



An updated consumer's guide to evenness and related indices

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Ecologists widely agree that species diversity consists of two components, richness (the number of species) and evenness (a measure of the equitability of the proportional abundances of those species). However, no consensus on an exact definition of evenness (or equitability) has emerged. Instead, numerous equitability indices have been used in the ecological literature, as different researchers have preferred indices with different mathematical properties. In this paper, I show that the phrase 'species diversity consists of two independent components, richness and evenness' logically leads to one particular definition of evenness ($\text{Evenness} = \text{Diversity/Richness}$). To facilitate accurate communication, I propose that the term 'evenness' be used only to refer to this phenomenon, and that other terms be used for the equitability indices that measure other things. Here I provide a review of popular equitability indices, explain what each measures in practice, and show how they relate to each other and to evenness itself. I also explore how the partitioning of diversity into richness and evenness components is related to the partitioning of diversity into alpha and beta components. Dissecting the indices makes it easier to see the conceptual differences among them. Such understanding is necessary to ensure that an appropriate index is chosen for the questions at hand, as well as to interpret the index values correctly and to assess when index values can and when they cannot be considered comparable.

Species diversity is traditionally thought to consist of two components, richness and evenness (Lloyd and Ghelardi 1964, Pielou 1966a, Sheldon 1969, Hurlbert 1971, Peet 1974, DeJong 1975, Solomon 1979, Taillie 1979, Alatalo 1981, Smith and Wilson 1996, Rousseau et al. 1999, Ricotta and Avena 2000, 2002, Gosselin 2001, Ricotta 2003, Olszewski 2004, Kindt et al. 2006, Symonds and Johnson 2008, Reitalu et al. 2009). Species richness refers to the number of species in the community of interest, and evenness to the equitability of the proportional abundances of those species.

Up to this point, there seems to be consensus. However, when it comes to actually defining evenness so that it can be quantified from data, opinions start to diverge. There are many different ways in which an index can reflect the degree of equitability among species abundances, and many different equitability or evenness indices have hence been proposed. There does not seem to be any agreement on which of the indices (if any) should be preferred, or why (Peet 1974, Alatalo 1981, Routledge 1983, Kvålseth 1991, Smith and Wilson 1996, Ricotta and Avena 2000, Gosselin 2001, Mouillot and Wilson 2002, Ricotta 2004).

Because different indices can quantify conceptually different things, two studies whose stated purpose is to document 'evenness' can actually focus on entirely different phenomena. Sometimes it is not even clear which phenomenon is being discussed, because many papers report results on 'evenness'

without specifying how it was quantified. Erroneous conclusions can easily be drawn if differences among indices are not taken into account when comparing results.

The situation is almost as confusing as in the case of beta diversity, which has also been associated with a bewildering multitude of indices. Many beta diversity indices have little or no logical connection to each other, but some are derived from the idea that gamma diversity consists of two components, alpha diversity and beta diversity (reviewed by Tuomisto 2010a, b).

Here I will first review what common evenness or equitability indices actually quantify, and then explore the relationships between the two ways of partitioning diversity (evenness–richness and alpha–beta).

In search of the best evenness index

Many researchers have approached the problem of defining evenness or equitability by listing desirable properties of an evenness index, and then evaluating how well different indices fulfil those criteria (Engen 1979, Alatalo 1981, Routledge 1983, Smith and Wilson 1996, Gosselin 2001, Ricotta et al. 2001). The most influential of such studies is the review by Smith and Wilson (1996). They assembled fifteen criteria for good evenness measures proposed in the literature, and treated four of these as essential requirements and ten as desirable features; one was rejected as undesirable.

Their four essential requirements have a long history (Dalton 1920) and can be rephrased as follows:

- 1) Evenness should be replication invariant: it should not change when a dataset is replicated such that each of its species gives rise to n new species of the same absolute abundance as the original one.
- 2) Evenness should decrease when abundance is transferred from a less abundant species to a more abundant one.
- 3) Evenness should decrease when an exceedingly rare species is added.
- 4) Evenness should be scale invariant, such that it depends on the proportional rather than absolute abundances of species.

After describing the essential requirements and desirable features of evenness, Smith and Wilson (1996) proceeded to evaluate how well fourteen evenness indices performed against these criteria. They found that five of the indices (E_{var} , 0, E_Q , E' and $E_{1/D}$ in their notation) fulfilled all essential requirements, but none had all the desirable features.

Another popular approach is to use compatibility with the Lorenz partial order as the main criterion for choosing among evenness measures (Taillie 1979, Nijssen et al. 1998, Rousseau et al. 1999, Gosselin 2001). The Lorenz curve shows the increase in cumulative proportional abundance of the species as a function of the proportion of species already considered, with species being ranked from the least abundant to the most abundant (Fig. 1). If all species are equally abundant, each new species adds the same amount of proportional abundance and the Lorenz curve becomes a straight line along the diagonal of the diagram. As the inequality in the species abundances increases, the Lorenz curve falls increasingly below the diagonal. Any evenness index that is Lorenz compatible must correctly indicate whether the Lorenz curve of one dataset is above or below that of another dataset. If the Lorenz curves of two datasets cross, then one is not intrinsically more even than the other, and two Lorenz compatible indices may rank them in opposite ways.

The essential requirements of Smith and Wilson (1996) pose no conflict with the Lorenz criterion, but many of

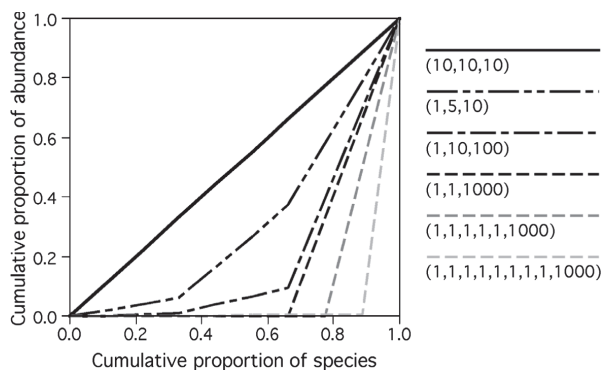


Figure 1. Lorenz curves of different datasets. Species along the x-axis are ranked from the least abundant to the most abundant. The absolute abundances of the species of each dataset are listed below the corresponding line type. Because the Lorenz curve is replication invariant, the same curve is obtained with the three-species dataset (1,5,10) and any dataset derived by exactly replicating its species, such as (1,1,5,5,10,10) and (1,1,1,5,5,5,10,10,10).

Settling for terminological clarity

The fact that no single index can be declared universally superior to the others does not mean that the indices are interchangeable. On the contrary, different evenness indices correspond to very different phenomena (such as relative diversity, entropy ratio and rate of increase in diversity). Choosing a relevant index for any particular purpose requires that it is understood which phenomenon each of the available indices quantifies. Similarly, and perhaps more obviously, different size indices (such as m , r , r^2 , πr^2 , r^3 and $4/3\pi r^3$) correspond to very different phenomena (such as mass, length, area and volume). Comparing index values without keeping track of which values represent length and which represent volume is both meaningless and potentially dangerous.

Similarly, accurate communication about issues related to evenness is only possible if indices that actually quantify different things are each called by a different name. The terminology is currently unstable, so the words ‘evenness’ and ‘equitability’ have been used as synonyms, as have ‘unevenness’ and ‘inequality’. I propose to use the terms ‘evenness’ and ‘unevenness’ in a specific quantitative sense (to be defined below; analogous to ‘length’), and the terms ‘equitability’ and ‘inequality’ in a more generic sense (analogous to ‘size’). I also propose descriptive unique names for the phenomena that correspond to aspects other than evenness in the strict sense.

If the use of the term 'evenness' is restricted to just one phenomenon, which one should that be? Ideally, this choice should be as compatible as possible with earlier practice. Let us therefore use as a starting point the most often repeated statement that involves the word 'evenness' in the ecological literature: 'diversity consists of two independent components, richness and evenness'. On the basis of this

postulate, we can infer some characteristics that an evenness measure should have.

Inference 1

Diversity, richness and evenness are each called by a different term, rather than by the same term with a different specifier. This suggests that 'independent' refers to conceptual independence, which implies that each term represents a different phenomenon (analogous to length and weight), rather than the same phenomenon as measured for a different part of a community (analogous to body length and tail length).

Inference 2

The statement that evenness and richness are independent can also refer to numerical independence, which implies that the two are free to vary independently of each other. In other words, there should be no mathematical necessity for the value of one component to change just because the value of the other does.

Inference 3

The purpose is to partition diversity into exactly two components, so the two should be sufficient to completely determine diversity. In other words, diversity should be expressible as a simple function of richness and evenness such that no other terms are needed in the equation.

Inference 4

When richness and evenness are combined, they are to produce a single value (diversity) as a result. Conceptually different phenomena are quantified using measurement units that cannot be transformed to each other by multiplying with a constant (for example, metres and feet represent the same phenomenon but metres and square metres do not). Therefore, if richness and evenness are to yield a single value, they have to be combined using multiplication rather than addition (just as when combining length and surface area: $2\text{ m} \times 3\text{ m}^2$ yields a single number, but $2\text{ m} + 3\text{ m}^2$ does not).

