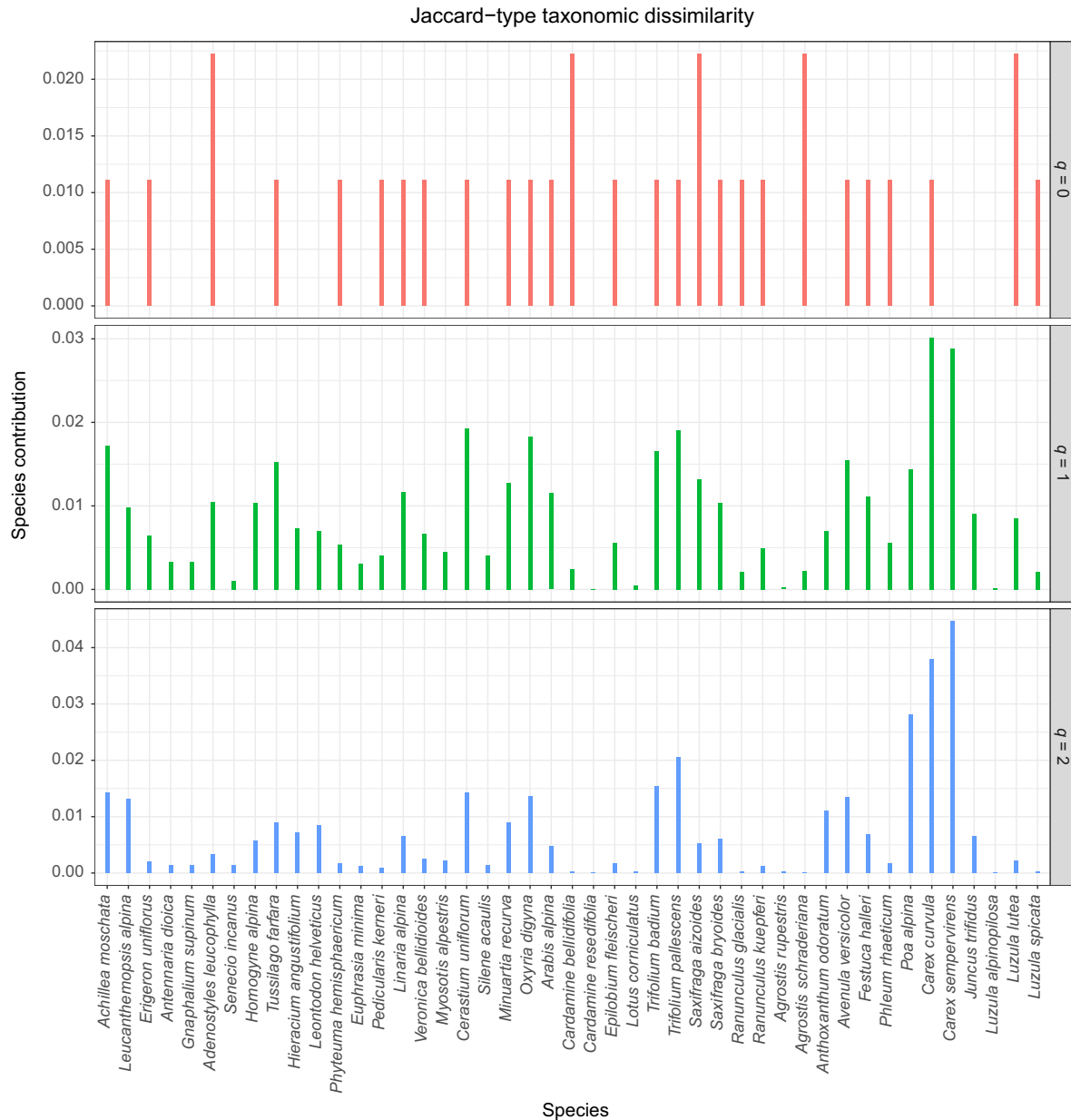


FIG. 3. The contribution of each species to the taxonomic Jaccard-type dissimilarity index. See Fig. 1 for species identities and relative abundances. The contribution pattern for the Sørensen-type dissimilarity index (as shown in Appendix S3: Fig. S1) is nearly identical except for the differences in magnitude.

internal node N2605 contributes a high portion of phylogenetic dissimilarity.

However, when the value of q is increased, the highest contributions to phylogenetic dissimilarity are increasingly provided by more internal nodes, meaning that for higher values of q , attention is progressively shifted from single species to species clades. This seems to be a very interesting outcome of this class of phylogenetic dissimilarity measures as changing the value of q allows a summarization of phylogenetic dissimilarity

at deeper evolutionary times. When $q = 2$, the species that lead to highest unevenness and largest weights are the two late-stage-dominant species *C. sempervirens* and *C. curvula* along with the more ubiquitous *P. alpina*, which is dominant in the early- and midsuccessional stages. These three graminoid species all descended from node N1054 but were found in different stages. This explains why the only dominant contribution to the phylogenetic dissimilarity of $q = 2$ comes from node N1054.

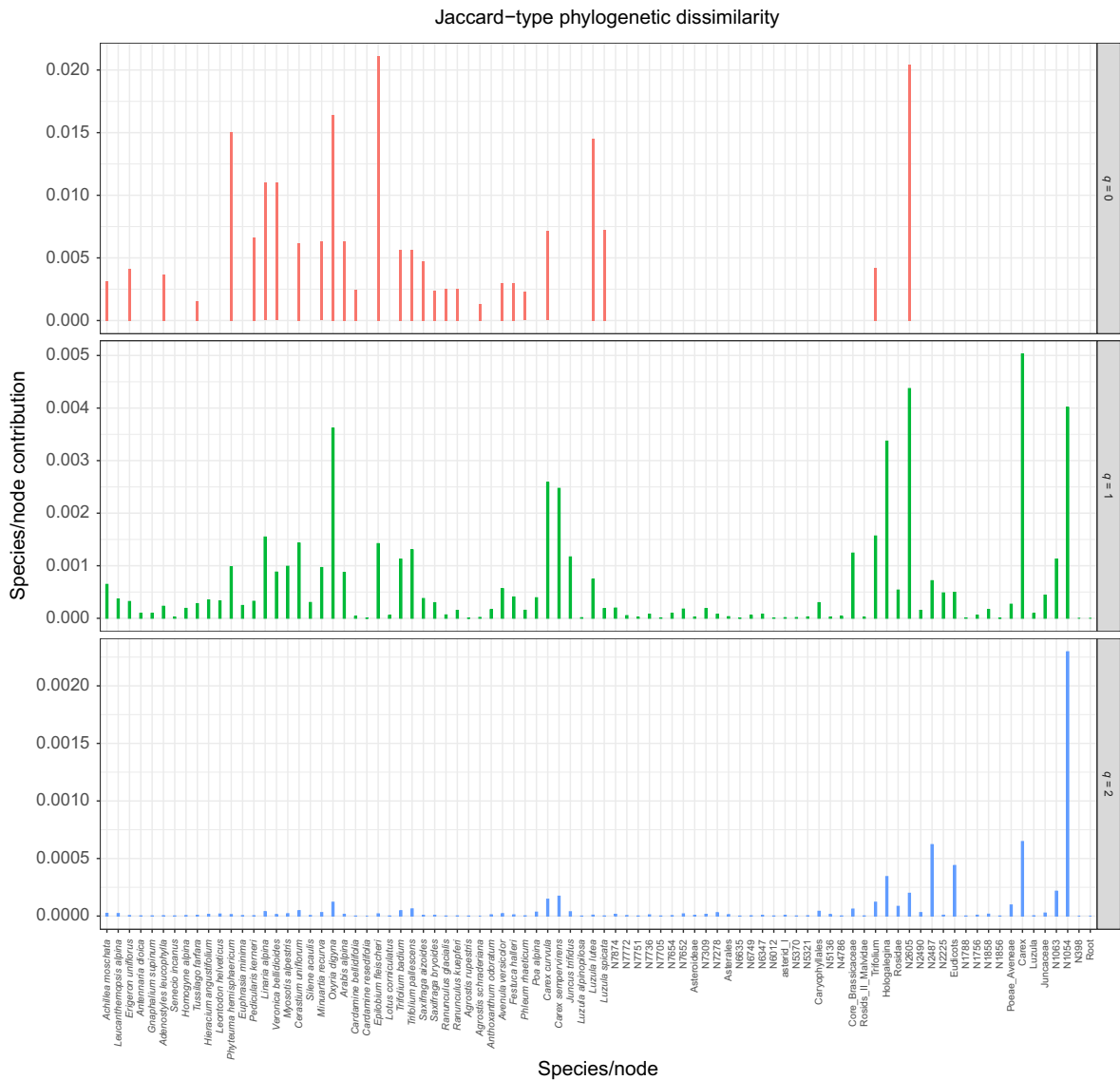


FIG. 4. The contribution of each species/node to the phylogenetic Jaccard-type phylogenetic dissimilarity index. See Fig. 1 for species relative abundances, species/node identities and the phylogenetic tree. The contribution pattern for the Sørensen-type dissimilarity index (shown in Appendix S3; Fig. S2) is nearly identical except for the differences in magnitude.

