Opinion is intended to facilitate communication between reader and author and reader and reader. Comments, viewpoints or suggestions arising from published papers are welcome. Discussion and debate about important issues in ecology, e.g. theory or terminology, may also be included. Contributions should be as precise as possible and references should be kept to a minimum. A summary is not required.

Entropy and diversity

***Lou Jost**, Baños, Tungurahua, Ecuador (loujost@yahoo.com).*

Entropies such as the Shannon–Wiener and Gini–Simpson indices are not themselves diversities. Conversion of these to effective number of species is the key to a unified and intuitive interpretation of diversity. Effective numbers of species derived from standard diversity indices share a common set of intuitive mathematical properties and behave as one would expect of a diversity, while raw indices do not. Contrary to Keylock, the lack of concavity of effective numbers of species is irrelevant as long as they are used as transformations of concave alpha, beta, and gamma entropies. The practical importance of this transformation is demonstrated by applying it to a popular community similarity measure based on raw diversity indices or entropies. The standard similarity measure based on untransformed indices is shown to give misleading results, but transforming the indices or entropies to effective numbers of species produces a stable, easily interpreted, sensitive general similarity measure. General overlap measures derived from this transformed similarity measure yield the Jaccard index, Sørensen index, Horn index of overlap, and the Morisita–Horn index as special cases.

What is diversity?

The plethora of diversity indices and their conflicting behavior has led some authors (Hurlbert 1971) to conclude that the concept of diversity is meaningless. Diversity is not meaningless but has been confounded with the indices used to measure it; a diversity index is not necessarily itself a "diversity". The radius of a sphere is an index of its volume but is not itself the volume, and using the radius in place of the volume in engineering equations will give dangerously misleading results. This is what biologists have done with diversity indices. The most common diversity measure, the Shannon–Wiener index, is an entropy, giving the uncertainty in the outcome of a sampling process. When it is calculated using logarithms to the base two, it is the minimum number of yes/no questions required, on the average, to determine the identity of a sampled species; it is the mean depth of a maximally-efficient dichotamous key. Tothmeresz (1995), Ricotta (2003) and Keylock (2005) have shown that most other nonparametric diversity indices are also generalized entropies. Entropies are reasonable indices of diversity, but this is no reason to claim that entropy *is* diversity.

In physics, economics, information theory, and other sciences, the distinction between the entropy of a system and the effective number of elements of a system is fundamental. It is this latter number, not the entropy, that is at the core of the concept of diversity in biology. Consider the simplest case, a community consisting of S equally-common species. In virtually any biological context, it is reasonable to say that a community with sixteen equally-common species is twice as diverse as a community with eight equally-common species. Thus, when all species are equally common, diversity should be proportional to the number of species. It is natural to set the proportionality constant to unity, so that a community with eight equally-common species has a diversity of eight species and a community with sixteen equally-common species has a diversity of sixteen species. The difference in behavior between an entropy and a diversity is clear here. The Shannon entropy $-\Sigma_{i=1}^{S} p_i \log_b p_i$ (calculated using base $b = 2$ for the logarithm) is 3.0 for the first community and 4.0 for the second community; the entropy of the second community is not twice that of the first. (For any choice of base b, if the entropy of the first community is x, the entropy of the second community is $x + \log_b 2$.) The entropy gives the uncertainty in the species identity of a sample, not the number of species in the community.

Accepted 3 January 2006
Subject Editor: Heikki Setälä

ISSN 0030-1299

This does not mean that Shannon entropy is a poor index of diversity; on the contrary, it is the most profound and useful of all diversity indices, but its value gives the uncertainty rather than the diversity. If it is chosen as a diversity index, then all communities that share a particular value of Shannon entropy are equivalent with respect to their diversity (according to this index). A diversity index thus creates equivalence classes among communities. In each of these equivalence classes there is one community whose species are all equally common. The intuitive definition of diversity just given applies to that community, showing that its diversity is equal to its number of species; all other communities in the equivalence class must also have this same diversity.

Finding the diversity of a community thus reduces to the problem of finding an equivalent community (one that has the same value of the diversity index as the community in question) composed of equally-common species. This is a matter of simple algebra: calculate the diversity index for D equally-common species (each species therefore with a frequency of 1/D), set the resulting expression equal to the actual value of the diversity index, and solve that equation for D. This value of D is the diversity of the community according to the chosen diversity index. Table 1 gives the results of this algorithm for some common diversity indices. The number D has been called the "effective number of species" by MacArthur (1965); in physics it is the number of states associated with a given entropy, and in economics it is called the "numbers equivalent" of a diversity measure (Patil and Taillee 1982). I will refer to it simply as the diversity.

Diversity of order q

Most nonparametric diversity indices used in the sciences (including all generalized entropies used in biology) are monotonic functions of $\Sigma_{i=1}^{S} p_i^q$, or limits of such functions as q approaches unity. These include species richness, Shannon entropy, all Simpson measures, all Renyi entropies (Renyi 1961, Pielou 1975), all HCDT or "Tsallis" entropies (Keylock 2005; our terminology follows Czachor and Naudts 2002), and many others. All such measures yield a single expression for diversity when the algorithm of the preceding section is applied to them:

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

[Proof 1] These are often called "Hill numbers", but they are more general than Hill's (1973) derivation suggests. The exponent and superscript q may be called the "order" of the diversity; for all indices that are functions of $\Sigma_{i=1}^{S} p_i^q$, the true diversity depends only on the value of q and the species frequencies, and *not on the functional form of the index.* This means that when calculating the diversity of a single community, it does not matter whether one uses Simpson concentration, inverse Simpson concentration, the Gini–Simpson index, the second-order Renyi entropy, or the Hurlbert–Smith–Grassle index with m = 2; all give the same diversity:

$$^{2}D = 1/\left(\sum_{i=1}^{S} p_i^2\right) \tag{2}$$

The superscript 2 on the diversity indicates that this is a diversity of order 2.