These basic considerations are sufficient to derive an equation that partitions diversity into the desired components:

$$\text{Diversity} = \text{Richness} \times \text{Evenness} \quad (1)$$

From Eq. 1 it follows that evenness can be defined as:

$$\text{Evenness} = \text{Diversity} / \text{Richness} \quad (2)$$

Jost (2010) pointed out that richness and evenness are not numerically independent of each other, because the minimum value that evenness can obtain in a dataset depends on richness (to be discussed in more detail after the concepts have been defined, below). In contrast, diversity and evenness are numerically independent, because one does not constrain the range of values that can be taken by the other in any way. Therefore, Jost (2010) proposed that we partition richness instead of diversity:

$$\text{Richness} = \text{Diversity} \times \text{Unevenness} \quad (3)$$

from which follows that unevenness is simply the inverse of evenness:

$$\text{Unevenness} = \text{Richness} / \text{Diversity} = 1 / \text{Evenness} \quad (4)$$

There is no logical conflict between the two ways of looking at the issue, so all four equations are equally valid. All also satisfy the inference that richness and evenness should be conceptually independent. However, the inference that richness and evenness should be numerically independent is only satisfied in part: the minimum value of evenness is dependent on the value of richness, but above that limit richness can vary although evenness remains unchanged, and vice versa. Given our pragmatic starting point, we can decide that this degree of numerical independence, together with full conceptual independence, is sufficient to satisfy the statement of independence in the definition of evenness proposed above. Thereby Eq. 2 qualifies as the logical mathematical expression of this definition.

The relationships spelled out in Eq. 1–4 seem simple enough, but there has been some disagreement on how to quantify richness, and especially diversity has been quantified using many different indices. Consequently, opinions differ on how the above equations should be applied to data, which has led to different definitions of evenness even among researchers who agree on the equations themselves. For example, it has been proposed that we first choose an evenness index, and then use it to define diversity according to Eq. 1 (Camargo 1992a, 1993, 1995, 2008, Bulla 1994, Rousseau et al. 1999). Alternatively, we can first choose a definition for diversity, and then use it to define evenness and unevenness according to Eq. 2 and 4, respectively. I will use the latter approach, because a logical and universally applicable definition of diversity is already available (Hill 1973).

In the rest of the present paper, I will focus on three main questions. 1) If we apply the above definitions of evenness and unevenness to a dataset, what do the resulting numbers actually mean? 2) What phenomena do other equitability indices represent, and how do these relate to each other? Indices to be discussed include diversity and evenness ratios, relative diversities and evennesses, rates of diversity increase, relative entropies, entropy differences and relative probabilities. 3) How does the partitioning of diversity into richness and evenness components relate to the partitioning of diversity into alpha and beta components?

Defining richness

Ecologists tend to agree that species richness (notated S) is a number of species. More generally, richness (notated R) can be defined as the number of types that a set of observed entities is classified into. Often the entities of interest are individual plants or animals, but they can also be ramets, units of surface area, units of biomass, or something else. The entities can be classified into any types that are relevant for the questions at hand, such as species, genera, families, haplotypes, functional types or size classes (Peet 1974, Solomon 1979). Whatever the classification of interest, richness equals the number of types needed to assign each entity

to an appropriate category. The unit of measurement changes with the classification used: species richness is measured in units of species (sp), genus richness in units of genera, functional richness in units of functional types, and so on (Tuomisto 2010c, 2011). Here I mostly focus on species, but the logic is the same for any classification.

To quantify richness in any particular case, we only need to decide which entities form the dataset of interest, and how they are classified into types. When these two choices have been made, a single perfectly accurate value of richness for that dataset will automatically follow. Of course, the richness of an existing dataset only provides a biased estimate of richness for a community that includes unseen individuals of unknown species identity. However, assessing the degree to which a dataset is adequate for a particular purpose is a separate question that is outside the scope of this paper. Here I simply treat richness (just as diversity and evenness) as a property that can be measured for whichever dataset we have at hand (see also Bulla 1994, Smith and Wilson 1996, Tuomisto 2010a, b, c).

Defining diversity and entropy

To quantify richness, it is only necessary to know how many types are present in the dataset of interest, which in practice means that richness is based on presence-absence data. In contrast, quantifying diversity requires the availability of abundance data, because diversity takes the equitability in species abundances into account (Eq. 1; for a more thorough discussion, see Tuomisto 2010c, 2011).

A logically satisfying definition of diversity is the effective number of types (MacArthur 1965, Hill 1973, Routledge 1979), also known as the ‘Hill number’ and ‘true diversity’ (Jost 2006, 2007, 2010, Tuomisto 2010a, c, 2011). This is calculated as:

$${}^qD = 1 / {}^q\bar{p}_i = 1 / \sqrt[q]{\sum_{i=1}^R (p_i p_i^{q-1})} \quad (5)$$

Here p_i is the proportional abundance of the i th species (or other type of interest) and ${}^q\bar{p}_i$ is the weighted generalised mean with exponent $q - 1$ of the p_i values, with p_i itself being used as the weight. In practice, qD quantifies the number of effective species in the dataset, i.e. how many equally-abundant species would give the observed mean proportional species abundance. The parameter q defines the kind of mean used. Increasing the value of q gives more weight to the most abundant species and less weight to the rare ones, which leads to higher ${}^q\bar{p}_i$ and lower qD (Jost 2006, 2007, Tuomisto 2010a). 0D (diversity with $q = 0$) is based on the weighted harmonic mean of the p_i values ${}^0\bar{p}_i$, and its numerical value is the same as that of richness R . 1D is based on the geometric mean and equals the exponential of the Shannon entropy, and 2D is based on the arithmetic mean and equals the inverse of the Simpson index (Hill 1973, Tuomisto 2010a, c). Negative values of q are not used, as they would lead to diversity exceeding richness.

The larger the largest p_i values, the larger the mean p_i and hence the smaller the number of equally-abundant species that would yield the same value of ${}^q\bar{p}_i$. These hypothetical

equally-abundant species can be called effective species (${}^q\text{sp}_E$) and they are the unit of measurement of species diversity qD (note the use of the superscript q in both cases to specify which mean is used). If richness is based on a classification to types other than species (such as genera, functional types or haplotypes), then the measurement unit of diversity changes accordingly (effective genera, effective functional types and so on).

Both richness and diversity follow the replication principle, i.e. their values double when each species in a dataset is divided into two exactly equally abundant new species. Many indices of diversity have been proposed (Patil and Taillie 1979, Solomon 1979, Tóthmérész 1995, Rousseau et al. 1999), and most of these do not follow the replication principle. Furthermore, each index quantifies a different phenomenon. Equating the raw values of diversity indices with diversity itself (qD) has therefore led to confusion (Jost 2006, 2007, Tuomisto 2010a, c).

The most popular diversity index has been the Shannon entropy H' (variously known as the Shannon, Shannon–Weaver, Shannon–Wiener or Shannon–Weiner index). The Shannon entropy quantifies the uncertainty in the species identity of an individual that is randomly chosen from the dataset. It equals $\log({}^1D)$, which is a special case with $q = 1$ of the Rényi entropy

$${}^qH' = \log({}^qD) \quad (6)$$

The value of q defines how the probability of choosing a particular individual is affected by the abundance of the species it belongs to. When $q = 1$, each individual has the same probability of being chosen, and hence the probability that the chosen individual represents species i equals p_i . When $q = 0$, the probability that a given individual is chosen is inversely related to the abundance of its species, such that each species has the same probability of being represented whatever its actual abundance. When $q > 1$, the individuals belonging to the most abundant species have a higher probability of being chosen, and with sufficiently large q , the chosen individual is almost certainly of the most abundant species in the dataset, which has proportional abundance $p_{i\text{max}}$. The uncertainty in the species identity of the randomly chosen individual (= Rényi entropy) hence decreases asymptotically towards $\log(1/p_{i\text{max}})$ as q increases towards infinity.

Other popular diversity indices are the Simpson index (Simpson 1949), which equals ${}^2\bar{p}_i = 1/{}^2D$, and the Gini–Simpson index, which equals $1 - 1/{}^2D$. The measurement unit of both is ${}^2\text{sp}_E^{-1}$. When two individuals are taken at random from the dataset (with replacement), the Simpson index equals the probability that both belong to the same species, and the Gini–Simpson index the probability that they belong to different species. The probability of interspecific encounter (PIE of Hurlbert 1971) can either equal the Gini–Simpson index or differ in that the two individuals are taken from the dataset without replacement. Sampling with replacement will be assumed here unless explicitly stated otherwise.

The Gini–Simpson index is a special case of an entropy that is known in ecology as the Tsallis or HCDT entropy (Jost 2006, Mendes et al. 2008):

$${}^qT = (1 - {}^qD^{1-q})/(q - 1) \quad (7)$$

The value of the HCDT entropy is related to the probability that q individuals chosen at random from the dataset (with replacement) represent at least two different species.

As we will see below, each one of these diversity indices has been associated with one or more equitability indices. Some of these indices have been obtained by deriving an equation analogous to Eq. 2 but using diversity index values (e.g. H') rather than diversity itself (qD). In addition, equitability indices have been derived using other principles, such that they do not necessarily constitute a component of diversity (or of a diversity index) at all.