DISCUSSION

We have presented some basic requirements for an evenness measure (Requirements 1a, 1b, 2, 3a, and 3b) and developed five classes of evenness measures (Table 1). All our measures are functions of species richness and diversity of order $q > 0$ and possess the required properties. Some additional properties (Properties P1–P4) of our measures are also derived. We have proposed the use of evenness profiles (Fig. 2) to quantify evenness in a single assemblage and compare them across multiple assemblages. The Jaccard- and Sørensen-type dissimilarity among assemblages can be expressed as weighted averages of individual species’ compositional unevenness

values (Eqs. 7a–c and Appendix S1: Section S4). The corresponding phylogenetic version is presented in Appendix S2. The contribution of each species/node to the Jaccard- and Sørensen-type taxonomic and phylogenetic dissimilarity measures can be quantified and displayed; see Figs. 3, 4.

Here, we discuss our requirements/properties in more detail and compare them with some other properties that were previously proposed by other researchers. The first requirement listed in the Smith and Wilson (1996) consumer’s guide to evenness indices is that an evenness measure should be “independent” of species richness. This concept of “independence” was interpreted differently by several authors. Smith and Wilson (1996)

believed that the independence could be verified by checking whether an evenness index is invariant for multiple replicated assemblages (i.e., replication invariance). Later, Gosselin (2006) interpreted this independence as an assertion that the value an evenness measure can take should not vary with species richness, and Kvålseth (2015) interpreted it as stating that richness S should not appear in an evenness formula.

We have adopted the resolution proposed by Chao and Chiu (2016) that the “independence” (or unrelatedness) of two measures means that for any diversity order $q \geq 0$, the range of values that one measure can take should be a fixed interval for any value of the other measure. The existence of such a fixed range facilitates comparability and meaningful ordering of evenness across different values of q and also across multiple assemblages. We have proved that our evenness measures are “independent” (or unrelated) not only of species richness but also of diversity of any order $q > 0$ in the following sense: all the proposed evenness measures (Table 1) attain a fixed maximum value of unity for a completely even assemblage (i.e., $\mathbf{p} = \bar{\mathbf{p}}$); all measures approach a fixed minimum value of 0 for the maximally uneven assemblage (i.e., $\mathbf{p} = \mathbf{p}^0$), regardless of the values of species richness and abundance-based diversity.

Independence is not equivalent to replication invariance

Several researchers (Sheldon 1969, Hill 1973, Tuomisto 2012) proposed a definition of “evenness” as the ratio of diversity and species richness; that is, ${}^qD/S$, for $q > 0$. Because qD is between 1 and S , Jost (2010) pointed out that the range of this index is in the interval $[1/S, 1]$, revealing the range is constrained by the value of species richness. Consequently, the index ${}^qD/S$, while replication invariant, is in fact “dependent” on species richness. This example clearly demonstrates that “independence” *cannot* be verified by replication invariance. The Gini evenness index provides another example, as will be discussed in the following.

Consequence of “dependence” on species richness

Here, we give a numerical example based on the measure ${}^qD/S$ for the special case of $q = 1$ to explain the consequence of “dependence”; a similar consequence arises for any other $q > 0$. Suppose that Assemblage I represents the maximally uneven two-species assemblage, that is, two species with relative abundances 0.999 and 0.001; we have ${}^1D/S = 1.008/2 = 0.504$. Assemblage II has 10 species with relative abundances $[3 \times 0.2874, 7 \times 0.0197]$ (3 species with relative abundances 0.2874 and 7 species with relative abundances 0.0197), which deviates to some extent from the maximally uneven 10-species assemblage. Intuitively, the two assemblages should not be equally even. However, for Assemblage II, we obtain almost the same evenness value based on the formula ${}^1D/S = 5.04/10 = 0.504$,

suggesting an intuitively unreasonable conclusion that the two assemblages are equally even.

The problem arises because the index ${}^1D/S$ in Assemblage I can only take values in $[0.5, 1]$ for any two-species assemblage; thus 0.504 means an almost minimally even (i.e., maximally uneven) assemblage. However, the same index in Assemblage II take values in the range $[0.1, 1]$; thus the same value 0.504 indicates a moderately even assemblage with 10 species. Therefore, a consequence of “dependence” on richness is that the same magnitude of evenness may quantify different degrees of equitability among species relative abundances if species richness differs. This leads to ambiguity in interpreting the measure ${}^1D/S$ to reflect evenness among assemblages.

To overcome this problem, we can normalize the measure to $[0, 1]$ using a simple transformation: $({}^qD/S - \min)/(\max - \min) = ({}^qD/S - 1/S)/(1 - 1/S) = ({}^qD - 1)/(S - 1)$, which is our third class of evenness measures (Table 1). Based on this normalized evenness measure, the evenness for Assemblage I is measured as 0.008, whereas the evenness for Assemblage II is 0.449, which reveals that Assemblage II is more even. This ordering then conforms to our intuition and is also consistent with that based on all our evenness measures listed in Table 1.

Lorenz partial-ordering and replication invariance

Taillie (1979) was the first to propose a Lorenz partial-ordering approach (Lorenz-ordering approach hereafter) to rank the evenness of assemblages. Gosselin (2001, 2006) advocated the Lorenz-ordering approach as a framework to define evenness indices. As discussed in the *Properties* section, our measures preserve Lorenz ordering only when species richness is fixed across assemblages (Property P2). Otherwise, the two approaches may give different orderings. In Appendix S4: Tables S1 and Fig. S1, we give an example in which the Lorenz curve of Assemblage I (two species) is everywhere above the curve of Assemblage II (five species). Lorenz ordering implies that Assemblage I is more even. However, all our measures reveal the reverse order. When species richness is not fixed, two drastically different properties exist between the Lorenz-ordering approach and our measures:

1. As intuitively explained in Property P4 (replication monotonicity) and rigorously proved in Appendix S1: Section S3, all our evenness measures always increase for multiple replicated assemblages except in the completely even case. This is consistent with Jost (2010) and Kvålseth (2015); they indicated that an evenness measure should *not* be replication invariant. By contrast, the Lorenz-ordering approach satisfies replication invariance because the Lorenz curve for any replicated assemblages is the same as that of the original one.
2. All our measures approach an absolute fixed minimum value, regardless of the value of species richness

(Requirement 3a). However, the minimum value a Lorenz-compatible evenness measure can take is necessarily dependent on species richness due to replication invariance; see Gosselin (2001: Fig. 2). As discussed in the preceding subsection for the measure ${}^qD/S$ and in the next subsection for the Gini index, such dependence causes interpretation problems. Nevertheless, this dependence can be eliminated through proper normalization. Both the normalized measure $({}^qD - 1)/(S - 1)$, as discussed previously, and the following normalized Gini evenness index satisfy replication monotonicity and approach an absolute minimum value of 0.