The order of a diversity indicates its sensitivity to common and rare species. The diversity of order zero (q = 0) is completely insensitive to species frequencies and is better known as species richness. All values of q less than unity give diversities that disproportionately favor rare species, while all values of q greater than unity disproportionately favor the most common species (Tsallis 2001, Keylock 2005). The critical point that weighs all species by their frequency, without favoring

Table 1. Conversion of common indices to true diversities.

Index x:	Diversity in terms of x:	Diversity in terms of p_i:
Species richness $x \equiv \sum_{i=1}^{S} p_i^0$	x	$\sum_{i=1}^{S} p_i^0$
Shannon entropy $x \equiv -\sum_{i=1}^{S} p_i \ln p_i$	exp(x)	$\exp\left(-\sum_{i=1}^{S} p_i \ln p_i\right)$
Simpson concentration $x \equiv \sum_{i=1}^{S} p_i^2$	1/x	$1/\sum_{i=1}^{S} p_i^2$
Gini–Simpson index $x \equiv 1-\sum_{i=1}^{S} p_i^2$	1/(1 − x)	$1/\sum_{i=1}^{S} p_i^2$
HCDT entropy $x \equiv \left(1-\sum_{i=1}^{s} p_i^q\right)/(q-1)$	$[(1-(q-1)x)]^{1/(1-q)}$	$\left(\sum_{i=1}^{S} p_i^q\right)^{1/(1-q)}$
Renyi entropy $x \equiv \left(-\ln \sum_{i=1}^{s} p_i^q\right)/(q-1)$	exp(x)	$\left(\sum_{i=1}^{S} p_i^q\right)^{1/(1-q)}$

either common or rare species, occurs when $q = 1$; Eq. 1 is undefined at $q = 1$ but its limit exists and equals

$$^{1}D = \exp\left(-\sum_{i=1}^{S} p_i \ln p_i\right) = \exp(H) \qquad (3)$$

This is the exponential of Shannon entropy, but it arises naturally here without any reference to information theory. The central role this quantity plays in biology, information theory, physics, and mathematics is not a matter of definition, prejudice, or fashion (as some biologists have claimed) but rather a consequence of its unique ability to weigh elements precisely by their frequency, without disproportionately favoring either rare or common elements. Biologists would have discovered it and used it as their main diversity index even if information theory did not exist.

Equation 1 has the properties intuitively expected of a diversity. For all values of q it always gives exactly S when applied to a community with S equally-common species. For all values of q it also possess the "doubling" property introduced by Hill (1973): suppose we have a community of S species with arbitrary species frequencies $p_1, \ldots p_i, \ldots p_s$, with diversity ^{q}D. Suppose we divide each species into two equal groups, say males and females, and we treat each group as a separate "species". Intuitively, we have doubled the diversity of the community by this reclassification, and indeed the diversity of the doubled community calculated according to Eq. 1 is always $2 \times {}^{q}D$ regardless of the values of the p_i. [Proof 2]

Alpha, beta, and gamma diversities

The Shannon entropies of multiple communities can be averaged to give what is known in information theory as the "conditional entropy", H_α, of the set of communities. Because Shannon entropy is a concave function, H_α is always less than or equal to the gamma entropy H_γ, the entropy of the pooled communities (Shannon 1948, Lande 1996). Though H_α is often called the "alpha diversity" in biology, it is of course really an entropy. It can be converted to the true alpha diversity by Eq. 3: $^{1}D_\alpha = \exp(H_\alpha)$. Likewise the amount of information provided by knowledge of the sample location is often called the beta diversity in biology but is actually an entropy. Like the alpha entropy, it can be converted to the true beta diversity by Eq. 3. The same tranformation also converts gamma entropy to true gamma diversity.

The relation between the Shannon alpha, beta, and gamma entropy follows directly from information theory:

$$H_\alpha + H_\beta = H_\gamma$$

By converting both sides of this equation to true diversities via Eq. 3, the relation between alpha, beta, and gamma diversity is obtained:

$$\exp(H_\alpha + H_\beta) = \exp(H_\gamma) \qquad (5a)$$

so

$$(\exp(H_\alpha))(\exp(H_\beta)) = \exp(H_\gamma) \qquad (5b)$$

or

$$(\text{alpha diversity})(\text{beta diversity}) = (\text{gamma diversity}) \qquad (5c)$$

Shannon or order 1 diversity thus necessarily follows Whittaker's (1972) multiplicative law. The minimum possible beta diversity is unity, which occurs when all communities are identical. The maximum possible beta diversity is N, the number of communities; this occurs when all N communities are completely distinct and equally weighted. Alpha and beta diversity are independent of each other regardless of the community weights.