Defining different aspects of equitability and inequality

Evenness and unevenness

When evenness is defined by inserting diversity as defined in Eq. 5 into Eq. 2, we obtain:

$${}^qE = {}^qD/R \quad (8)$$

Similarly, unevenness obtained by using diversity in Eq. 4 is:

$${}^qU = R/{}^qD \quad (9)$$

Because evenness and unevenness are dependent on the proportional abundances of the species, the value of q is shown as a superscript, just as in the case of diversity. For any given dataset, large values of q lead to lower qE and higher qU than small values of q , because qD decreases when q increases, but R does not change (see Defining diversity and entropy, above). Among-dataset comparisons are therefore only meaningful if all measures are based on the same q .

In practice, qE quantifies how many effective types there are for each actual type in the dataset of interest. When the types of interest are species, the measurement unit of evenness is ${}^q\text{sp}_E/\text{sp}$. The highest value that evenness can take (${}^qE_{\max}$) is $1 {}^q\text{sp}_E/\text{sp}$. This is obtained when there are as many effective as actual species, i.e. when either all species are equally abundant or $q = 0$. When $q > 0$, diversity qD decreases towards $1 {}^q\text{sp}_E$ as the proportional abundance of the most abundant species increases towards unity. As a result, the smallest possible value of evenness (${}^qE_{\min}$) is $(1 {}^q\text{sp}_E)/R$. The minimum value is exactly reached only when $R = 1 \text{ sp}$ (in which case the minimum equals the maximum), because each species that is present in a dataset has to have a non-zero abundance. However, here we can assume that the dataset is so large that when all species but one are represented with a single individual, then p_{\max} rounds to unity with high accuracy.

Similarly, qU quantifies how many actual species (or other types of interest) there are for each effective species in the dataset of interest, and its measurement unit is $\text{sp}/{}^q\text{sp}_E$. The minimum value ${}^qU_{\min} = 1 \text{ sp}/{}^q\text{sp}_E$ is obtained when all species are equally abundant, and the maximum value ${}^qU_{\max} = R/(1 {}^q\text{sp}_E)$ is approached when all species but one have vanishingly small abundances.

Both qE and qU are Lorenz compatible (Taillie 1979, Nijssen et al. 1998, Gosselin 2001, Jost 2010), and they also fulfil the four essential requirements of Smith and Wilson (1996). Both measures are replication invariant: when a dataset is duplicated, both R and qD double, which leaves their ratios qE and qU unchanged. Both qE and qU follow the transfer principle: when individuals are transferred from a less abundant species to an already more abundant species, R remains the same but qD decreases, which causes qE to decrease and qU to increase. When an exceedingly rare species is added to the dataset, qE decreases and qU increases because R increases but qD remains practically the same. Finally, both qE and qU are scale invariant: they are not

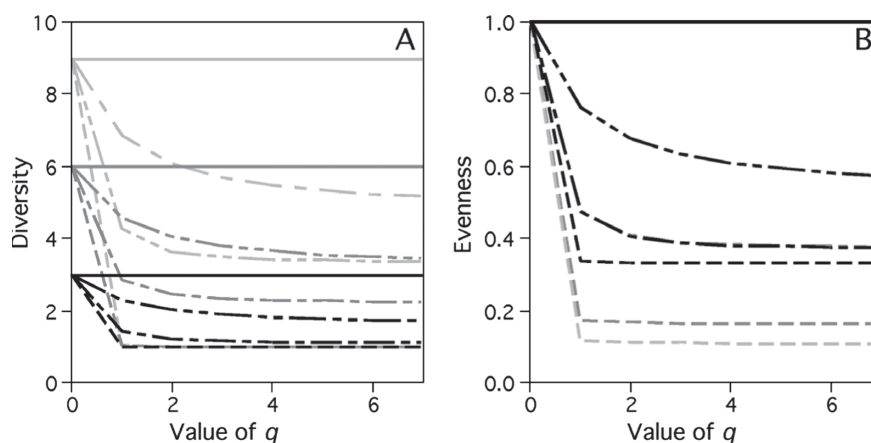


Figure 2. Diversity (A) and evenness (B) in datasets with different species abundance distributions as a function of the parameter q , which defines the mean used when quantifying mean proportional species abundance. The harmonic mean is used at $q = 0$, the geometric mean at $q = 1$, the arithmetic mean at $q = 2$ and the maximum value in the limit as q approaches infinity. Black lines correspond to the datasets with three species shown in Fig. 1. The three uppermost mid and pale gray lines correspond to datasets with six and nine species, respectively, which are obtained by replicating the three uppermost three-species datasets. Replicating a dataset by a given factor (here 2 or 3) multiplies diversity by the same factor but leaves evenness unchanged, so the corresponding curves are identical in (B). The datasets with lowest evenness correspond to the three lowermost lines in Fig. 1. These are not replicates of each other, which is why their evenness curves are not identical in (B).

affected by changes in absolute abundances as long as relative abundances remain the same.

As q is varied, different species abundance distributions lead to different trajectories of diversity qD , and hence of evenness qE and unevenness qU (Fig. 2; see also Ricotta and Avena 2000, 2002, Ricotta 2003, Kindt et al. 2006, Jost 2010). Plotting either qD , qE or qU as a function of q can therefore visualise dataset properties related to species abundance patterns. For datasets with the same R , a graph that plots qE against q is similar to a graph that plots qD against q , except for the units of measurement on the vertical axis. For datasets that differ in R , graphs showing qE and qD against q provide different, and complementary, insights (compare panels A and B in Fig. 2).

Evenness as defined in Eq. 8 has been used in several studies, with the most popular variants being 1E and 2E (Table 1). Smith and Wilson (1996) noted that out of the fourteen equitability indices they compared, 2E ($E_{1/D}$ in their notation; Table 2) is the only one that conforms to Eq. 2, but this was not among their requirements for an evenness index.

Diversity ratio, evenness ratio and unevenness ratio

Hill (1973) used as an equitability index a ratio of two diversities obtained with different values of q , rather than a ratio of diversity and richness. This diversity ratio can also be expressed as an evenness ratio (notation adapted to that used elsewhere in the present paper):

$$D_{q_2/q_1} = {}^{q_2}D/{}^{q_1}D = ({}^{q_2}D/R)/({}^{q_1}D/R) = {}^{q_2}E/{}^{q_1}E = E_{q_2/q_1} \quad (10)$$

In other words, Hill's measure expresses diversity (or evenness) calculated with one value of q as a proportion of diversity (or evenness) calculated with another value of q . Such a measure is useful when one is interested in quantifying by what factor the perceived diversity (or evenness) of a dataset changes when q is changed from q_1 to q_2 (i.e. the mean used when calculating mean species proportional abundance is changed).

The inverse of the evenness ratio can be interpreted as an unevenness ratio:

$$1/E_{q_2/q_1} = (1/{}^{q_2}E)/(1/{}^{q_1}E) = {}^{q_2}U/{}^{q_1}U = U_{q_2/q_1} = E_{q_1/q_2} \quad (11)$$

In other words, when q is changed from q_1 to q_2 , unevenness changes by the same factor as evenness does when q is changed the other way round.

As can be seen in Eq. 10, diversity ratio and evenness ratio are mathematically equivalent, so they always give the same end result. The following considerations therefore apply to both. The unevenness ratio, being the inverse of the other two, approaches unity in the same situations but increases when the other two decrease.

The behaviour of the diversity ratio depends both on how equal the proportional species abundances p_i are, and on the values of q_1 and q_2 . If all species are equally abundant, diversity as calculated with any value of q equals R , so the diversity ratio necessarily equals unity. The more unequal the species abundances, the more different the diversity values at different values of q , and the further away from unity the diversity ratio for any given combination of q_1 and q_2 . In general, diversity decreases as q increases. This causes the

Table 1. Examples of ecological studies that have used or discussed different 'equitability' indices. Most indices are explained in Table 2, but those marked with * are actually indices of diversity rather than equitability, and are explained in the main text only (see Defining diversity and entropy). Indices marked with # do not follow the uniform notation proposed in the present paper but the notation of Smith and Wilson (1996) as shown in the last column of Table 2.