Normalized Gini evenness index

The overall amount of unevenness in a Lorenz curve can be measured by the Gini coefficient. Assume that the elements of the species relative abundance vector $\mathbf{p} = (p_1, p_2, \dots, p_S)$ are ordered such that $p_{(1)} \geq p_{(2)} \geq \dots \geq p_{(S)}$; the Gini unevenness coefficient can be expressed as $(S + 1 - 2 \sum_{i=1}^S ip_{(i)})/S$ and the corresponding Gini evenness index is $G = (2 \sum_{i=1}^S ip_{(i)} - 1)/S$. The Gini evenness index is replication invariant but “dependent” on richness in the sense that it takes values in the interval $[1/S, 1]$. This follows from the fact that the Gini evenness index attains a fixed maximum value of 1 for $\mathbf{p} = \bar{\mathbf{p}}$, and the minimum value is $1/S$ when $\mathbf{p} = \mathbf{p}^0$. A similar interpretational problem as that found for the measure ${}^qD/S$ also arises for the Gini evenness index. For example, the Gini evenness index for the previously described maximally uneven two-species assemblage (Assemblage I with species relative abundances 0.999 and 0.001) is 0.5005, suggesting a minimally even assemblage, because Assemblage I can only take values in $[0.5, 1]$. By contrast, the Gini evenness index for Assemblage II = $[3 \times 0.2874, 7 \times 0.0197]$ (10 species) is 0.438. This lower evenness value, however, indicates a moderately even assemblage, because the same index in Assemblage II take values in the range $[0.1, 1]$. However, the Gini evenness index implies that the maximally uneven Assemblage I is “more even” than Assemblage II, which is contradictory to intuition.

Again, a simple remedy is to normalize the Gini evenness measure to $[0, 1]$ using a simple transformation: $G^* = (G - \min)/(\max - \min) = (2 \sum_{i=1}^S ip_{(i)} - 2)/(S - 1)$, a measure first developed by Solomon (1979). This normalized evenness measure possesses all our requirements/properties, including replication monotonicity. The normalized Gini evenness indices for Assemblage I and Assemblage II are calculated, respectively, as 0.002 and 0.338, which reveals the reverse ordering; that is, Assemblage II is more even. This ordering is also consistent with that based on all our evenness measures. Additional discussion on some other evenness measures and related statistical issues are provided in Appendix S4.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.2852/supinfo>

DATA AVAILABILITY

Data used in this paper and the R code “Evenness” for computing our proposed evenness indices and making all relevant plots are available in Zenodo: <https://doi.org/10.5281/zenodo.3341384>.

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Quantifying evenness and linking it to diversity, beta diversity, and similarity. *Ecology*

Appendix S1. Mathematical Details

S1. Majorization, Schur-concavity, and the Lorenz curve

As we indicated in Requirement 1a for an evenness measure in the main text, the most essential property shared by evenness and diversity for a fixed value of species richness is the principle of transfer, which is equivalent to the strict Schur-concavity property. Intuitively, Schur-concavity of evenness means that evenness increases as dispersion of abundances decreases, whereby “dispersion” of abundances is defined by the concept of majorization (Marshall, Olkin and Arnold 2011). Here we briefly present the concepts of majorization and Schur-concavity. The related topic of the Lorenz curve is also briefly reviewed.

For an assemblage with species relative abundance vector $\mathbf{p} = (p_1, p_2, \dots, p_S)$, the vector \mathbf{p} majorizes another species relative abundance vector $\mathbf{p}^* = (p_1^*, p_2^*, \dots, p_S^*)$, denoted as $\mathbf{p} \succ \mathbf{p}^*$, if $p_{(1)} \geq p_{(1)}^*$, $p_{(1)} + p_{(2)} \geq p_{(1)}^* + p_{(2)}^*$, \dots , $\sum_{i=1}^{S-1} p_{(i)} \geq \sum_{i=1}^{S-1} p_{(i)}^*$ and $\sum_{i=1}^S p_{(i)} = \sum_{i=1}^S p_{(i)}^* = 1$, where $p_{(i)}$ ’s and $p_{(i)}^*$ ’s are elements of the vectors \mathbf{p} and \mathbf{p}^* respectively arranged in descending order, i.e., $p_{(1)}$ and $p_{(1)}^*$ are for the most abundant species,

$p_{(1)} \geq p_{(2)} \geq \dots \geq p_{(S)}$ and $p_{(1)}^* \geq p_{(2)}^* \geq \dots \geq p_{(S)}^*$. Intuitively, $\mathbf{p} \succ \mathbf{p}^*$ means that the elements of vector \mathbf{p} are more unequal or more dispersed than are the elements of vector \mathbf{p}^* , given the sum of the elements of the two vectors is unity. The vector \mathbf{p} is defined to strictly majorize \mathbf{p}^* , denoted as $\mathbf{p} \succ \mathbf{p}^*$, if \mathbf{p} majorizes \mathbf{p}^* and is not a permutation of \mathbf{p}^* . A function g is called Schur-concave if $\mathbf{p} \succ \mathbf{p}^*$ implies $g(\mathbf{p}) \leq g(\mathbf{p}^*)$. A function g is called strictly Schur-concave if $\mathbf{p} \succ \mathbf{p}^*$ implies $g(\mathbf{p}) < g(\mathbf{p}^*)$. Note that in the definition of (strict) majorization and (strict) Schur-concavity, some elements of the two vectors are allowed to be exactly zero. For example, we have $(0.5, 0.5, 0, 0) \succ (0.4, 0.3, 0.2, 0.1)$.

In ecological context, the Lorenz curve for any species relative abundance vector

$\mathbf{p}=(p_1, p_2, \dots, p_S)$ plots the cumulative relative abundance (i.e., proportion of cumulative of individuals) with respect to the proportion of cumulative number of species. That is, for the vector with descending elements $p_{(1)} \geq p_{(2)} \geq \dots \geq p_{(S)}$, the Lorenz curve is the polygon joining the points $(0, 0)$ and $(\sum_{j=1}^k p_{(j)}, k/S)$, or equivalently, joining the points $(0, 0)$ and $(k/S, \sum_{j=0}^{k-1} p_{(S-j)})$, $k = 1, 2, \dots, S$. We use the latter definition throughout the main text and appendices. For a completely even assemblage, the Lorenz curve is a straight diagonal line of equality. If both vectors have the same number of non-zero elements, then $\mathbf{p} \succ \mathbf{p}^*$ if and only if the Lorenz curve for \mathbf{p}^* is nowhere below the Lorenz curve of \mathbf{p} . In other words, the Lorenz curve of \mathbf{p}^* is closer to the diagonal line of equality than \mathbf{p} , implying \mathbf{p}^* is more even than \mathbf{p} for the Lorenz-ordering approach.

Requirement 1a (i.e., strict Schur-concavity for an evenness measure) states that if two species relative abundance vectors satisfy $\mathbf{p} \succ \mathbf{p}^*$ and both vectors have the same number of non-zero elements (i.e., species richness is fixed), then the evenness for the two vectors must satisfy $E(\mathbf{p}) < E(\mathbf{p}^*)$. This requirement then implies the second property (P2): Lorenz ordering is preserved for any evenness measure when species richness is fixed across assemblages. In Appendix S4, we give an example to show that our proposed evenness measures (in Table 1 of the main text) may yield different Lorenz orderings if species richness differs among assemblages. See the *Discussion* section of the main text for comparisons of our framework with the Lorenz partial-ordering approach.

S2. Kullback-Leibler divergence, and unevenness measures as normalized absolute slopes of some profiles

The Kullback-Leibler divergence is an important measure in various disciplines. We first introduce the general framework of Kullback-Leibler divergence in terms of two sets of species relative abundances which are denoted respectively by (p_1, p_2, \dots, p_S) and $(\pi_1, \pi_2, \dots, \pi_S)$, $\sum_{i=1}^S p_i = \sum_{i=1}^S \pi_i = 1$. The Kullback-Leibler divergence between the two relative abundance vectors (p_1, p_2, \dots, p_S) and $(\pi_1, \pi_2, \dots, \pi_S)$ is defined as

$$A_{KL}(p_1, p_2, \dots, p_S \parallel \pi_1, \pi_2, \dots, \pi_S) = \sum_{i=1}^S p_i \log \frac{p_i}{\pi_i}.$$

Here, by convention, $0 \log \frac{0}{\pi} = 0$ and $p \log \frac{p}{0} = \infty$. For the first class of divergence

measures, we have

$$\begin{aligned}\lim_{q \rightarrow 1} \Delta_1(\mathbf{p}^q, \bar{\mathbf{p}}^q) &= \lim_{q \rightarrow 1} \frac{1}{q-1} \left[({}^q D)^{1-q} - S^{1-q} \right] = -1 \circ \mathbf{p} + 1 \circ \bar{\mathbf{p}} \\ &= \sum_{i=1}^S p_i \log \frac{p_i}{(1/S)} = \Delta_{KL}(p_1, p_2, \dots, p_S \parallel 1/S, \dots, 1/S).\end{aligned}$$