Keylock (2005), following Lande (1996), has criticized the use of diversities (Hill numbers) because they are often not concave functions, and so alpha diversity might sometimes be greater than gamma diversity. This would be a valid criticism if we averaged individual diversities directly ($w_1D(H_1)+w_2D(H_2)+\ldots$) to obtain the alpha diversity; an alpha diversity calculated this way would indeed sometimes exceed the gamma diversity. However, there is no theoretical justification for averaging diversities in this way. Diversities are not substitutes for entropies but rather transformations of them after all entropic calculations (such as calculation of the alpha entropy) have been done. The logic is analogous to working with variances when their mathematical properties (such as additivity) are useful, and then converting the result to a standard deviation at the end for comparison with experiment. Let H stand for any generalized entropy or diversity index, and let D(H) be the function that transforms H into a true diversity. If the underlying entropies are concave, then H_α will be less than or equal to H_γ (Lande 1996). Hence if the transformation function D(H) is monotonically increasing, the transformed alpha entropy $D(H_\alpha)$ will be less than or equal to the transformed gamma entropy $D(H_\gamma)$. In the Shannon case, the function that converts entropy H to diversity D is the exponential function, which is monotonically increasing: if $x \le y$, then $\exp(x) \le \exp(y)$. Because Shannon entropy is concave, H_α is always less than or equal to H_γ, and so it follows that $\exp(H_\alpha)$ is always less than or equal to $\exp(H_\gamma)$. Shannon alpha diversity is always less than or equal to Shannon gamma diversity, and the concavity of D(H) plays no role in this.

The other commonly-used concave entropy is the Gini–Simpson index. If one defines the alpha Gini–Simpson index H_α of a set of communities as the average of the Gini–Simpson indices of the individual communities (as is traditional in biology, though see below), then by concavity H_α is always less than or equal to H_γ (Lande 1996). This index is transformed to a true diversity by the function $1/(1-H)$ (which is obtained by the algorithm described in the first section). The Gini–Simpson index always lies within the interval [0, 1), and in this domain the transformation function $1/(1-H)$ is a monotonically increasing function of H. Hence if x and y are numbers in the range [0, 1) and if x is less than or equal to y, $1/(1-x)$ must be less than or equal to $1/(1-y)$. Since H_α is always less than or equal to H_γ, the alpha diversity $1/(1-H_\alpha)$ will therefore always be less than or equal to the gamma diversity $1/(1-H_\gamma)$. The concavity of the transformation function is irrelevant.

It is important to note that the alpha (or conditional) entropy is not uniquely defined for the Gini–Simpson index or other non-Shannon diversity measures (Taneja 1989, Yamano 2001). In physics, for example, the currently accepted definition of the conditional Gini–Simpson index is not $w_1H_1 + w_2H_2 + \ldots$ but $[(w_1^2)H_1 + (w_2^2)H_2 + \ldots]/[w_1^2 + w_2^2 + \ldots]$ (Tsallis et al. 1998, Abe and Rajagopal 2001). There are many other definitions in the literature (Taneja 1989). Each satisfies a different subset of the theorems which apply to their Shannon counterpart, and no definition satisfies them all. The traditional biological definition of Gini–Simpson alpha entropy agrees with the current physics definition only when community weights are equal. These ambiguities apply also to the definition of beta for non-Shannon measures. Until these issues are resolved at a deeper level, one should avoid the use of the Gini–Simpson index to calculate alpha and beta for unequally-weighted samples or communities. The issues involved are explained in more detail in Appendix 2. In the following applications we restrict ourselves to the case of equal weights.

Application

The distinction between an entropy and a true diversity is not merely semantic; confusion between entropy and diversity has serious practical consequences. Entropies and other diversity indices have a wide variety of ranges and behaviors; if applied to a system of S equally common species, some vary as S, some as log S, some as 1/S, some as 1–1/S, etc. Some have unlimited ranges while others are always less than unity. A general formula or equation designed to accept raw indices is likely to give reasonable results for some of these but not for others. By calling all of these indices “diversities” and treating them as if they were interchangeable in formulas or analyses requiring diversities, we will often generate misleading results. Converting indices to true diversities gives them a set of common behaviors and properties, permitting the development of truly general index-independent formulas and analytical techniques.

Consider for example a popular general similarity or homogeneity measure (Lande 1996, Veech et al. 2002) based on raw diversity indices:

$$L \equiv \text{alpha diversity index/gama diversity index} = H_\alpha/H_\gamma \tag{6}$$

(H here refers to any generalized entropy or diversity index, not necessarily the Shannon entropy.) This similarity measure is designed to be used with species richness, Shannon entropy, the Gini–Simpson index, or any other concave measure. It is intended to give the proportion of total regional “diversity” contained in the average single community, but it does not distinguish entropies from diversities, and this causes problems.

When applied to N equally-weighted communities it gives sensible results when used with species richness (which is after all a true diversity, the diversity of order zero). In this case the similarity measure has a well-defined maximum of 1.0 when the communities are all identical, and a well-defined minimum of 1/N when the communities are completely dissimilar. However, when this same similarity measure is used with Shannon entropy or the Gini–Simpson index, its value approaches unity as community diversity becomes large, no matter how dissimilar the communities! [Proof 3] Whittaker (1972) first noted this problem in ratios of gamma and alpha Shannon entropies. The inflation of similarity arises because most entropies, including Shannon entropy and the Gini-Simpson index, have a nearly flat slope when diversity is high; if a set of communities is very diverse, H_α and H_γ will therefore be nearly equal, and as alpha becomes large their ratio will be approach unity regardless of their similarity. This makes the measure uninterpretable as a summary statistic; a similarity of 0.999 using the Gini–Simpson index in Eq. 6 may mean communities are nearly identical, may mean they are moderately similar, or may mean they are completely distinct.