Index	References
1E	Sheldon 1969, Buzas and Gibson 1969, Buzas and Hayek 1996, Hayek and Buzas 1997, 1998, Small and McCarthy 2002, Camargo 2008
2E	Weiher and Keddy 1999, Wilsey and Potvin 2000, Mouillot and Wilson 2002, Brosse et al. 2003, De Deyn et al. 2003, Ma 2005, Martin et al. 2005, Bock et al. 2007, Scrosati and Heaven 2007, Wilsey and Stirling 2007, Camargo 2008
$D_{q/0}$	Alatalo 1981, Taillie 1979, Patil and Taillie 1982, Ricotta and Avena 2000, 2002, Ricotta 2003, Jost 2010
$D_{2/1}$	Rotenberry 1978, Alatalo 1981, Ricotta and Avena 2000
$J'_{1/\max}$ or $J'_{1/0}$ or ${}^1J'$	Sheldon 1969, Tramer 1969, Kricher 1972, DeBenedictis 1973, DeJong 1975, Errhif et al. 1997, Qian et al. 1997, Wills et al. 1997, Rex et al. 2000, Wilsey and Potvin 2000, Stirling and Wilsey 2001, He and Legendre 2002, Miranda et al. 2002, Woodd-Walker et al. 2002, Olszewski 2004, Cao and Hawkins 2005, Ma 2005, Veneklaas et al. 2005, Wilsey and Stirling 2007, Lamb and Cahill 2008, Reitalu et al. 2009, Anticamara et al. 2010, Castro et al. 2010, Kardol et al. 2010, Villéger et al. 2010, Spatharis et al. 2011
H'_{1-0}	Hill 1973, Ricotta 2003, Kindt et al. 2006
$T_{2/\max}$ or PIE'	Hurlbert 1971, Fager 1972, DeJong 1975, Smith and Wilson 1996, Cook 2008
* H'	Jabot and Chave 2009, Anticamara et al. 2010
* 2T or PIE	Weiher and Keddy 1999, Stevens and Willig 2002, Dangles and Malmqvist 2004, Olszewski 2004, Davis 2005, Vellend 2005, Ulrich and Zalewski 2007, Jarvis et al. 2008, Anticamara et al. 2010, Blois et al. 2010
* ${}^2H'$	Walker and Cyr 2007
* 2D or 1D	Gardezi and Gonzales 2008, Anticamara et al. 2010
# O	Mouillot and Wilson 2002, Stevens and Willig 2002
# E' or Gini coefficient	Camargo 1992a, 1993, Drobner et al. 1998, Mouillot and Leprêtre 1999, Nijs and Roy 2000, He and Legendre 2002, Mouillot and Wilson 2002, Stevens and Willig 2002, Ma 2005, Wittebolle et al. 2009, Poggio and Ghersa 2011
# E_{var}	Drobner et al. 1998, Weiher and Keddy 1999, Mouillot and Wilson 2002, Ma 2005, Laird and Schamp 2006, Symonds and Johnson 2008, Bernhardt-Römermann et al. 2011, Nimmo et al. 2011
# NHC	Weiher and Keddy 1999
# E_Q	Drobner et al. 1998, Mouillot and Wilson 2002, Ma 2005

Table 2. Characterization of equitability indices that have been used in the ecological literature. The uniform notation used elsewhere in the present paper is shown in the second column. Equation numbers are given in the third column for those indices that are covered in detail in the text. The last column shows the notation used by Smith and Wilson (1996), and if an equal sign is present, it also specifies how the variant used by Smith and Wilson (1996) would be expressed in the uniform notation. qD is species diversity, R is the total number of individuals in the dataset, and m_i is the number of individuals belonging to species i . Subscript min and max refer to the minimum and maximum values, respectively, that the variable in question can take given R and assuming very large m . Measurement units: sp are actual species, qsp_E are effective species, ind are individuals, and bits, nats and decits are units of uncertainty as quantified with log bases 2, e and 10, respectively.

Type of measure	Present notation	Calculation	Interpretation	Range of values	Measurement unit	Lorenz compatible	Notation in S&W
Absolute evenness	qE	$= {}^qD/R$ (Eq. 8)	Evenness of order q ; the number of effective species per actual species	$]1/R, 1]$	${}^qsp_E/sp$	yes	$E_{1/D} = {}^2E$
Relative diversity or relative evenness	$D_{q/\max}$ or $E_{q/\max}$	$= {}^qD/{}^qD_{\max}$ $= {}^qE/{}^qE_{\max}$ (Eq. 12)	Diversity or evenness expressed as a proportion of its maximum value (alternatively expressible as a percentage)	$]1/R, 1]$ (alternatively $[100/R, 100]$)	unitless as derived from ${}^qsp_E/{}^qsp_E$ or ${}^qsp_E/sp$ (alternatively %)	yes	
Relative diversity or relative evenness	${}^qD'_{q/\max}$ or ${}^qE'_{q/\max}$	$= \frac{{}^qD - {}^qD_{\min}}{{}^qD_{\max} - {}^qD_{\min}}$ $= \frac{{}^qE - {}^qE_{\min}}{{}^qE_{\max} - {}^qE_{\min}}$ (Eq. 13)	Diversity or evenness expressed in relation to its possible range (alternatively expressible as a percentage)	$]0, 1]$ (alternatively $]0, 100]$)	unitless as derived from ${}^qsp_E/{}^qsp_E$ or ${}^qsp_E/sp$ (alternatively %)	no	
Diversity ratio, evenness ratio or unevenness ratio	$D_{q2/q1}$ or $E_{q2/q1}$ or $U_{q1/q2}$	$= {}^qD/{}^{q1}D$ $= {}^qE/{}^{q1}E$ $= {}^{q1}U/{}^{q2}U$ (Eq. 10–11)	The factor by which diversity or evenness changes when q is changed from q_1 to q_2 or the factor by which unevenness changes when q is changed the other way round	Strictly positive and ≤ 1 when $q_1 < q_2$; $= 1$ when $q_1 = q_2$; ≥ 1 when $q_1 > q_2$	${}^{q2}sp_E/{}^{q1}sp_E$ which may also be derived from $\frac{{}^{q2}sp_E/sp}{{}^{q1}sp_E/sp}$ or $\frac{sp/{}^{q1}sp_E}{sp/{}^{q2}sp_E}$	only if $q_1 = 0$ and $q_2 \neq 0$ (or if $q_1 \neq 0$ and $q_2 = 0$, but then increases with inequality)	$E_{2,1} = E_{2/1}$
Rate of change	qF	$= ({}^qD - 1)/(R - 1)$ (Eq. 14–15)	Average rate of change in diversity as richness increases from 1 to R (numerical value as that of ${}^qD'$)	$]0, 1]$	${}^qsp_E/sp$	no	$E_{\text{Heip}} = {}^1F$
Rate of change	$F_{q2/q1}$	$= ({}^{q2}D - 1)/({}^{q1}D - 1)$ (Eq. 16–17)	Average rate of change in diversity of order q_2 as diversity of order q_1 increases from 1 to 1D	Strictly positive and ≤ 1 when $q_1 < q_2$; $= 1$ when $q_1 = q_2$; ≥ 1 when $q_1 > q_2$	${}^{q2}sp_E/{}^{q1}sp_E$	no	$F_{2,1} = F_{2/1}$
Entropy ratio	${}^qJ'$	$= \log({}^qD)/\log(R)$ (Eq. 21)	The uncertainty in the species identity of a randomly chosen individual expressed as a proportion of the uncertainty in the identity of a randomly chosen species	$]0, 1]$	unitless, derivation depends on the base of the logarithm, e.g. bit/bit, nat/nat or decit/decit	no	$J' = {}^1J'$ $E_{-\ln D} = {}^2J'$
Entropy ratio	$J'_{q/\max}$	$= \log({}^qD)/\log({}^qD_{\max})$ (Eq. 20)	The uncertainty in the species identity of a randomly chosen individual expressed as a proportion of its maximum possible value	$]0, 1]$	unitless, derivation depends on the base of the logarithm, e.g. bit/bit, nat/nat or decit/decit	no	

(Continued)

Table 2. (Continued)

Type of measure	Present notation	Calculation	Interpretation	Range of values	Measurement unit	Lorenz compatible	Notation in S&W
Entropy ratio	J_{q_2/q_1}	$= \frac{\log(q_2 D) - \log(q_1 D)}{\log(q_2 D)} \quad (\text{Eq. 22})$	The factor by which the perceived uncertainty in the species identity of a randomly chosen individual changes when q is changed from q_1 to q_2	Strictly positive and ≤ 1 when $q_1 < q_2$; $= 1$ when $q_1 = q_2$; ≥ 1 when $q_1 > q_2$	unitless, derivation depends on the base of the logarithm, e.g. bit/bit, nat/nat or decit/decit	no	
Entropy difference	$H'_{q_2 - q_1}$	$\begin{aligned} &= q_2 H' - q_1 H' \\ &= \log(q_2 D) - \log(q_1 D) \\ &= \log(D q_2 / q_1) \\ &= \log(E_{q_2/q_1}) \\ &= -\log(U_{q_2/q_1}) \quad (\text{Eq. 25-27}) \end{aligned}$	The amount by which the uncertainty in the species identity of a randomly chosen individual changes when q is changed from q_1 to q_2	≤ 0 when $q_1 < q_2$; $= 0$ when $q_1 = q_2$; ≥ 0 when $q_1 > q_2$	depends on the base of the logarithm, e.g. bit, nat or decit	only if $q_1 = 0$ and $q_2 \neq 0$ (or if $q_1 \neq 0$ and $q_2 = 0$, but then increases with inequality)	
Entropy difference	$\log(qE)$	$\begin{aligned} &= \log(qD) - \log(R) \\ &= \log(qD/R) \quad (\text{Eq. 28}) \end{aligned}$	The amount by which the uncertainty in the species identity of a randomly chosen individual exceeds the uncertainty in the identity of a randomly chosen species	≤ 0	depends on the base of the logarithm, e.g. bit, nat or decit	yes	
Relative probability	$T_{q/\max}$	$= \frac{1 - qD^{1-q}}{1 - qD_{\max}^{1-q}} \quad (\text{Eq. 31})$	Probability of picking q individuals of at least two species expressed as a proportion of that probability when all species are equally abundant	$]0, 1]$	unitless as derived from $q \text{sp}_E^{1-q/q} \text{sp}_E^{1-q}$	no	E_{1-D} or $E_{\text{Mcl}} = T_{2/\max}$
Mean pairwise similarity		$= 1 - \frac{\sum_{i=1}^{R-1} \sum_{j=i+1}^R p_i - p_j }{R}$	The one-complement of mean pairwise differences in species proportional abundances	$[1/R, 1]$	sp^{-1} as derived from (ind/sp)/ind (R is taken as a unitless counting parameter)	yes	E'
Cumulative abundance		$= \sum_{i=1}^R \min(p_i, 1/R)$	Sum of those parts of species proportional abundances that do not exceed $1/R$	$[1/R, 1]$	sp^{-1} as derived from (ind/sp)/ind	no	O
Relative cumulative abundance		$= \frac{O - 1/R}{1 - 1/R}$	O expressed in relation to its possible range (alternatively expressable as a percentage)	$]0, 1]$	unitless as derived from $\text{sp}^{-1}/\text{sp}^{-1}$ (alternatively %)	no	E
Transformed rate of change		if $F_{2/n} > 0.707107$ then: $= F_{2/n} \cdot 0.636611 \cdot \arcsin F_{2/n}$ else: $= F_{2/n}^{2/3}$ $= 1 - \frac{2}{\pi} \arctan \frac{\sum_{j=1}^R \left(\ln(m_j) - \sum_{j=1}^R \ln(m_j)/R \right)^2}{R}$? (Non-linear transformation of $F_{2/n}$)	? (alternatively $]0, 100])$?	no	$G_{2,1}$
Transformed variance			? (Non-linear transformation of the variance in the logarithms of the absolute abundances of the species)	$]0, 1]$?	no	E_{var}
Regression slope		$= b'$	Slope of the Dominance/Diversity curve as fitted by least-squares regression	≤ 0	?	no	NHC
Transformed regression slope		$= -2/\pi \arctan(b')$? (Non-linear transformation of NHC)	$]0, 1]$?	no	E_Q