That is, when q tends to 1, the first class of divergence measures tends to the Kullback-Leibler divergence between $\mathbf{p} = (p_1, p_2, \dots, p_S)$ and the mean vector $\bar{\mathbf{p}} = (1/S, 1/S, \dots, 1/S)$

Unevenness measures as normalized slopes of some profiles

Following Olszewski's (2004) approach, we show that our first class of unevenness measures of any order q represents the normalized absolute slope of the Tsallis entropy profile. Here the Tsallis entropy is defined as ${}^q H_T = (\sum_{i=1}^S p_i^q - 1)/(1-q)$, $q \geq 0$, $q \neq 1$, and the sub-index “T” is referred to as “Tsallis”. Consider the magnitude or absolute value of the slope ${}^q L_T$ connecting the two points $(0, {}^0 H_T)$ and $(q, {}^q H_T)$ in a profile based on Tsallis entropy, leading to

$${}^q L_T = \frac{{}^0 H_T - {}^q H_T}{q} = \frac{(S-1)(1-q) - \sum_{i=1}^S p_i^q + 1}{q(1-q)}, \quad q \geq 0, \quad q \neq 1.$$

This slope represents an unevenness measure because it attains the minimum when $\mathbf{p} = \bar{\mathbf{p}}$, and attains the maximum when $\mathbf{p} = \mathbf{p}^0$, i.e., $\min({}^q L_T) = [(S-1)(1-q) - S^{1-q} + 1]/[q(1-q)]$ and $\max({}^q L_T) = (S-1)/q$. Then the normalized absolute unevenness measure turns out to be $1 - {}^q E_1(\mathbf{p})$, i.e.,

$$\frac{{}^q L_T - \min({}^q L_T)}{\max({}^q L_T) - \min({}^q L_T)} = 1 - {}^q E_1(\mathbf{p}).$$

Using a similar proof, we can show that the third and fifth classes of evenness measures (in Table 1 of the main text) are respectively the normalized absolute slopes of Hill-numbers and Rényi-entropy (logarithm of Hill numbers) profiles.

S3. Property P3 (evenness of $\mathbf{p}^\lambda = \lambda \bar{\mathbf{p}} + (1-\lambda)\mathbf{p}^0$) and Property P4 (replication monotonicity)

Property P3 (evenness of $\mathbf{p}^\lambda = \lambda \bar{\mathbf{p}} + (1-\lambda)\mathbf{p}^0$)

If a relative abundance vector is expressed as a convex combination of $\bar{\mathbf{p}}$ and \mathbf{p}^0 , i.e., $\mathbf{p}^\lambda = \lambda \bar{\mathbf{p}} + (1-\lambda)\mathbf{p}^0$, then we have the vector $\mathbf{p}^\lambda = (1-\lambda + \lambda/S, \lambda/S, \dots, \lambda/S)$. When $\lambda > \lambda^*$, it is readily seen that $\mathbf{p}^{\lambda^*} \succ \mathbf{p}^\lambda$. Strict Schur-concavity implies that the evenness of \mathbf{p}^λ is a monotonically increasing function of λ . Here we evaluate the evenness of \mathbf{p}^λ for Smith and Wilson's (1996) measure, which is expressed as ${}^2E_1(\mathbf{p}) = (1 - \sum_{i=1}^S p_i^2)/(1 - 1/S)$, i.e., the first class of measures of $q = 2$ in Table 1 of the main text. Based on the elements of the vector \mathbf{p}^λ , we obtain

$$\sum_{i=1}^S p_i^2 = (1 - \lambda + \lambda/S)^2 + (S-1)(\lambda/S)^2 = 1 - 2\lambda(1 - 1/S) + \lambda^2(1 - 1/S).$$

The above then leads to ${}^2E_1(\mathbf{p}^\lambda) = \lambda(2 - \lambda)$, which is an increasing function of λ . Thus, Kvålseth's (2015) stringent requirement (i.e., the evenness for \mathbf{p}^λ must be λ) is relaxed to be an increasing function of λ based on our measures.

For Pielou's J' (the first class of evenness measures of $q = 1$), we have

$$J' = {}^1E_1(\mathbf{p}^\lambda) = \frac{-(1 - \lambda + \lambda/S) \log(1 - \lambda + \lambda/S) - [\lambda(S-1)/S] \log(\lambda/S)}{\log S}.$$

Regarding the above formula as a function of λ and taking the derivative with respect to λ , we have

$$\frac{d {}^1E_1(\mathbf{p}^\lambda)}{d\lambda} = \frac{(1 - 1/S) \log[1 + (1 - \lambda)\lambda/S]}{\log S} > 0.$$

This proves that Pielou's J' for the vector \mathbf{p}^λ is an increasing function of λ . Analogous results can be obtained for any of the other measures listed in Table 1 of the main text.

Property P4 (replication monotonicity)

Assume an assemblage consists of K replicates of the original assemblage (referred to as a K -replicated-assemblage). Each replicate has the same number of species and the same species abundances as the original one, but with completely different, unique species in each replicate. Then the diversity (including richness) of the K -replicated-assemblage becomes K

times that of the original single assemblage. Thus the evenness of the K -replicated-assemblage based on the first class of measures can be expressed as the following function of K :

$$h(K) = \frac{1 - (K \times {}^qD)^{1-q}}{1 - (K \times S)^{1-q}}, \quad q \neq 1;$$

$$= \frac{\log(K \times {}^qD)}{\log(K \times S)}, \quad q = 1.$$

Taking the derivative with respect to K , we obtain

$$\frac{dh(K)}{dK} = \frac{(q-1)K^{-q}[({}^qD)^{1-q} - S^{1-q}]}{[1 - (KS)^{1-q}]^2}, \quad q \neq 1;$$

$$= \frac{\log S - \log({}^qD)}{K[\log(KS)]^2}, \quad q = 1.$$

The two derivatives are positive if ${}^qD < S$, whereas they are 0 if ${}^qD = S$. The replication monotonicity property then follows from the fact that $h(K)$ is an increasing function of K if ${}^qD < S$ (non-completely-even), and $h(K) = 1$ if ${}^qD = S$ (completely even). A similar proof can be applied to the other four classes of evenness measures.

S4. Linking species compositional unevenness to the Sørensen-type dissimilarity measures

Let the weight of species i of order q be ${}^qw_{2i} = \sum_{u=1}^N z_{iu}^q / \sum_{v=1}^S \sum_{m=1}^N z_{vm}^q$, $i = 1, 2, \dots, S$. Then the weighted average of individual species' compositional unevenness values based on our second class of unevenness measure $1 - {}^qE_2(\mathbf{p}^{(i)})$ leads to the abundance-based Sørensen-type dissimilarity/non-overlap measure $1 - C_{qN}$ (Chao and Chiu 2016, their Eq. 12b). That is, we have

$$\sum_{i=1}^S ({}^qw_{2i}) [1 - {}^qE_2(\mathbf{p}^{(i)})] = \sum_{i=1}^S \frac{\sum_{u=1}^N z_{iu}^q}{\sum_{v=1}^S \sum_{m=1}^N z_{vm}^q} \frac{\{1 / [\sum_{k=1}^N (z_{ik} / z_{i+})^q] - N^{q-1}\}}{1 - N^{q-1}} \quad (S1)$$

$$= \frac{\sum_{i=1}^S \sum_{k=1}^N (z_{ik}^q - \bar{z}_{i+}^q)}{(1 - N^{1-q}) \sum_{v=1}^S \sum_{m=1}^N z_{vm}^q} = 1 - C_{qN}. \quad (S2)$$

This non-overlap measure $1 - C_{qN}$ for all $q \geq 0$ quantifies the effective average proportion of species in an individual assemblage that are not shared by any other assemblages (Chao & Chiu, 2016, p. 922). Eqs. (S1) and (S2) link species compositional unevenness to Sørensen-type dissimilarity measures for $q > 0$; the Sørensen-type dissimilarity measure

$1 - C_{qN}$ in Eq. (S2) is also valid for $q = 0$ (i.e., only species presence/absence data are counted).