This problem can be avoided by converting the entropies to true diversities before taking their ratio, obtaining:

$$M \equiv {}^qD(H_\alpha)/{}^qD(H_\gamma) \tag{7}$$

where ${}^qD(H)$ means the diversity associated with the entropy H. The reciprocal of this formula has been proposed as a measure of beta diversity for the Shannon case (MacArthur 1965), and for the Gini–Simpson index (Olszewski 2005). The conversion to true diversities puts these diversity indices on a common footing, eliminating the erratic behavior of Eq. 6 when used with different indices. Most importantly, because both alpha and gamma diversities have the “doubling” property described earlier, their ratio is immune to the false inflation of similarity which is characteristic of a ratio of entropies. Unlike a ratio of entropies, it has a fixed minimum value (indicating complete dissimilarity) of 1/N for N equally-weighted communities, whether used with species richness, Shannon entropy, or the Gini–Simpson index, and regardless of the alpha diversity of the communities. [Proof 4] Thus we can easily tell whether a set of N equally-weighted communities is distinct and we can meaningfully compare the similarity values based on different indices and between different sets of N communities (whose alpha diversities may differ).

The difference between the ratio of entropies and the ratio of true diversities can be seen by applying each of them to two imaginary equally-weighted bird communities with no species in common: a community in Costa Rica and one in Indonesia, each with 50 equally common bird species. Since no species are shared between Costa Rica and Indonesia, the pooled diversity is 100 equally-common species. Equation 6 gives the proportion of total pooled "diversity" contained in the average community as 0.5 using species richness, 0.85 using the Shannon entropy, and 0.99 using the Gini–Simpson index. Inflation is apparent in the latter two values, which are close to unity (which would indicate maximal similarity) even though the communities have no similarity at all. Furthermore, the similarity values vary erratically depending on the diversity index used, even though the species probabilities in the individual and pooled communities are perfectly uniform, with no dominance or concentration effects that could account for the differences. Since the value that indicates complete dissimilarity depends in a complex way on the alpha diversity and on the index used, these similarity values cannot be directly compared between different sets of communities and cannot be easily interpreted.

In contrast the similarity of these two completely distinct communities using true diversities, Eq. 7, is 0.50 for all these diversity measures, reflecting the fact that if two communities are completely distinct and equally-weighted the average community must contain half the total pooled diversity. *When two equally-weighted communities are completely dissimilar, we would obtain this same value of 0.50 even if the communities each had very different numbers of species, and even if each species were not equally-common, and no matter whether we used diversities calculated from species richness, Shannon entropy, or the Gini–Simpson index.* The measure accurately and robustly indicates the degree of similarity without confounding this with total diversity.

The ratio of true diversities not only has superior mathematical properties but is also more biologically meaningful than the ratio of entropies. This can be best demonstrated on a real two-community system, the canopy and understory fruit-feeding butterfly communities of a South American rain forest (DeVries and Walla 2001). The published raw data set (11696 individuals) is large enough to eliminate bias in the estimates of diversity measures, and the statistical weights of the two communities are within 1% of equality, making it an ideal test. The distinctness of the canopy versus understory butterfly communities is obvious from inspection of the published raw data (rearranged here as Table 2); on the average a species is more than 30 times more common in its preferred community than in its nonpreferred community, and the difference reaches or exceeds a significance level of 0.001 for 63 of the 74 species in the published data. A reasonable similarity measure should reveal this distinctness. However, the similarity measure Eq. 6, the ratio of entropies, gives an inflated similarity value of 0.95 for the two communities using the Gini–Simpson index. Most ecologists looking at this 95% similarity value would wrongly assume that the forest is homogeneous in the vertical dimension and that the canopy and understory communities are very similar in species composition. In contrast Eq. 7, the ratio of true diversities, shows that the average community really shares not 95% but only 59% of the total diversity, using the Gini–Simpson index. This value is close to the theoretical minimum of 50% for two completely dissimilar equally-weighted communities, showing that the canopy and understory communities are really very distinct from each other. The authors of the butterfly study used additional methods to demonstrate the importance of the canopy/understory distinction, concluding that "the vertical dimension is a major structural component in tropical forest butterfly communities" (Engen et al. 2002). The similarity measure based on entropies, Eq. 6, hides this structure while the similarity measure based on true diversities, Eq. 7, highlights it. Additive partitioning studies which rely exclusively on Eq. 6 for the evaluation of their results need to be re-examined using the corrected measure, Eq. 7.

Other useful similarity measures can be derived from Eq. 7 for use with equally-weighted samples or communities of a region. The minimum value of Eq. 7 for N equally-weighted samples or communities, 1/N, obviously depends on the number of samples or communities in the region. The measure can be transformed onto the interval [0,1] to facilitate comparisons between regions with different numbers of samples or communities. Since ${}^{q}D(H_{\alpha})/{}^{q}D(H_{\gamma})$ goes from 1/N to 1, the linear transformation

$$S \equiv [{}^{q}D(H_{\alpha})/{}^{q}D(H_{\gamma}) - 1/N]/[1 - 1/N] \qquad (8)$$

ranges from 0 to 1. This new measure equals zero when all the samples or communities are completely distinct, equals unity when all are identical, and is linear in the proportion of total diversity contained in the average sample or community. When this measure is applied to two equally-weighted samples or communities, it simplifies to the Jaccard index (Jaccard 1902) when used with species richness, and to the Morisita–Horn index (Horn 1966) when used with the Gini–Simpson index. [Proof 5] For the butterfly data mentioned above, it gives 0.18 with the Gini–Simpson index.