diversity ratio to be smaller than unity when $q_1 < q_2$, equal to unity when $q_1 = q_2$, and larger than unity when $q_1 > q_2$. The exact behavior of the diversity ratio is difficult to predict, however, as are the minimum and maximum values it can take. As the difference between q_1 and q_2 increases, the diversity ratio deviates more from unity. At the same time, increasing both q_1 and q_2 (even if their difference remains the same) causes the deviation from unity to decrease, because then both qD and qE tend towards the same value ($1/p_{i\max}$; see Defining diversity and entropy, above).

Diversity ratio and evenness ratio do not equal evenness as defined in Eq. 2, and unevenness ratio does not equal unevenness as defined in Eq. 4. Evenness qE is the ratio of two conceptually different phenomena, diversity qD and richness R . The diversity of a dataset can change while richness stays constant and vice versa, the only constraint being that ${}^qD \leq R$ because $q \geq 0$, which limits qE to values equal to or smaller than unity. In contrast, the diversity ratio is a ratio of two variables representing the same phenomenon, namely diversity. Its numerator qD cannot change without the denominator qD also changing, unless either q_1 or q_2 (but not both) equals zero. Furthermore, the diversity ratio is not bounded by unity, but can exceed it if $q_1 > q_2$.

In the special case when $q_1 = 0$, the numerical value of the diversity ratio $D_{q_2/0}$ equals that of evenness qE , because the numerical value of 0D always equals that of R . Several authors addressing $D_{q_2/0}$ have indeed found it appropriate as an equitability measure (Table 1). The diversity ratio $D_{2/1}$ has also been used as a measure of equitability (Table 1). However, D_{q_2/q_1} is only Lorenz compatible when either $q_1 = 0$ or $q_2 = 0$, so using $D_{2/1}$ as a measure of equitability leads to logical inconsistencies.

Jost (2010) equated richness R with diversity of order zero 0D , and hence treated evenness qE and the diversity ratio $D_{q/0}$ as synonyms. However, above it was inferred that the terms ‘richness’ and ‘diversity’ should refer to conceptually different phenomena (see Settling for terminological clarity). Conceptually different terms cannot be synonymous and are not interchangeable in mathematical equations: the result represents a different phenomenon depending on which of the alternatives is used in the calculation (just as would happen if length were changed for volume).

Relative diversity, relative evenness and relative unevenness

Hurlbert (1971) asserted that equitability measures can be derived by expressing the observed value of a diversity index in relative terms. Relative measures can be obtained either by dividing the observed index value by the maximum possible value, or by ranging (i.e., first subtracting the minimum value and then dividing by the possible range). Such measures are not evenness in the sense of Eq. 2, but they can be useful for other purposes. When the first approach is applied to diversity qD or evenness qE it gives:

$$\begin{aligned} D_{q/\max} &= {}^qD / {}^qD_{\max} = ({}^qD/R) / ({}^qD_{\max}/R) \\ &= {}^qE / {}^qE_{\max} = E_{q/\max} \end{aligned} \quad (12)$$

This relative diversity (or relative evenness) measure simply expresses the observed diversity (or evenness) as a proportion

of the maximum value it could take in a dataset with the observed number of species. The maximum value of this relative measure is unity, and the minimum value is ${}^qD_{\min}/{}^qD_{\max}$ (which equals ${}^qE_{\min}/{}^qE_{\max}$). Here ${}^qD_{\max}$ (or ${}^qE_{\max}$) is the largest and ${}^qD_{\min}$ (or ${}^qE_{\min}$) the smallest value the original variable could take. If the ranging equation is used, the relative measure becomes (note the apostrophe; see also Hurlbert 1971, Jost 2010):

$$\begin{aligned} D'_{q/\max} &= ({}^qD - {}^qD_{\min}) / ({}^qD_{\max} - {}^qD_{\min}) \\ &= ({}^qD/R - {}^qD_{\min}/R) / ({}^qD_{\max}/R - {}^qD_{\min}/R) \\ &= ({}^qE - {}^qE_{\min}) / ({}^qE_{\max} - {}^qE_{\min}) = E'_{q/\max} \end{aligned} \quad (13)$$

This ranges the original variable to the interval $]0, 1]$, and in practice specifies the relative position of the observed diversity (or evenness) between the smallest and largest value it could theoretically take.

A major conceptual difference between absolute and relative measures is that the absolute measures only depend on actually observed properties of the dataset of interest (R , qD and qE), and their values are therefore unambiguous. In contrast, the relative measures also depend on hypothetical properties (${}^qD_{\max}$ or ${}^qE_{\max}$ and ${}^qD_{\min}$ or ${}^qE_{\min}$). Since these were not actually observed, they can be defined in different ways, and each definition leads to a different relative measure. One option is to define the maximum and minimum limits on the basis of what is possible in a very large dataset with the observed number of species R (Jost 2010). A second option is to define the limits on the basis of what is possible given R and the observed number of individuals m (Hurlbert 1971). Then ${}^qD_{\min}$ is the diversity that is obtained when $R - 1$ species are represented by a single individual each, and the R th species by $m - (R - 1)$ individuals. ${}^qD_{\max}$ is the diversity obtained when all species are as equally abundant as possible, but unless m/R is an integer, some species will still be slightly more abundant than others. A third option is to use as the reference point the diversity obtained with R species following an arbitrarily chosen species abundance distribution. For example, Lloyd and Ghelardi (1964) expressed observed diversity as a proportion of the diversity that would be obtained if species abundances followed MacArthur’s broken stick model. Because species abundances in this model are far from equal, the relative diversity values obtained are much larger than if theoretical maxima had been used, and could also exceed unity. In the following, it is assumed that the maxima are based on the first option, i.e. the numerical value of ${}^qD_{\max}$ equals that of R and 0D .

The relative measures of Eq. 12 ($D_{q/\max}$ and $E_{q/\max}$) obtain the same value as evenness itself ${}^qE = {}^qD/R$, the diversity ratio $D_{q/0} = {}^qD/{}^0D$ and the evenness ratio $E_{q/0} = {}^qE/{}^0E$. If $q > 0$, all five measures range in the interval $[1/R, 1]$, but their measurement units differ. The unit of qE is ${}^q\text{sp}_E/\text{sp}$, the unit of $D_{q/0}$ and $E_{q/0}$ is ${}^q\text{sp}_E/{}^0\text{sp}_E$ and the unit of $D_{q/\max}$ and $E_{q/\max}$ is ${}^q\text{sp}_E/{}^q\text{sp}_E$, which simplifies to a unitless value. If $q = 0$, also the diversity ratio and evenness ratio become unitless and the values of all five measures equal unity.

The ranged value obtained with Eq. 13 is contained in the interval $]0, 1]$; it cannot exactly equal zero, because the minimum diversity of unity (and the minimum evenness of $1/R$) is only exactly reached in datasets that consist of a single species. In this case, the minimum equals the maximum and

the ranged value becomes undefined. The ranged value is undefined also when $q = 0$, because the value of 0D is the same irrespectively of species abundances.

Relative measures of unevenness qU can be derived in a similar way. In a large dataset ($m \gg R$), unevenness potentially varies in the interval $[1, R]$ (unit $\text{sp}/{}^q\text{sp}_E$). This can be expressed in relative terms either by expressing qU as a proportion of ${}^qU_{\max}$ (as in Eq. 12), or by ranging qU to the unitless interval $[0, 1]$ (see also Jost 2010).