When q tends to 1, the weight becomes the proportion of a species' total abundance ${}^1w_{2i} = z_{i+} / \sum_{j=1}^S z_{j+} = z_{i+} / z_{++}$, and the species compositional unevenness measure $1 - {}^qE_2(\mathbf{p}^{(i)})$ tends to Pielou's unevenness measure based on the among-assemblage relative abundance vector of species i , i.e., $\mathbf{p}^{(i)} = \{z_{i1}/z_{i+}, z_{i2}/z_{i+}, \dots, z_{iN}/z_{i+}\}$. Therefore, we have $1 - C_{1N} = 1 - U_{1N}$ as derived in Eq. 12c of Chao and Chiu (2016). The dissimilarity measure $1 - C_{qN}$ is also a monotonic transformation of multiplicative beta diversity ${}^qD_\beta$, i.e., $1 - C_{qN} = [({}^qD_\beta)^{1-q} - 1] / (N^{1-q} - 1)$, for $q \neq 1$, and $1 - C_{1N} = \log({}^1D_\beta) / \log N$. Thus, beta diversity can be expressed as a function of the second class of unevenness measures:

$${}^qD_\beta = \left(1 + (N^{1-q} - 1) \sum_{i=1}^S ({}^qw_{2i}) [1 - {}^qE_2(\mathbf{p}^{(i)})] \right)^{1/(1-q)}, \quad q > 0, q \neq 1.$$

The measure $1 - C_{0N}$ reduces to the classic N -assemblage richness-based Sørensen dissimilarity index. Thus, the class of measures $1 - C_{qN}$ generalizes the classic Sørensen index to incorporate species abundances (if $q > 0$). When the data matrix $[z_{ik}]$ is replaced by the within-assemblage relative abundances, this measure for $q=1$ and 2 reduces respectively to the traditional N -assemblage Horn (1966) and Morisita-Horn (Morisita 1959) dissimilarity measures. This class of measures is valid for all types of abundance data, thus generalizing the traditional Horn and Morisita-Horn measures to compare all types of data.

Based on Eqs. (S1)–(S2), the contribution of each species to the Sørensen-type non-overlap measure can be obtained. For any $q > 0$, the contribution of species i is simply $({}^qw_{2i})[1 - {}^qE_2(\mathbf{p}^{(i)})]$, i.e., the product of the second-kind weight and the second-class of unevenness measure for $\mathbf{p}^{(i)}$. The contribution of any species is positive if ${}^qE_2(\mathbf{p}^{(i)}) < 1$, whereas the contribution is 0 if ${}^qE_2(\mathbf{p}^{(i)}) = 1$, which means species i has an equal abundance among the N assemblages.

For the special case of $q = 1$, the contribution of species i to the Jaccard- and Sørensen-type measures is identical because $1 - C_{1N} = 1 - U_{1N}$. That is, the contribution of

species i reduces to the product of the species weight and Pielou's unevenness measure based on $\mathbf{p}^{(i)}$, which can be simplified to $(z_{++} \log N)^{-1} \sum_{k=1}^N z_{ik} \log(z_{ik} / \bar{z}_{i+})$. Also, we have

$${}^1D_\beta = \exp\left(\log N \sum_{i=1}^S ({}^1w_{1i}) [1 - {}^1E_2(\mathbf{p}^{(i)})]\right).$$

For $q = 0$, if we define $0^0 \equiv 0$ so that any absent species does not contribute to the computation, then the contribution of species i can be obtained from Eq. (S2) and expressed as

$$\frac{\sum_{k=1}^N (z_{ik}^0 - \bar{z}_{i+}^0)}{(1 - N^{1-q}) \sum_{v=1}^S \sum_{m=1}^N z_{vm}^0} = \frac{N - Y_i}{(\sum_{j=1}^S Y_j)(N - 1)} = \frac{N - Y_i}{(N\bar{S})(N - 1)},$$

where \bar{S} denotes the average species richness per assemblage. The above contribution is positive if species i is not detected in at least one of the N assemblages, and is 0 if species i is detected in all assemblages.

References for Appendix S1

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Appendix S2. Extending Our Framework to a Phylogenetic Version

S1. An illustrative example

We assume that there are N assemblages and S species (as tip nodes) connected by a rooted ultrametric phylogenetic tree. All phylogenetic diversity measures are computed from a given fixed time reference point that is ancestral to all taxa considered in the study. Suppose that the tree depth is T and there are B branches/nodes in the pooled tree, $B \geq S$. Let L_i denote the length of the i -th branch, and define z_{ik} (node/branch abundance) as the total abundance descending from node/branch i , $i = 1, 2, \dots, B$. A simple example for $N = 2$, $S = 5$, and $B = 8$ is given in Figure S1, and the corresponding node abundances are given in Table S1.

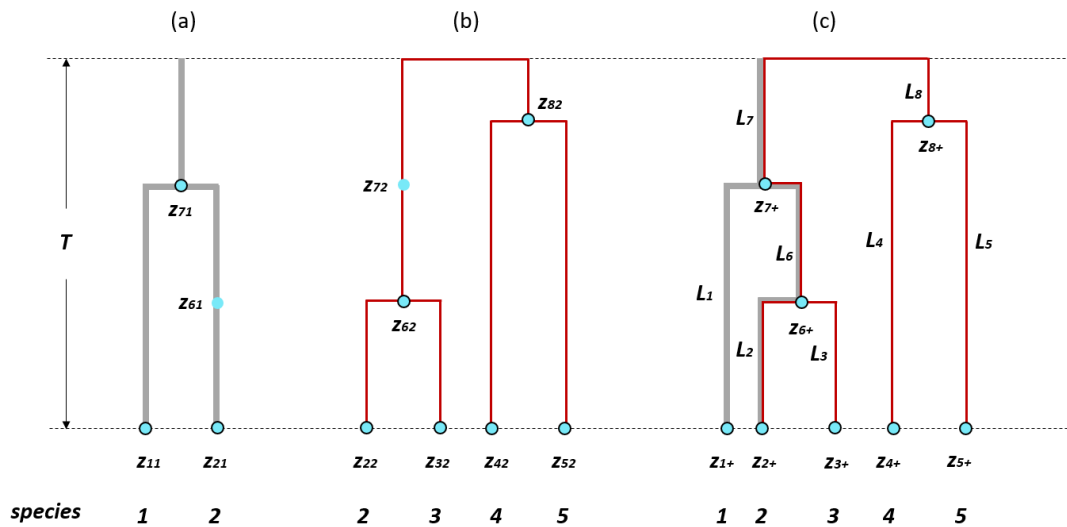


Figure S1. (a) Phylogenetic tree for Assemblage I (grey) with species (1, 2) and tip-node abundances (z_{11} , z_{21}). (b) Phylogenetic tree for Assemblage II (red) with species (2, 3, 4, 5) and tip-node abundances (z_{22} , z_{32} , z_{42} , z_{52}). (c) Pooled tree for five species (1, 2, 3, 4, 5) with five tip-node abundances (z_{1+} , z_{2+} , z_{3+} , z_{4+} , z_{5+}) and corresponding branch lengths (L_1 , L_2 , L_3 , L_4 , L_5), along with three internal-node abundances (z_{6+} , z_{7+} , z_{8+}) with branch lengths (L_6 , L_7 , L_8). The whole pooled phylogenetic tree includes 8 nodes and their corresponding branch

lengths. The branch/node abundances for each assemblage and the pooled assemblage are tabulated in Table S1. Blue closed dots denote nodes in each tree. When the phylogenetic tree of each individual assemblage is embedded in the pooled tree, one additional node (blue open circle) is added so that the diversity of each individual assemblage can be computed from the pooled tree with 8 nodes.

Table S1. Branch/node abundance set of Assemblages I, II and the pooled assemblage for the phylogenetic tree given in Figure S1.