Sometimes the focus of a study is not on the amount of homogeneity or shared diversity in a region but on the amount of species overlap between two communities. This requires a direct comparison between communities, whose original statistical weights are then irrelevant and

Table 2. Canopy and understory butterfly communities in a tropical rain forest (modified from DeVries and Walla 2001). Butterfly species, along with their number of captures in the canopy and understory, are listed in descending order of abundance and include the 74 most common species (those with 8 or more captures). The canopy and understory butterfly communities are not similar to each other; nearly all species are much more abundant in one community than in the other.

Species	Canopy	Understory	Species	Canopy	Understory
Historis acheronta	1882	26	*Callicore hesperis*	44	1
Panacea prola	1028	535	*Opsiphanes invirae*	40	5
Nessaea hewitsoni	19	984	*Baeotus deucalion*	40	1
Morpho achilles	5	751	*Archaeprepona licomedes*	1	39
Taygetis sp. 1	8	621	*Taygetis mermeria*	0	40
Colobura dirce	273	250	*Memphis arachne*	36	1
Bia actorion	8	426	*Mycelia capenas*	31	5
Catoblepia berecynthia	3	336	*Paulogramma pyracmon*	32	0
Historis odius	299	11	*Diarthria clymena*	29	0
Catoblepia xanthus	4	289	*Catoblepia soranus*	0	27
Panacea divalis	244	21	*Chloreuptychia herseis*	0	27
Caligo idomenius	2	242	*Catonephele numilia*	25	1
Catonephele acontius	176	67	*Cithaerias aurorina*	0	21
Callicore hystapes	201	1	*Chloreuptychia arnaea*	0	19
Panacea regina	182	14	*Cissia erigone*	0	19
Caligo eurilochus	2	184	*Pareuptychia binocula*	1	17
Memphis florita	136	33	*Caligo teucer*	0	17
Batesia hypochlora	36	113	*Chloreuptychia hewitsonii*	0	17
Morpho menelaus	1	131	*Memphis polycarmes*	15	1
Archaeprepona demophon	63	63	*Mageuptychia nr. helle-1*	9	7
Hamadryas arinome	108	14	*Hamadryas feronia*	15	0
Mageuptychia antonoe	117	3	*Archaeprepona demophoon*	14	0
Smyrna blomfildia	100	1	*Hamadryas chloe*	2	12
Tigridia acesta	29	65	*Pierella lena*	0	14
Opsiphanes cassina	72	18	*Cissia myncea*	5	8
Callicore cyllene	81	0	*Mageuptychia analis*	6	7
Haetera piera	0	77	*Pierella astyoche*	0	13
Prepona laertes	74	2	*Taygetis virgilia*	0	13
Hamadryas amphinome	72	3	*Cissia proba*	0	12
Hamadryas laodamia	60	0	*Pareuptychia ocirrhoe*	1	11
Caligo placidianus	0	57	*Agrias sardanapolis*	10	0
Opsiphanes quiteria	8	49	*Baeotus amazonicus*	9	0
Zaretis itys	50	4	*Cissia terrestris*	3	6
Temenis laothe	49	3	*Prepona pylene*	8	0
Taygetis sp. 3	0	51	*Antirrhea avernus*	0	8
Archaeprepona amphimachus	5	44	*Chloreuptychia tolumnia*	1	7
Taygetis sp. 2	0	49	*Taygetis valentina*	0	8

are taken to be equal in the calculation of alpha, beta, and gamma. The most useful kind of overlap measure has been called a "true overlap measure" (Wolda 1981): when two communities each consist of S equally-common species, with C shared species, a true overlap measure gives the value C/S, the fraction of one community which overlaps with the other. A true overlap measure for HCDT entropies can be derived from Eq. 7, since the (q-1)th power of the ratio of alpha to gamma diversities is linear in C/S. We can transform that ratio onto the interval [0,1] to obtain the true measure of overlap:

$$\text{Overlap (of order q)} \equiv \{[{}^{q}D(H_{\alpha})/{}^{q}D(H_{\gamma})]^{q-1} - [1/2]^{q-1}\}/\{1-[1/2]^{q-1}\} \qquad (9)$$

[Proof 6] This yields the Sørensen index (Sørensen 1948) when q = 0, the Horn index of overlap (Horn 1966) in the limit as q approaches 1, and the Morisita–Horn index (Horn 1966) when q = 2. [Proof 7] For the butterfly data the overlap between canopy and understory communities using the Gini-Simpson index is 18%. For order 2 diversities Eqs. 8 and 9 necessarily give the same values. For q other than 2.0 the values will differ between Eq. 8 and 9.

Conclusions

The confusion between entropy and diversity fuels much of the debate about diversity measures, obscures patterns in field studies, and hinders theoretical progress. Most diversity indices are entropies, not diversities, and their mathematical behavior usually does not correspond to biologists' theoretical or intuitive concept of diversity. All indices can be transformed into true diversities, which possess a uniform set of mathematical properties that accurately capture the diversity concept.