As defined in Eq. 8, evenness qE quantifies how many effective species a dataset contains for each actual species. Sheldon (1969) criticised 1E for decreasing when R is changed by taking an individual from the most abundant species and allocating it to a new species. Increasing R in this way hardly affects qD but causes the single effective species to be divided among an increasing number of actual species, which forces the Lorenz curve further away from the diagonal and decreases qE (Fig. 1–2; see also Gosselin 2001). In contrast, the ranged measure $E'_{q/\max}$ gives near-zero values for all of Sheldon's datasets, because each one of them has maximally unequal species abundances. If R increases as a result of replicating the dataset, the Lorenz curves of all replicate datasets are identical. In this case, qE does not change but $E'_{q/\max}$ does when R is changed.

qE is replication invariant, but its minimum value depends on richness. In contrast, the minimum value of the ranged measure $E'_{q/\max}$ (Eq. 13) is zero no matter what the species richness of a dataset, so $E'_{q/\max}$ cannot be replication invariant. The fewer species a dataset contains (and hence the larger ${}^qE_{\min}$), the larger the difference between the absolute and ranged evenness value.

Absolute and relative evenness serve different purposes, just as absolute and relative measures do in other contexts (e.g. when measuring species abundances). Unfortunately, absolute and relative evenness can easily be confused in practical applications, because each only takes non-negative values smaller than unity. Expressing relative evenness as a percentage rather than as a proportion would help discriminate between the two: it is quite obvious that 50% is not the same thing as $0.5 \text{ sp}_E/\text{sp}$. As always with percentages, care needs to be taken to explicitly specify the reference range of the percentages, i.e. if 0% corresponds to zero diversity or evenness (as in $D_{q/\max}$ and $E_{q/\max}$) or to a given minimum value of diversity or evenness (as in $D'_{q/\max}$ and $E'_{q/\max}$).

Rate of increase in diversity

Heip (1974) wanted an equitability measure whose minimum value does not depend on R , and introduced the index:

$${}^1F = ({}^1D - 1)/(R - 1) \quad (14)$$

This can be generalised to any value of q and rewritten (since any dataset must have at least one actual and one effective species):

$${}^qF = ({}^qD - {}^qD_{\min})/(R - R_{\min}) \quad (15)$$

qF does not equal evenness as defined in Eq. 2, but instead quantifies the average rate of increase in diversity as richness increases from one species to R . The measurement unit of

qF is the same as that of evenness qE , namely ${}^q\text{sp}_E/\text{sp}$, but numerical values differ. Instead of varying in the interval $[1/R, 1]$ as qE does, qF varies in the interval $[0, 1]$ just as do the ranged measures $D'_{q/\max}$ and $E'_{q/\max}$ (Eq. 13). If the dataset of interest is large ($m \gg R$), the numerical value of ${}^qD_{\max}$ equals that of R , and the numerical values of qF , $D'_{q/\max}$ and $E'_{q/\max}$ are identical (compare Eq. 13 and 15). Indeed, Jost (2010) considered $E'_{q/\max}$ and qF as synonyms, but doing so conflicts with the inference that richness and diversity should represent conceptually different phenomena.

Alatalo (1981) derived a new measure by modifying Hill's diversity ratio $D_{2/1} = {}^2D/{}^1D$ such that minimum diversity (unity) was subtracted from the numerator and the denominator separately:

$$F_{2/1} = ({}^2D - 1)/({}^1D - 1) \quad (16)$$

This measure can be generalised to any pair of q values as follows:

$$F_{q_2/q_1} = ({}^{q_2}D - {}^{q_2}D_{\min})/({}^{q_1}D - {}^{q_1}D_{\min}) \quad (17)$$

This quantifies the average rate of increase in diversity of order q_2 as diversity of order q_1 increases from unity (its minimum value) to ${}^{q_1}D$. Jost (2010) interpreted $F_{2/1}$ as a relative measure obtained by ranging the evenness ratio E_{q_2/q_1} to the interval $[0, 1]$ in a similar way as ranged evenness can be related to Heip's measure (Eq. 13, 15). However, the interpretation of F_{q_2/q_1} in these terms is not accurate. This can be seen by dividing all terms in Eq. 16 by 1D :

$$F_{2/1} = ({}^2D/{}^1D - 1/{}^1D)/({}^1D/{}^1D - 1/{}^1D) \quad (18)$$

For this to qualify as a ranging equation (such as Eq. 13), the ${}^1D/{}^1D$ term should equal the maximum value obtainable by ${}^2D/{}^1D$, and $1/{}^1D$ should equal the minimum. However, $1/{}^1D$ is not an accurate minimum value for ${}^2D/{}^1D$, because 2D and 1D covary: if 2D approaches unity, 1D must do so as well, which causes their ratio to approach its maximum value of unity. In fact, it seems impossible to define a generally applicable minimum value for the diversity ratio (see Diversity ratio, evenness ratio and unevenness ratio), and if one does not exist, then the diversity ratio cannot be ranged to a fixed interval at all.

Relative entropy and entropy ratios (based on Rényi or Shannon entropy)

Pielou (1966a, b) derived an equitability measure by expressing the observed Shannon entropy as a proportion of the maximum Shannon entropy that would be obtained if all R species were equally abundant. Then ${}^1D_{\max}$ equals R and 0D , so the same measure can be expressed in different ways:

$$J' = H'/H'_{\max} = \log({}^1D)/\log({}^1D_{\max}) = \log({}^1D)/\log(R) = \frac{\log({}^1D)}{\log({}^1D)/\log({}^0D)} \quad (19)$$

All versions of J' give the same numerical value when calculated for the same dataset. However, they can be interpreted in somewhat different ways, and their generalisations to Rényi entropies based on values of q other than unity are also different. The generalisation involving maximum values is:

$$J'_{q/\max} = \log({}^qD)/\log({}^qD_{\max}) \quad (20)$$

This is a measure of relative entropy that is analogous to the relative diversity $D_{q/\max}$ of Eq. 12. It quantifies the uncertainty in the species identity of an individual that is taken at random from the dataset as a proportion of the uncertainty that would be observed if all species were equally abundant. Here the value of q determines how the probability that a given individual is chosen depends on the proportional abundance of its species (see Defining diversity and entropy). The generalisation involving richness is:

$${}^qJ' = \log({}^qD)/\log(R) \quad (21)$$

This is an entropy ratio that is analogous to evenness qE of Eq. 8, where the numerator and the denominator represent conceptually different things. In ${}^qJ'$, the uncertainty in the species identity of a randomly chosen individual (at a certain q) is expressed as a proportion of the uncertainty in the identity of a randomly chosen species (which is independent of q). Note that the randomly chosen entity is an individual in the numerator but a species in the denominator. The generalisation involving two different values of q is:

$$J'_{q_2/q_1} = \log({}^{q_2}D)/\log({}^{q_1}D) \quad (22)$$

This is an entropy ratio that is analogous to the diversity ratio D_{q_2/q_1} of Eq. 10. Here the uncertainty in the species identity of a randomly chosen individual at one value of q is divided by the corresponding uncertainty at another value of q . In other words, J'_{q_2/q_1} quantifies by what factor the perceived entropy of a dataset changes when q is changed from q_1 to q_2 . Just as the corresponding diversity ratio, this entropy ratio is smaller than unity when $q_1 < q_2$, equal to unity when $q_1 = q_2$, and larger than unity when $q_1 > q_2$. In contrast, both relative entropy $J'_{q/\max}$ and the entropy ratio ${}^qJ'$ are restricted to the interval $[0, 1]$.

The Shannon and Rényi entropies can be calculated using any log base, although log bases 2 and e have been most popular in ecological studies. Because $\log_b x / \log_b a = \log_a x$, Eq. 20 can be rewritten (choosing $b = 2$ just for the sake of clarity):

$${}^qJ' = \log_2({}^qD)/\log_2(R) = \log_R({}^qD) \quad (23)$$

Here it can be seen that ${}^qJ'$ (and hence J') equals Rényi entropy as calculated with log base R (Pielou 1966b). Diversity and richness follow the replication principle, i.e. their values double when each species is duplicated. The corresponding logarithms increase by a fixed amount instead, and with log base 2 the increase equals one unit for each doubling of qD and R . The relative increase in the logarithm is therefore smaller with large than with small original values. Consequently, J' and its variants are not replication invariant (as evenness itself is) but they increase with R even when the Lorenz curves of all datasets are identical (Hill 1973, Alatalo 1981; Fig. 1).

From Eq. 21 it can be seen that ${}^qJ'$ results from the partitioning of $\log({}^qD)$ into two components, one of which is $\log(R)$. To understand what this partitioning means in terms of diversity itself, we can solve Eq. 23 for qD by taking the exponential function with base R of both sides:

$$\exp_R({}^qJ') = \exp_R(\log_R({}^qD)) = {}^qD = R^{qJ'} \quad (24)$$

In other words, Pielou's J' quantifies how many times richness needs to be multiplied by itself to equal diversity. Because diversity cannot exceed richness, ${}^qJ'$ cannot exceed unity, so this can also be thought of as taking the $1/{}^qJ'$ th root of R to obtain diversity. Either way, it is clear that ${}^qJ'$ allows expressing diversity as a transformation of richness rather than dividing diversity into two conceptually different components. Equations 20 and 22 can be solved in a similar way to express diversity as a transformation of its maximum possible value or of diversity obtained with another value of q , respectively.