Branch/Node i	Assemblage I	Assemblage II	Pooled
1	z_{11}	0	$z_{1+} = z_{11}$
2	z_{21}	z_{22}	$z_{2+} = z_{21} + z_{22}$
3	0	z_{32}	$z_{3+} = z_{32}$
4	0	z_{42}	$z_{4+} = z_{42}$
5	0	z_{52}	$z_{5+} = z_{52}$
6	$z_{61} = z_{21}$	$z_{62} = z_{22} + z_{32}$	$z_{6+} = z_{21} + z_{22} + z_{32}$
7	$z_{71} = z_{11} + z_{21}$	$z_{72} = z_{22} + z_{32}$	$z_{7+} = z_{11} + z_{21} + z_{22} + z_{32}$
8	0	$z_{82} = z_{42} + z_{52}$	$z_{8+} = z_{42} + z_{52}$

S2. Linking node compositional unevenness and Jaccard-type phylogenetic dissimilarity

Chiu et al. (2014) extended the taxonomic Jaccard- and Sørensen-type dissimilarity measures, i.e., $1 - U_{qN}$ and $1 - C_{qN}$, discussed in the main text and in Appendix S1: Section S4, to their phylogenetic version: $1 - \bar{U}_{qN}(T)$ and $1 - \bar{C}_{qN}(T)$. As discussed in the main text, a time parameter T (tree depth) is affixed to each measure to signify that it is a function of tree depth. Analogous procedures to those presented in the Section *Linking unevenness and beta/dissimilarity for multiple assemblages* of the main text can be developed. Here we only focus on linking species/node compositional unevenness to phylogenetic dissimilarity indices; its linking to phylogenetic beta diversity is omitted. First, species compositional unevenness

is extended to each node. That is, for the i -th *node*, $i = 1, 2, \dots, B$, the node compositional unevenness measure is computed as a normalized divergence between the N -element *node* relative abundance vector $\mathbf{a}^{(i)} = \{z_{i1}/z_{i+}, z_{i2}/z_{i+}, \dots, z_{iN}/z_{i+}\}$ and the mean vector $\bar{\mathbf{p}}(N) = (1/N, 1/N, \dots, 1/N)$; here we extend the index i to include all nodes in the phylogenetic tree.

Consider the weight ${}^q w_{li} = z_{i+}^q / \sum_{j=1}^B L_j z_{j+}^q$ for the i -th node, $i = 1, 2, \dots, B$. The weighted average of individual nodes' compositional unevenness values of $1 - {}^q E_1(\mathbf{a}^{(i)})$ becomes

$$\sum_{i=1}^B L_i ({}^q w_{li}) [1 - {}^q E_1(\mathbf{a}^{(i)})] = \sum_{i=1}^B L_i \frac{z_{i+}^q}{\sum_{j=1}^B L_j z_{j+}^q} \frac{[\sum_{k=1}^N (z_{ik}/z_{i+})^q - N^{1-q}]}{1 - N^{1-q}} \quad (\text{S1})$$

$$= \frac{\sum_{i=1}^B L_i \sum_{k=1}^N (z_{ik}^q - \bar{z}_{i+}^q)}{(N^q - N) \sum_{j=1}^B L_j \bar{z}_{j+}^q} = 1 - \bar{U}_{qN}(T), \quad (\text{S2})$$

which is the Jaccard-type phylogenetic dissimilarity/non-overlap measure $1 - \bar{U}_{qN}(T)$ derived in Chiu et al. (2014). This measure for *all* $q \geq 0$ quantifies the effective proportion of non-shared branches in the pooled assemblage. Note that when q tends to 1, the weight becomes the proportion of a species' node abundance ${}^1 w_{li} = z_{i+} / \sum_{j=1}^B L_j z_{j+} = z_{i+} / (T z_{++})$, and the node compositional unevenness measure $1 - {}^q E_1(\mathbf{a}^{(i)})$ tends to Pielou's unevenness measure based on $\mathbf{a}^{(i)} = \{z_{i1}/z_{i+}, z_{i2}/z_{i+}, \dots, z_{iN}/z_{i+}\}$. In the special case of $q = 1$, we have

$$\begin{aligned} \lim_{q \rightarrow 1} \sum_{i=1}^B L_i ({}^q w_{li}) [1 - {}^q E_1(\mathbf{a}^{(i)})] &= \sum_{i=1}^B L_i \frac{z_{i+}}{T z_{++}} \left[1 - \frac{\sum_{k=1}^N (-z_{ik}/z_{i+}) \log(z_{ik}/z_{i+})}{\log N} \right] \\ &= \frac{1}{T z_{++} \log N} \sum_{i=1}^B \sum_{k=1}^N L_i z_{ik} \log \frac{z_{ik}}{z_{i+}} = 1 - \bar{U}_{1N}(T). \end{aligned} \quad (\text{S3})$$

For $q = 0$ and $N = 2$, the measure $1 - \bar{U}_{02}(T)$ reduces to the Jaccard-type *UniFrac* measure developed by Lozupone and Knight (2005) and the PD-dissimilarity measure developed by Faith et al. (2009).

It follows from Eqs. (S1)–(S2) that the contribution of each node to the phylogenetic

Jaccard-type non-overlap measure can be quantified as $L_i({}^q w_{li})[1 - {}^q E_1(\mathbf{a}^{(i)})]$ for $q > 0$.

Note the contribution of any node is positive if ${}^q E_1(\mathbf{a}^{(i)}) < 1$, whereas the contribution is 0 if

${}^q E_1(\mathbf{a}^{(i)}) = 1$, meaning node i has equal descending abundances among the N assemblages.

For the special case of $q = 1$, the contribution of node i based on Eq. (S3) is

$(T z_{++} \log N)^{-1} L_i \sum_{k=1}^N z_{ik} \log(z_{ik} / \bar{z}_{i+})$. Let Y_i^* denote the number of assemblages in which

descendants of node i are detected. For the special case of $q = 0$, the contribution of node i can be obtained from Eq. (S2) and expressed as

$$\frac{L_i \sum_{k=1}^N (z_{ik}^0 - \bar{z}_{i+}^0)}{(N^q - N) \sum_{j=1}^B L_j \bar{z}_{j+}^0} = \frac{L_i}{(\sum_{j=1}^B L_j)} \frac{(N - Y_i^*)}{(N - 1)},$$

which is positive if descendants of node i are not detected in all of the N assemblages, and is 0 if descendants of node i are detected in all assemblages.

S3. Linking node compositional unevenness and Sørensen-type phylogenetic dissimilarity

Consider another type of weight ${}^q w_{2i} = \sum_{u=1}^N z_{iu}^q / \sum_{v=1}^B L_v \sum_{m=1}^N z_{vm}^q$ for the i -th node. Then the weighted average of individual nodes' compositional unevenness value of $1 - {}^q E_2(\mathbf{a}^{(i)})$ becomes

$$\sum_{i=1}^B L_i ({}^q w_{2i}) [1 - {}^q E_2(\mathbf{a}^{(i)})] = \sum_{i=1}^B L_i \frac{\sum_{u=1}^N z_{iu}^q}{\sum_{v=1}^B L_v \sum_{m=1}^N z_{vm}^q} \frac{\{1 / [\sum_{k=1}^N (z_{ik} / z_{i+})^q] - N^{q-1}\}}{1 - N^{q-1}} \quad (\text{S4})$$

$$= \frac{\sum_{i=1}^B L_i \sum_{k=1}^N (z_{ik}^q - \bar{z}_{i+}^q)}{(1 - N^{1-q}) \sum_{v=1}^B \sum_{m=1}^N L_v z_{vm}^q} = 1 - \bar{C}_{qN}(T), \quad (\text{S5})$$

which is the Sørensen-type phylogenetic non-overlap measure $1 - \bar{C}_{qN}(T)$ derived in Chiu et al. (2014). This measure for *all* $q \geq 0$ quantifies the effective average proportion of branches in an individual assemblage that are not shared by any other assemblages. As above, when q tends to 1, the resulting dissimilarity reduces to the one in Eq. (S3). For $q = 0$ and $N = 2$, this similarity measure $\bar{C}_{02}(T)$ reduces to the measure *PhyloSor* (Phylo-Sørensen) developed by Bryant et al. (2008) and Ferrier et al. (2007). Analogously, we can quantify the contribution of each node, $i = 1, 2, \dots, B$.

As with the Jaccard-type phylogenetic non-overlap measure, the contribution of node i for the Sørensen-type phylogenetic non-overlap measure can be quantified as

$L_i({}^q w_{2i})[1 - {}^q E_2(\mathbf{a}^{(i)})]$ for $q > 0$. For the special case of $q = 1$, the contribution of node i is the same as that in the Jaccard-type phylogenetic non-overlap measure. For the special case of $q = 0$, the contribution of node i can be obtained from Eq. (S5) and expressed as

$$\frac{L_i \sum_{k=1}^N (z_{ik}^0 - \bar{z}_{i+}^0)}{(1 - N^{-1}) \sum_{v=1}^B \sum_{m=1}^N L_v z_{vm}^0} = \frac{L_i}{(\sum_{j=1}^B L_j Y_j)} \frac{(N - Y_i^*)}{(N - 1)},$$

which is positive if descendants of node i are not detected in all of the N assemblages, and is 0 if descendants of node i are detected in all assemblages.