Conversion of indices to true diversities facilitates interpretation of results. If researchers find a pre-treatment Shannon entropy of 4.5 and a post-treatment Shannon entropy of 4.1, they usually go no further than to say that the difference is small, and then fall back on statistical tests to see if the difference is statistically significant. It is more informative to give the diversities instead of the entropies; in this case, the diversities are 90 species and 60 species respectively. It is now easy to see that the difference between pre- and post-treatment diversities is not small but enormous. The question of the real magnitude of the drop is important and is separate from its statistical significance. It is essential to have informative, interpretable diversity and similarity measures, so we can go beyond mere statistical conclusions.

It is especially useful to convert to true diversities when dealing with multiple kinds of indices. If a community has a species richness of 100, a Shannon entropy of 3.91 and Gini–Simpson index of 0.967, it is not obvious how these compare. Converting to diversities gives 100, 50 and 30 species; the big drops in the diversities as q increases indicate a high degree of dominance in the community. If the communities had been completely without dominance (all species equally likely) the diversities would have been 100 species for all values of q.

Shannon beta entropy is additive but this forces Shannon beta diversity to be multiplicative; both sides in the debate over the additivity or multiplicativity of beta are correct, but one side is talking about entropy while the other is talking about diversity.

Each diversity index has unique properties that are useful for specific applications (this is the real point of Hurlbert's criticism of diversity as a unified concept). The present paper is not intended to argue against the appropriate use of raw indices in these index-specific applications. However, since raw diversity indices exhibit a wide variety of mathematical behaviors, they cannot all give reasonable results when directly inserted into a general diversity equation or formula. Converting raw indices to true diversities (Hill numbers) makes possible the construction of meaningful index-independent general equations, measures, or formulas involving diversity.

Acknowledgements – I acknowledge helpful talks with Dr. Thomas Walla and Harold Greeney. This work was supported by grants from John and Ruth Moore to the Population Biology Foundation.

References

Abe, S. and Rajagopal, A. 2001. Nonadditive conditional entropy and its significance for local realism. – Phys. Lett. A 289: 157–164.

Aczel, J. and Daroczy, Z. 1975. On measures of information and their characterization. – Academic Press.

Czachor, M. and Naudts, J. 2002. Thermostatistics based on Kolmogorov-Nagumo averages: unifying framework for extensive and nonextensive generalizations. – Phys. Lett. A 298: 369–374.

DeVries, P. and Walla, T. 2001. Species diversity and community structure in neotropical fruit-feeding butterflies. – Biol. J. Linn. Soc. 74: 1–15.

Engen, S., Lande, R., Walla, T. et al. 2002. Analyzing spatial structure of communities using the two-dimensional Poisson lognormal species abundance model. – Am. Nat. 160: 60–73.

Hill, M. 1973. Diversity and evenness: a unifying notation and its consequences. – Ecology 54: 427–432.

Horn, H. 1966. Measurement of "overlap" in comparative ecological studies. – Am. Nat. 100: 419–424.

Hurlbert, S. 1971. The nonconcept of diversity: a critique and alternative parameters. – Ecology 52: 577–586.

Jaccard, P. 1902. Lois de distribution florale dans la zone alpine. – Bull. Soc. Vaudoise Sci. Nat. 38: 69–130.

Keylock, C. 2005. Simpson diversity and Shannon-Wiener index as special cases of a generalized entropy. – Oikos 109: 203–207.

Lande, R. 1996. Statistics and partitioning of species diversity, and similarity among multiple communities. – Oikos 76: 5–13.

Lewontin, R. 1972. The apportionment of human diversity. – Evol. Biol. 6: 381–398.

MacArthur, R. 1965. Patterns of species diversity. – Biol. Rev. 40: 510–533.

Olszewski, T. 2004. A unified mathematical framework for the measurement of richness and evenness within and among communities. – Oikos 104: 377–387.

Patil, G. and Taillie, C. 1982. Diversity as a concept and its measurement. – J. Am. Statist. Ass. 77: 548–561.

Pielou, E. 1975. Ecological diversity. – Wiley.

Renyi, A. 1961. On measures of entropy and information. – In: Neymann, J. (ed.), Proc. 4th Berkeley Symp. Math. Statist. Probabil. (Vol. 1). Univ. of California Press, pp. 547–561.

Ricotta, C. 2003. Parametric scaling from species relative abundances to absolute abundances in the computation of biological diversity: a first proposal using Shannon's entropy. – Acta Biotheor. 51: 181–188.

Shanon, C. 1948. A mathematical theory of communication. – Bell System Tech. J. 27: 379–423, 623–656.

Sørensen, T. 1948. A method of establishing groups of equal amplitude in plant sociology based on similarity of species content. – K. dan Vidensk Selsk Biol. Skr. 5: 1–34.

Taneja, I. 1989. On generalized information measures and their applications. – Adv. Electron. Electron Phys. 76: 327–413.

Tsallis, C. 2001. Nonextensive statistical mechanics and thermodynamics: historical background and present status. – In: Abe, S. and Okamoto, Y. (eds), Nonextensive statistical mechanics and its applications, series lecture notes in physics. Springer-Verlag, pp. 3–98.

Tsallis, C., Mendes, R. and Plastino, A. 1998. The role of constraints within generalized nonextensive statistics. – Phys. A 261: 534–554.

Tothmeresz, B. 1995. Comparison of different methods for diversity ordering. – J. Veg. Sci. 6: 283–290.

Veech, J., Summerville, K., Crist, T. et al. 2002. The additive partitioning of species diversity: recent revival of an old idea. – Oikos 99: 3–9.

Whittaker, R. 1972. Evolution and measurement of species diversity. – Taxon 21: 213–251.