It is clear that $J'_{q/\max}$, J'_{q_2/q_1} and ${}^qJ'$ are useful measures (see also Jost 2010). However, they do not quantify evenness in the sense of Eq. 2, because they are obtained by partitioning entropy into two components rather than by partitioning diversity. In spite of this logical inconsistency, Pielou's J' appears to have been the most popular "evenness" index in ecological studies (Table 1).

Entropy difference (based on Rényi or Shannon entropy)

After having disqualified Pielou's J' because it is not replication invariant, Hill (1973) pointed out that the following measure is replication invariant:

$$\begin{aligned} H'_{1-0} &= {}^1H' - {}^0H' = \log({}^1D) - \log({}^0D) \\ &= \log({}^1D/{}^0D) = \log(D_{1/0}) \end{aligned} \quad (25)$$

This measure can be generalised to any two values of q :

$$\begin{aligned} H'_{q_2-q_1} &= {}^{q_2}H' - {}^{q_1}H' = \log({}^{q_2}D/{}^{q_1}D) = \log(D_{q_2/q_1}) \\ &= \log(E_{q_2/q_1}) \end{aligned} \quad (26)$$

$H'_{q_2-q_1}$ is the logarithm of both diversity ratio D_{q_2/q_1} and evenness ratio E_{q_2/q_1} . Entropy difference $H'_{q_2-q_1}$ simply quantifies by how much the amount of entropy perceived in the dataset increases when q is changed from q_1 to q_2 . If all species are equally abundant, entropy difference between any two values of q equals zero. Otherwise, entropy difference is negative when $q_1 < q_2$ (because then entropy decreases), equal to zero when $q_1 = q_2$, and positive when $q_1 > q_2$. Entropy difference can also be expressed in terms of unevenness as follows (Eq. 11):

$$H'_{q_2-q_1} = \log(E_{q_2/q_1}) = \log(U_{q_1/q_2}) = -\log(U_{q_2/q_1}) \quad (27)$$

A similar entropy difference can be derived from evenness itself:

$$\log({}^qE) = \log({}^qD/R) = \log({}^qD) - \log(R) \quad (28)$$

This quantifies how much larger the entropy in species identity is when an individual is taken at random from the dataset than when a species is taken at random. If $q = 0$ or all species are equally abundant, both entropies are equal and their difference is zero. Otherwise, the entropy difference is negative, because qD and hence $\log({}^qD)$ decreases when either q increases or the species abundances become less equal. The same value but with positive sign is obtained by taking the logarithm of unevenness:

$$\log({}^qU) = \log(R/{}^qD) = \log(R) - \log({}^qD) \quad (29)$$

Equation 28 is the basis of the *SHE* analysis of Buzas and Hayek (1996), the purpose of which is to partition Shannon's H' into Species and Evenness components. However, if one is really interested in species richness and evenness, rather than in their logarithms, partitioning qD in accordance with Eq. 8 would be more straightforward and less confusing than partitioning $\log({}^qD)$ in accordance with Eq. 28.

Although entropy differences have been used as equitability measures (Table 1), they quantify neither evenness as defined in Eq. 2 nor unevenness as defined in Eq. 4.

Relative probability and entropy ratio (based on HCDT or Tsallis entropy)

McIntosh (1967) proposed both absolute and relative diversity indices based on species absolute abundances, and Pielou (1969, cited in Smith and Wilson 1996) suggested using one of these relative indices to quantify equitability:

$$T_{2/\max} = \frac{m - \sqrt{\sum_{i=1}^R m_i^2}}{m - \sqrt{m^2/R}} = \frac{1 - \sqrt{\sum_{i=1}^R p_i^2}}{1 - \sqrt{R(1/R)^2}} = \frac{1 - 1/{}^2D}{1 - 1/{}^2D_{\max}} \quad (30)$$

In Eq. 30 it can be seen that although the McIntosh index was derived using absolute abundances, it can also be expressed in terms of relative abundances. It turns out to be mathematically equivalent to a relative version of the Gini–Simpson index. The Gini–Simpson index itself is a special case of the HCDT or Tsallis entropy qT (Eq. 7), so the relative measure of Eq. 30 can be generalized to any value of q as follows (Mendes et al. 2008):

$$T_{q/\max} = (1 - {}^qD^{1-q}) / (1 - {}^qD_{\max}^{1-q}) \quad (31)$$

qT itself has the term $(q - 1)$ in the denominator, but in the relative measure this term cancels out. When $q \geq 2$, $T_{q/\max}$ expresses the probability that q individuals chosen at random from a dataset (with replacement) represent at least two different species as a proportion of the probability that would be obtained if all species were equally abundant. This relative probability is analogous to relative diversity of Eq. 12. The measure makes mathematical sense also when $q < 2$, but then the interpretation needs to be phrased differently.

If the q individuals are taken without replacement, the resulting index equals Hurlbert's *PIE* ranged to the interval $]0, 1]$ ($= PIE'$). This ranged probability is analogous to ranged diversity of Eq. 13, and its interpretation needs to take into account the same considerations on how the minimum and maximum values are chosen.

Both $T_{2/\max}$ and PIE' have been used as equitability measures (Table 1). They are useful when one wishes to express in relative terms the probability of obtaining at least two different species in a pre-selected number of randomly chosen individuals. However, none of these measures quantifies evenness as defined in Eq. 2.

Diversity or a diversity index

Several studies have equated the raw value of a diversity index, or the value of diversity itself, with 'evenness'. The

Shannon entropy has been used occasionally, and the Gini–Simpson index and *PIE* have been even more popular. The Rényi entropy of order two has also been used, as has diversity² D itself (Table 1).

The problem with this approach is that the main purpose of diversity indices is to summarise into one measure aspects of both richness and evenness. If an index succeeds in doing so, it cannot logically continue to equal evenness. These measures therefore do not quantify evenness as defined in Eq. 2.

Measures not based on diversity

Out of the fourteen 'evenness' indices examined by Smith and Wilson (1996), seven can be expressed as functions of diversity (Table 2). One of these ($E_{1/D}$) corresponds to absolute evenness in the sense of the present paper, one quantifies relative evenness (E_{Heip}) and one the rate of increase in diversity at one value of q in relation to diversity at another value of q ($F_{2,1}$). Two of the indices are ratios of Rényi entropies (J' and E_{-lnD}) and two are ratios of probabilities (E_{1-D} and E_{Mcl}), which themselves are transformations of diversity.

The other seven indices of Smith and Wilson (1996) are not functions of diversity at all, but have instead been derived using other principles. The O index (Camargo 1992b, Bulla 1994; Table 2) calculates the sum of those parts of the proportional species abundances that do not exceed $1/R$. This measure hence reflects changes in the proportional abundances of species rarer than $1/R$ in a way that is consistent with the Lorenz curve, but it is insensitive to any changes in abundance among species more abundant than $1/R$. As a whole, the O index is therefore not Lorenz compatible, but it has been used as an equitability measure in some ecological studies (Table 1). The E index expresses O as a proportion of its possible range, and E could hence also be given as a percentage. Since O is not Lorenz compatible, neither is E .

The Camargo index E' quantifies how similar, on average, the proportional abundances of species are to each other (Table 2). It equals the one-complement of the Gini coefficient, which is a popular measure of inequality in economics (not to be confused with the Gini–Simpson diversity index). The Gini coefficient equals twice the area between the observed Lorenz curve and the diagonal of perfectly equitable species abundances, so the Camargo index E' equals twice the area below the Lorenz curve (Fig. 1). Both of these indices have been used in ecology as equitability or inequality measures (Table 1).

The E_{ar} measure of Smith and Wilson (1996; Table 2) quantifies a transformed variance of transformed species abundances. What this index means in ecological terms is not immediately obvious, but since Smith and Wilson recommended it as a general-purpose equitability measure, it has been used in several studies (Table 1). The NHC index equals the slope of the log-transformed rank-abundance curve, and the E_Q index transforms NHC to the $]0, 1]$ range (Table 2).

Each one of the indices quantifies a real (but different) aspect of the data, and can hence be relevant in some ecological studies. However, these indices cannot be expressed

as functions of diversity and richness, and therefore they do not quantify evenness as defined in Eq. 2. In addition, three of the indices are nonlinear transformations of a variable, which makes it difficult to describe exactly what they quantify in practice ($G_{2,1}$, E_{var} and E_Q ; see Table 2).