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Appendix S3. Numerical Examples

S1. Numerical values of six classes of evenness measures for the worked example presented in the main text

In Figure 2 of the main text, we plot for the worked example the evenness profiles as a function of order q ($0 \leq q \leq 2$) based on the six classes of measures in Table 1 (denoted as E1–E6) for 45 Alpine species in three succession stages: early, mid and late. See Figure 1 of the main text for species relative abundances. Detailed numerical results are provided in Table S1 below.

Table S1. Evenness values for $q = 1$ and 2 based on the six classes of measures in Table 1 of the main text (denoted as E1–E6) for Alpine species in three succession stages: early, mid and late (Caccianiga et al. 2006, Ricotta et al. 2016, 2018). See Figure 2 of the main text for the plot of each measure’s profile as a function of order q ($0 \leq q \leq 2$).

Evenness measure	Order q	Succession stage		
		Early	Mid	Late
E1	$q=1$	0.882	0.884	0.899
	$q=2$	0.973	0.977	0.972
E2	$q=1$	0.882	0.884	0.899
	$q=2$	0.508	0.506	0.565
E3	$q=1$	0.647	0.641	0.706
	$q=2$	0.508	0.506	0.565
E4	$q=1$	0.985	0.987	0.985
	$q=2$	0.973	0.977	0.972
E5	$q=1$	0.882	0.884	0.899
	$q=2$	0.817	0.823	0.836
E6	$\alpha=1$	0.614	0.598	0.650
	$\alpha=2$	0.836	0.847	0.834

S2. Contribution of each species/node to the Sørensen-type taxonomic and phylogenetic dissimilarity measures

Figure 3 of the main text depicts the contribution of each species to the Jaccard-type taxonomic dissimilarity index. The contribution pattern for the taxonomic Sørensen-type dissimilarity index as shown below is nearly identical except for the differences in magnitude.

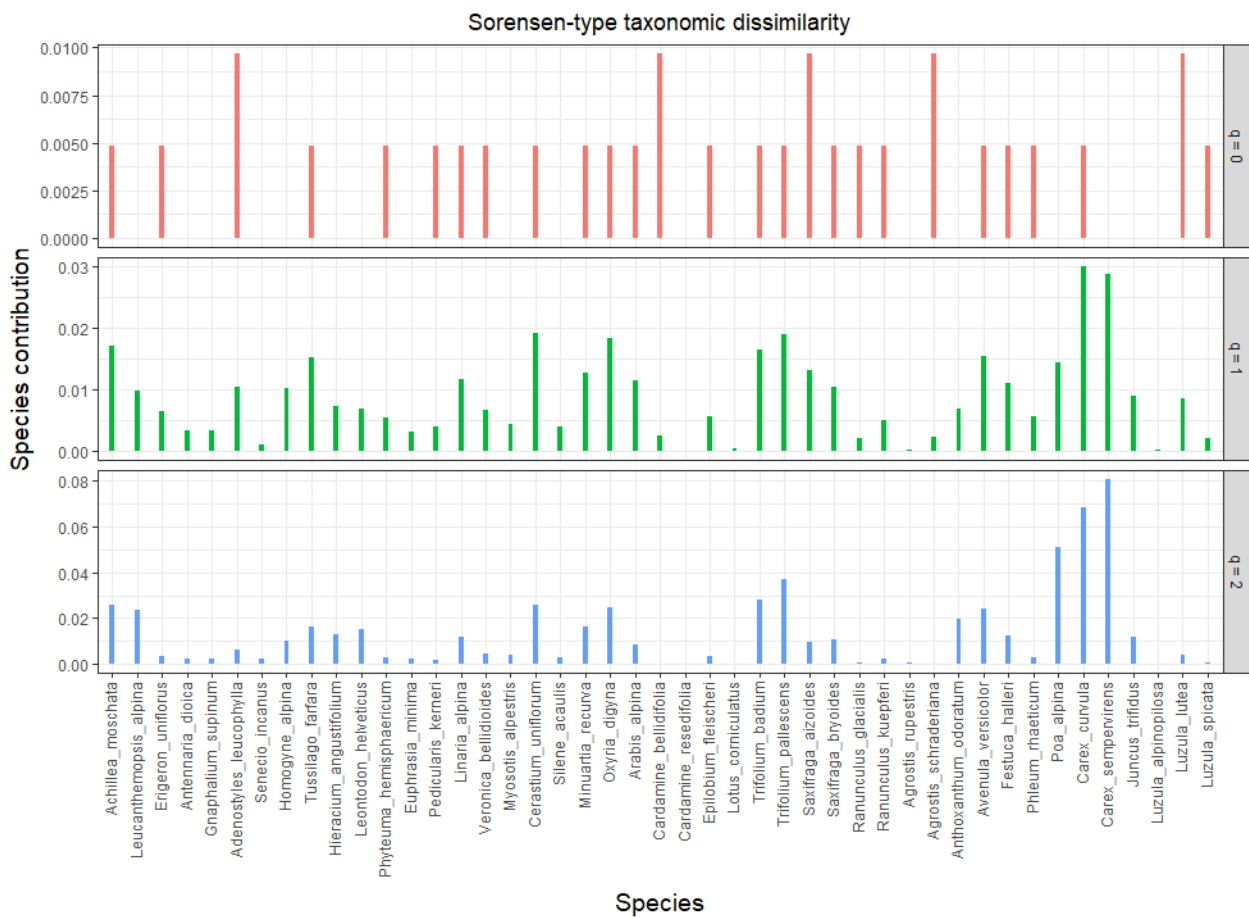


Figure S1. The contribution of each species to the taxonomic **Sørensen-type** dissimilarity index. See Figure 1 of the main text for species identities and relative abundances. The contribution pattern for the Jaccard-type dissimilarity index (as shown in Figure 3 of the main text) is nearly identical except for the differences in magnitude.

[illegible]

3

All data used in our worked example and the R code “Evenness” for computing our proposed evenness indices and making all relevant plots are supplied at Anne Chao’s Github (<https://github.com/AnneChao>) and also available in Zenodo: <https://doi.org/10.5281/zenodo.3341384>.

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Appendix S4. Additional Discussion

S1. When species richness is not fixed among assemblages, our measures and the Lorenz-curve approach may give different orderings

Our Requirement 1a (principle of transfer or strict Schur-concavity) for an evenness measure states that if two species relative abundance vectors satisfy strict majorization (i.e., $\mathbf{p} \succ \mathbf{p}^*$, see Appendix S1: Section S1 for definition) and both vectors have the same number of non-zero elements (i.e., species richness is fixed), then the evenness for the two vectors must satisfy $E(\mathbf{p}) < E(\mathbf{p}^*)$. This provides a way of ranking or ordering evenness among assemblages with the same number of species. In the conventional definition of majorization and Schur-concavity, some elements in any species relative abundance vector are allowed to be zero. For example, we have $(0.5, 0.5, 0, 0) \succ (0.4, 0.3, 0.2, 0.1)$. Here, the vector $(0.4, 0.3, 0.2, 0.1)$ can be obtained by a finite number of transfers from the vector $(0.5, 0.5, 0, 0)$. However, if the vector $(0.5, 0.5, 0, 0)$ were interpreted as a completely even two-species assemblage, then strict Schur-concavity and the principle of transfer cannot be applied to these two vectors. Otherwise, there would exist a four-species assemblage with evenness higher than the completely even two-species assemblage; a contradiction thus arises.

The above example reveals that strict Schur-concavity and the principle of transfer must be restricted to the case of fixed species richness among assemblages. For the above-mentioned example, we must interpret each 0 in the vector $(0.5, 0.5, 0, 0)$ as the abundance of a vanishingly small species so as to allow the Schur-concavity requirement to be met for a fixed value of $S = 4$ for *both* vectors, i.e., $(0.5, 0.5, 0+, 0+) \succ (0.4, 0.3, 0.2, 0.1)$. Then it follows from Schur-concavity that the evenness of the four-species assemblage with relative abundance vector $(0.4, 0.3, 0.2, 0.1)$ is higher than the evenness of the *four-species* assemblage where two species have relative abundances near 0.5 and the other two species have abundances near 0.