Wolda, H. 1981. Similarity indices, sample size and diversity. – Oecologia 50: 296–302.

Yamano, T. 2001. A possible extension of Shannon's information theory. – Entropy 3: 280–292.

Appendix 1. Proofs

Note: H represents any generalized entropy or diversity index.

Proof 1

If $H(\Sigma_{i=1}^{S}(p_i)^q)$ is continuous and monotonic (hence invertible) and has a value x, then the algorithm in the text to find its diversity gives:

$$H\left(\sum_{i=1}^{D}(1/D)^q\right)=x$$

$$H(D\cdot(1/D)^q)=(x)$$

$$(1/D)^{(q-1)}=H^{-1}(x)$$

$$D=[1/(H^{-1}(x))]^{1/(q-1)}$$

Since $x=H(\Sigma_{i=1}^{S}(p_i)^q)$, $H^{-1}(x)=H^{-1}(H(\Sigma_{i=1}^{S}(p_i)^q))=\Sigma_{i=1}^{S}(p_i)^q$, so D is independent of the function $H(\ldots)$ and the diversity associated with any such diversity index can be expressed as:

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

Proof 2

If the original community had $\Sigma_{i=1}^{S}(p_i)^q$ equal to x, doubling each element of the sum while halving each probability is equivalent to replacing each element p_i^q by $(2^{1-q})(p_i^q)$. Thus the sum for the doubled system is $(2^{1-q})(x)$. Any monotonic function $H(\Sigma_{i=1}^{S}(p_i)^q)$ gives a diversity of $(\Sigma_{i=1}^{S}(p_i)^q)^{1/1-q}$, by Proof 1. Thus the diversity of the doubled system is $[(2^{1-q})(x)]^{1/(1-q)}=2[x^{1/(1-q)}]=2x$.

Proof 3

As shown by Lande (1996) for concave diversity measures, $H_\alpha <= H_\gamma$; H_α/H_γ is maximal and equals unity when all communities are identical, and for a given value of H_α, H_α/H_γ is minimal when all communities are distinct. Any H_α/H_γ is therefore bounded between these values.The following proofs show that the lower bound approaches unity as alpha becomes high; hence all H_α/H_γ approach unity when alpha is high.

Shannon case. When all communities are distinct, only one of the p_{ij} in each term of H_γ,

$$-\sum_{i=1}^{S}(w_1p_{i1}+w_2p_{i2}+\ldots)\ln(w_1p_{i1}+w_2p_{i2}+\ldots)$$

is nonzero, so H_γ separates into

$$-\sum_{i=1}^{S}w_1p_{i1}\ln(w_1p_{i1})+-\sum_{i=1}^{S}w_2p_{i2}\ln(w_2p_{i2})+\ldots$$

which simplifies to

$$-w_1\sum_{i=1}^{S}(p_{i1})(\ln w_1+\ln p_{i1})+$$

$$-w_2\sum_{i=1}^{S}(p_{i2})(\ln w_2+\ln p_{i2})+\ldots$$

$$=-w_1\sum_{i=1}^{S}p_{i1}\ln p_{i1}+(-w_1\ln w1)\sum_{i=1}^{S}p_{i1}+$$

$$-w_2\sum_{i=1}^{S}p_{i2}\ln p_{i2}+(-w_2\ln w_2)\sum_{i=1}^{S}p_{i2}+\ldots$$

$$=w_1H_1+(-w_1\ln w_1)(1)+w_2H_2+(-w_2\ln w_2)(1)$$

$$=H_\alpha+H_w$$

where H_w is the entropy of the community weights. Thus H_α/H_γ for completely distinct communities is $H_\alpha/(H_\alpha+H_w)$ or $1/(1+H_w/H_\alpha)$. H_w is fixed by the weights so as H_α becomes large, H_w/H_α approaches zero and H_α/H_γ approaches 1.

Gini–Simpson case. When all communities are distinct (no shared species) only one of the p_{ij} in each term of H_γ,

$$1-\sum_{i=1}^{S}(w_1p_{i1}+w_2p_{i2}+\ldots)^2,$$

is nonzero, so H_γ separates into

$$1-\left[\sum_{i=1}^{S}w_1^2p_{i1}^2+\sum_{i=1}^{S}w_2^2p_{i2}^2+\ldots\right]$$

and so H_α/H_γ can be written

$$\left\{1-\left[\sum_{i=1}^{S}w_1p_{i1}^2+\sum_{i=1}^{S}w_2p_{i2}^2+\ldots\right]\right\}\bigg/$$

$$\left\{1-\left[\sum_{i=1}^{S}w_1^2p_{i1}^2+\sum_{i=1}^{S}w_2^2p_{i2}^2+\ldots\right]\right\}$$

where the numerator is the alpha component of the Gini–Simpson index. As the alpha diversity becomes large, each of the sums making up the numerator approach zero. The same sums appear in the denominator (though with different weight coefficients) so all the summations in both the numerator and denominator approach zero. Then H_α/H_γ is $(1-\varepsilon)/(1-\delta)$ and as ε and δ approach zero this approaches unity.