Different ways of partitioning diversity: richness–evenness and alpha–beta

The diversity of a dataset was above partitioned into richness and evenness components. Another approach that has attracted much attention recently is the partitioning of gamma diversity into alpha and beta components. Although at least one study has referred to both partitions (Martin et al. 2005), their relationship has not been formally established. I will here show that although each approach has a different aim, they follow similar logic, are fully compatible with each other and can be applied to a dataset simultaneously. Conceptually and numerically independent alpha and beta components are obtained as follows (Routledge 1979, Jost 2006, 2007, Tuomisto 2010a, c, 2011):

$${}^qD_\gamma = {}^qD_\alpha \times {}^qD_\beta \quad (32)$$

Here ${}^qD_\gamma$ or gamma diversity is the total diversity observed in the dataset of interest, which I have simply notated qD (without the subscript) up to now. Gamma diversity is calculated using Eq. 5. Partitioning gamma diversity into alpha and beta components requires that the dataset consists of (or gets divided into) subunits, and that each individual (or other entity of interest) belongs to exactly one subunit. This partitioning can be thought of as a reallocation of the ${}^qD_\gamma$ effective species into effective compositional units, which are hypothetical subunits that have the same number of effective species as the original subunits do on average, but share no effective species. Then alpha diversity (${}^qD_\alpha$) quantifies the mean effective density of species per effective compositional unit, and beta diversity (${}^qD_\beta$) quantifies the number of effective compositional units obtained. Alpha diversity is quantified as (see Tuomisto 2010a, c for derivation):

$${}^qD_\alpha = 1 - q \sqrt[q]{\sum_{j=1}^N w_j ({}^qD_{\alpha j})^{1-q}} \quad (33)$$

This is the weighted generalised mean with exponent $1 - q$ of the ${}^qD_{\alpha j}$ values, which quantify the effective density of

species per subunit for each subunit j . N is the number of subunits, and w_j is the nominal weight of subunit j , i.e. the proportion of all individuals that belong to subunit j . The effective weight of each subunit also depends on the value of q , such that large values of q diminish the importance of the nominal weights w_j and give more weight to the smallest ${}^qD_{\alpha j}$ values instead (Tuomisto 2010a, c).

The logical structure of the equation that partitions gamma diversity into alpha and beta components (${}^qD_\gamma = {}^qD_\alpha \times {}^qD_\beta$) is similar to the logical structure of the equation that partitions richness into unevenness and diversity components ($R = {}^qU \times {}^qD$). In both equations, all three terms are conceptually independent (they represent different things) and their values are equal to or larger than unity. The two terms on the right side of both equations are also numerically independent of each other (one does not constrain the value of the other in any way), and the first one of them is conceptually a concentration measure (see the units of measurement in Table 3). As we saw earlier (Eq. 1–4), the equation that partitions richness can be rearranged so as to partition diversity into evenness and richness components. In this case, richness constrains the minimum value of evenness, and evenness also differs from the other terms in that its maximum value is unity.

The alpha–beta partitioning expresses species diversity at one spatial (or temporal) resolution as a product of mean concentration of species diversity in subunits at a finer resolution and the minimum number of such subunits needed to reach the observed total species diversity. The richness–evenness partitioning expresses species diversity as a product of the actual number of species and a term indicating how close the species abundances are to a perfectly even distribution.

Each partitioning gives components that can be used also in other contexts. The partitioning of diversity into evenness and richness components can be applied equally well to gamma diversity, alpha diversity and beta diversity. Similarly, both richness and evenness can be partitioned into alpha and beta components (Table 3). The two ways of partitioning diversity can be combined in different ways. For example,

$$\begin{aligned} {}^qE_\beta &= {}^qE_\gamma / {}^qE_\alpha = ({}^qD_\gamma / R_\gamma) / ({}^qD_\alpha / R_\alpha) \\ &= ({}^qD_\gamma / {}^qD_\alpha) / (R_\gamma / R_\alpha) = {}^qD_\beta / R_\beta \end{aligned} \quad (34)$$

Gamma richness is partitioned into alpha and beta components in the same way as gamma diversity (Tuomisto 2010c,

Table 3. Different ways of partitioning diversity and richness into conceptually independent components. Measurement units assume that the classification of interest is that of individuals to species, but the derivations are the same even if other types are used instead (such as genera, functional types or haplotypes).

Partitioning	Measurement units	Possible values
$R = {}^qU \times {}^qD$	$\text{sp} = \text{sp}/\text{sp}_E \times {}^q\text{sp}_E$	all components ≥ 1
${}^qD = {}^qE \times R$	${}^q\text{sp}_E = {}^q\text{sp}_E/\text{sp} \times \text{sp}$	$1/R < {}^qE \leq 1$, other components ≥ 1
${}^qD_\gamma = {}^qD_\alpha \times {}^qD_\beta$	${}^q\text{sp}_E = {}^q\text{sp}_E/\text{CU}_E \times {}^q\text{CU}_E$	all components ≥ 1
${}^qE_\gamma = {}^qE_\alpha \times {}^qE_\beta$	${}^q\text{sp}_E/\text{sp} = ({}^q\text{sp}_E/\text{CU}_E)/(\text{sp}/\text{CU}) \times {}^q\text{CU}_E/\text{CU}$	$1/R_\gamma \leq {}^qE_\gamma \leq 1$, values of ${}^qE_\alpha$ and ${}^qE_\beta$ depend on subunit weights and the value of q
$R_\gamma = R_\alpha \times R_\beta$	$\text{sp} = \text{sp}/\text{CU} \times \text{CU}$	all components ≥ 1
${}^qD_\gamma = {}^qE_\gamma \times R_\gamma$	${}^q\text{sp}_E = {}^q\text{sp}_E/\text{sp} \times \text{sp}$	$1/R_\gamma \leq {}^qE_\gamma \leq 1$, other components ≥ 1
${}^qD_\alpha = {}^qE_\alpha \times R_\alpha$	${}^q\text{sp}_E/\text{CU}_E = ({}^q\text{sp}_E/\text{CU}_E)/(\text{sp}/\text{CU}) \times \text{sp}/\text{CU}$	${}^qE_\alpha$ depends on subunit weights and the value of q , other components ≥ 1
${}^qD_\beta = {}^qE_\beta \times R_\beta$	${}^q\text{CU}_E = {}^q\text{CU}_E/\text{CU} \times \text{CU}$	${}^qE_\beta$ depends on subunit weights and the value of q , other components ≥ 1

2011). The total number of actual species in the dataset (gamma richness R_γ) can be thought to consist of the mean actual density of species per compositional unit (alpha richness R_α) and the number of compositional units (beta richness R_β).

In turn, ${}^qE_\gamma$ measures how many effective species there are for each actual species in the entire dataset. Its value depends on how evenly the observed individuals are distributed among the actual species at the level of the entire dataset. ${}^qE_\gamma$ necessarily equals unity at $q = 0$ and is generally constrained to the interval $[1/R_\gamma, 1]$ (provided that $q \geq 0$). ${}^qE_\alpha$ measures the ratio of mean effective species density over mean actual species density at the subunit level, and ${}^qE_\beta$ quantifies how many effective compositional units there are for each actual compositional unit in the dataset (Eq. 34, Table 3).

The values of ${}^qE_\alpha$ and ${}^qE_\beta$ depend not only on how evenly the individuals are distributed among the actual species at the subunit level, but also on how evenly the individuals are distributed among the subunits. ${}^qE_\alpha$ and ${}^qE_\beta$ are constrained to values ≤ 1 only if all subunit weights w_i are equal when calculating ${}^qD_\alpha$ (Eq. 33). For example, if the subunits with the largest w_i values have the highest effective species density and $q < 1$, ${}^qD_\alpha$ can exceed R_α , which is an unweighted mean of the actual species densities (Tuomisto 2010a, c, 2011), and then ${}^qE_\alpha$ can exceed unity. It is noteworthy that ${}^qD_\alpha$ is conceptually a measure of diversity concentration, which contrasts with ${}^qD_\beta$ and ${}^qD_\gamma$ both of which are measures of plain diversity (of species and of compositional units, respectively). As a consequence, both ${}^qE_\gamma$ and ${}^qE_\beta$ conform with the definition of evenness as given in Eq. 2, but ${}^qE_\alpha$ is conceptually an evenness ratio.

Conclusions

There has been much uncertainty about the relative merits of different evenness indices and little consensus on which phenomenon evenness corresponds to. A part of the confusion seems to be caused by a failure to separate two distinct questions. Firstly, which of the available measures is most useful in practical applications? Secondly, which measure should be called ‘evenness’? These questions do not need to have the same answer.

Most of the measures that have been associated with ‘evenness’ are useful in some contexts. They quantify, for example, absolute and relative diversity ratios, entropy ratios, entropy differences, mean abundance differences, variances and regression slopes. Which measure is most informative in any particular situation depends entirely on what the questions of interest are. However, all useful measures that somehow link to the equitability of species abundances should not be called ‘evenness’, because doing so erodes the informative value of the term and leads to confusing the phenomena represented by the different measures. Instead, one of the phenomena should be universally referred to as ‘evenness’, and the other phenomena should each be called something different (suggestions can be found in the subheadings above).

Deciding which measure to bestow the name ‘evenness’ on implies no opinion on which measure is most important or most useful, so the decision can be entirely based

on convenience. Because there is broad consensus in the ecological literature that diversity consists of richness and evenness components, it is most convenient that ‘evenness’ be defined in agreement with this statement. This leads to $\text{Evenness} = \text{Diversity/Richness}$.

Diversity can be multiplicative partitioned in different ways. In particular, its partitioning into richness and evenness components has links to its partitioning into alpha and beta components, and both can be applied to a dataset simultaneously. Consequently, not only diversity but also richness and evenness can be partitioned into alpha and beta components, with each component quantifying a different aspect of the data. It remains to be seen how these approaches can be exploited to increase our understanding of issues that have real ecological meaning and significance.

Because measures representing different phenomena can behave in very different ways, great care is needed when choosing a measure for a particular purpose, interpreting results and comparing them among studies. Referring to multiple measures by the same term (such as evenness) should be avoided, because it easily leads to drawing conclusions on one phenomenon when in fact the chosen measure quantified another.

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