Lorenz-ordering provides another way of ranking evenness among assemblages. An assemblage with relative abundance vector \mathbf{p}^* is more even than an assemblage with relative abundance vector \mathbf{p} if the Lorenz curve of \mathbf{p}^* is nowhere below the Lorenz curve of \mathbf{p} . The notion of majorization reviewed in Appendix S1: Section S1 plays an important role in Lorenz-ordering. That is, $\mathbf{p} \succ \mathbf{p}^*$ if and only if the Lorenz curves for \mathbf{p}^* is nowhere below the Lorenz curve of \mathbf{p} . This link between majorization and Lorenz-ordering is true only under the condition that species richness is fixed. In the example described above, if the vector $(0.5, 0.5, 0, 0)$ were interpreted as a completely even two-species assemblage, then Lorenz-ordering cannot be applied to the two vectors $(0.5, 0.5, 0, 0) \succ (0.4, 0.3, 0.2, 0.1)$. This is because the two-species assemblage with relative abundances $(0.5, 0.5)$ would be completely even, implying the Lorenz curve for this two-species assemblage would be the diagonal line of equality. Then, there could not be any other four-species assemblage whose Lorenz curve is everywhere above the diagonal line. By contrast, if both assemblages have the same species richness of $S = 4$, it is readily seen that the Lorenz curve for the four-species assemblage with abundance vector $(0.4, 0.3, 0.2, 0.1)$ is everywhere above the Lorenz curve for the four-species assemblage with abundance vector $(0.5, 0.5, 0, 0)$. The above argument also offers a justification for our property 2 (P2) in the *Properties* section of the main text that Lorenz ordering for our measures is preserved when species richness is fixed across assemblages.

We now give an example to show that when species richness is not fixed, our measures and Lorenz-ordering may yield different orderings. The species abundances in two assemblages (I and II) are given in Table S1. Figure S1 shows that the Lorenz curve of Assemblage I (two species) is everywhere above the curve of Assemblage II (5 species); Lorenz ordering implies that Assemblage I is more even. For example, the Gini evenness indices for Assemblage I and Assemblage II are calculated respectively as 0.667 and 0.550. By contrast, all our measures tabulated in Table S2 clearly reveal the reverse order. In accordance with our theory, this problem resulted from the two assemblages having different numbers of species. From our perspective, when species richness values are different, the Lorenz partial-order approach cannot be used to rank the degree of evenness across assemblages, mainly due to the “dependence” of any Lorenz-compatible measure on species richness; see the main text for details.

However, as we demonstrated in the *Discussion* section of the main text, the dependence can be eliminated by normalization. As shown in Table S2, the normalized Gini evenness indices for Assemblage I and Assemblage II are calculated respectively as 0.334 and 0.438, which reveals the reverse ordering from the Gini evenness index. The normalized index yields an ordering which is consistent with all of our measures.

Table S1. Species raw abundances of two assemblages (I and II)

Species	Assemblage I	Assemblage II
A	10	10
B	2	10
C		2
D		1
E		1

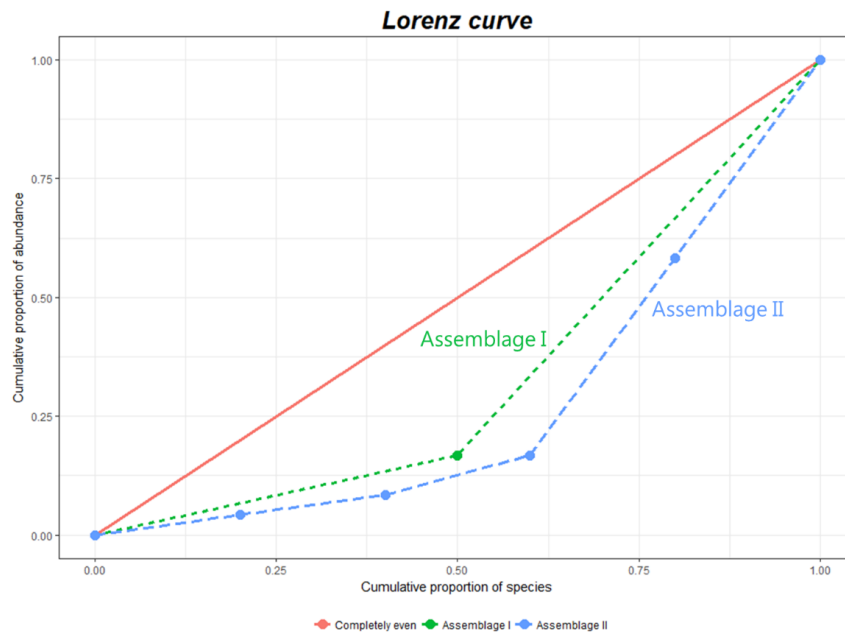


Figure S1. The Lorenz curves of the two assemblages described in Table S1.

Table S2. The six classes of evenness measures for the two assemblages described in Table S1; the measures E1–E6 correspond to the six classes of evenness indices in Table 1 of the main text. Note that the Gini evenness index (in red) gives a different ordering from other measures.

Evenness measure	Order q	Assemblage I	Assemblage II
E1	$q=1$	0.650	0.747
	$q=2$	0.556	0.803
E2	$q=1$	0.650	0.747
	$q=2$	0.385	0.449
E3	$q=1$	0.569	0.581
	$q=2$	0.385	0.449
E4	$q=1$	0.725	0.874
	$q=2$	0.556	0.803
E5	$q=1$	0.650	0.747
	$q=2$	0.469	0.639
E6	$\alpha=1$	0.333	0.458
	$\alpha=2$	0.333	0.556
Gini evenness index		0.667	0.550
Normalized Gini evenness index		0.334	0.438

The R function (Lorenz.R) for computing and plotting Lorenz curves of assemblages are included in the R code “Evenness” available at Anne Chao’s Github (<https://github.com/AnneChao>) and in Zenodo: <https://doi.org/10.5281/zenodo.3341384>.

S2. Some other evenness measures

In their consumer’s guide to evenness indices, Smith and Wilson (1996) recommended the use of their own measure E_{var} as the best general-purpose evenness measure. Tuomisto (2012) defined “evenness” as the ratio of diversity and species richness (i.e., ${}^qD/S$) in her updated consumer’s guide. Both of the recommended measures are replication invariant. Kvålseth (2015) showed that the measure E_{var} violates the fundamental principle of transfer (Requirement 1a) and is thus *not* a valid evenness index. As discussed in the Discussion of the main text, the range of ${}^qD/S$ depends on species richness and thus violates the independence requirement (Requirement 3a).

Hill (1997) proposed a class of evenness measures as a ratio of two Hill numbers, ${}^qD/{}^bD$

(see Eq. 1 of the main text), for all possible pairs of diversity orders q and b . Note that any ratio of two Hill numbers satisfies replication invariance; it tends to the maximum value of unity for completely even communities, and also tends to unity for the most uneven assemblage (Peet 1974). Thus, any ratio of two Hill numbers cannot be a legitimate evenness measure. Similar arguments can be applied to Hill's (1997) replication-invariant index, $(^3D/^2D)^2$. Alatalo (1981) proposed a modified Hill's ratio: $(^2D-1)/(^1D-1)$, but it does not possess the fundamental principle of transfer (Kvålseth 2015) and thus cannot be a legitimate evenness measure.

S3. Statistical estimation

All the proposed evenness measures in Table 1 of the main text are in terms of abundance-based diversity (i.e., $q > 0$) and species richness. In practice, diversity needs to be estimated from sampling data. It is well known that the observed diversity values (including the observed species richness) in a sample underestimate the true parameters (Chao and Jost 2015). For severely under-sampled data, the estimation of species richness ($q = 0$) is a very difficult statistical issue; at best one can only obtain a lower bound. Thus, all evenness measures cannot be accurately estimated from incomplete samples. In this case, to make fair comparisons among samples, ecologists have used rarefaction and extrapolation to compare species diversity at a standardized sampling effort or sample completeness (as measured by sample coverage); see Chao et al. (2014). The sample-size- and coverage-based integration of rarefaction and extrapolation represents a unified framework for estimating diversities and for comparing multiple assemblages based on these estimates. A similar sample-size- and coverage-based rarefaction/extrapolation approach can be applied to infer evenness profiles.

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