Proof 4

Proof 1 can be used to write the desired inequality as

$$1/N \le {}^qD(H_\alpha)/{}^qD(H_\gamma) \equiv \left\{(1/N)\left[\sum_{i=1}^{S} p_{i1}^q + \sum_{i=1}^{S} p_{i2}^q + \ldots\right] \Big/ \sum_{i=1}^{S}[(1/N)(p_{i1}+p_{i2}+\ldots)]^q\right\}^{1/(1-q)}$$

which can be rewritten

$$1 \le \left\{\left[\sum_{i=1}^{S} p_{i1}^q + \sum_{i=1}^{S} p_{i2}^q + \ldots\right] \Big/ \sum_{i=1}^{S}[(p_{i1}+p_{i2}+\ldots)]^q\right\}^{1/(1-q)}$$

Case q >1. The above inequality can then be rewritten

$$\sum_{i=1}^{S}[(p_{i1}+p_{i2}+\ldots)]^q \ge \left[\sum_{i=1}^{S} p_{i1}^q + \sum_{i=1}^{S} p_{i2}^q + \ldots\right]$$

with the inequality reversing because we are taking the reciprocal of both sides. Each term $(p_{i1}+p_{i2}+\ldots)^q$ of the left-hand summation is greater than or equal to $p_{i1}^q + p_{i2}^q + \ldots$ since $(x)^q$ is a convex function, so the inequality is true.

Case q <1. For this case the proof is the same; the inequality can be written

$$\sum_{i=1}^{S}[(p_{i1}+p_{i2}+\ldots)]^q \le \left[\sum_{i=1}^{S} p_{i1}^q + \sum_{i=1}^{S} p_{i2}^q + \ldots\right]$$

and this is true term by term since for this case $(x)^q$ is a concave function.

Case q =1. The inequality can be proven by noting that the limit of ${}^qD(H_\alpha)/{}^qD(H_\gamma)$ as q approaches 1 exists, so ${}^qD(H_\alpha)/{}^qD(H_\gamma)$ is continuous at q =1; the above inequality holds since it holds for q >1 and q <1.

We prove equality when the communities are completely distinct by noting that for q not equal to 1 the gamma diversity for distinct communities separates into

$$\left\{(1/N)^q \sum_{i=1}^{S} p_{i1}^q + (1/N)^q \sum_{i=1}^{S} p_{i2}^q + \ldots\right\}^{1/(1-q)}$$

so the ratio ${}^qD(H_\alpha)/\,{}^qD(H_\gamma)$ becomes

$$\left\{1/N\left[\sum_{i=1}^{S} p_{i1}^q + \sum_{i=1}^{S} p_{i2}^q + \ldots\right] \Big/ \left[(1/N)^q \sum_{i=1}^{S} p_{i1}^q + (1/N)^q \sum_{i=1}^{S} p_{i2}^q + \ldots\right]\right\}^{1/(1-q)} = 1/N$$

For q =1, ${}^1D(H)$ is exp(H) by the algorithm in the text and also by taking the limit of the result of Proof 1 as q approaches 1. When all communities are distinct and equally weighted, H_γ separates into

$$-\sum_{i=1}^{S}(1/N\ p_{i1})\ \ln(1/N\ p_{i1}) + -\sum_{i=1}^{S}(1/N\ p_{i2}) \times \ln(1/N\ p_{i2}) + \ldots$$

which simplifies to

$$\begin{aligned}
&-1/N\sum_{i=1}^{S}(p_{i1})(\ln 1/N + \ln p_{i1}) + \\
&\quad -1/N\sum_{i=1}^{S}(p_{i2})(\ln 1/N + \ln p_{i2}) + \ldots \\
&\quad = -1/N\sum_{i=1}^{S} p_{i1}\ \ln p_{i1} + (-1/N \ln 1/N)\sum_{i=1}^{S} p_{i1} + \\
&\quad -1/N\sum_{i=1}^{S} p_{i2}\ \ln p_{i2} + (-1/N \ln 1/N)\sum_{i=1}^{S} p_{i2} + \ldots \\
&\quad = (1/N)H_1 + (-1/N \ln 1/N)(1) \\
&\quad + (1/N)H_2 + (-1/N \ln 1/N)(1) + \ldots \\
&\quad = H_\alpha + N(-1/N \ln 1/N) = H_\alpha + \ln N
\end{aligned}$$

so ${}^1D(H_\gamma) = \exp(H_\alpha + \ln N) = N \exp(H_\alpha)$.
Hence the ratio ${}^1D(H_\alpha)/{}^1D(H_\gamma) = \exp(H_\alpha)/N\exp(H_\alpha) = 1/N$.

Proof 5

$[{}^qD(H_\alpha)/{}^qD(H_\gamma) - 1/N]/[1 - 1/N]$ for two equally-weighted communities is $[({}^q\lambda_\alpha/{}^q\lambda_\gamma)^{1/(1-q)} - 0.5]/[0.5]$. For q =0 this becomes

$$\begin{aligned}
&\left\{\left[(0.5)\sum_{i=1}^{S} p_{i1}^0 + (0.5)\sum_{i=1}^{S} p_{i2}^0\right] \Big/ \left\{\sum_{i=1}^{S}[0.5\ p_{i1} + 0.5\ p_{i2})^0] - 0.5\right\}\right\}/\{0.5\} \\
&= \{[0.5\ N_1 + 0.5\ N_2]/[N_{tot}] - 0.5\}/\{0.5\} \\
&= \{[N_1 + N_2] - N_{tot}\}/\{N_{tot}\} \\
&= (N_{shared})/(N_1 + N_2 - N_{shared}) = N_{shared}/N_{tot}
\end{aligned}$$

which is the Jaccard index.

For q =2 the measure can be written

$$= \left\{\left[\sum_{i=1}^{S}(0.5\ p_{i1} + 0.5\ p_{i2})^2\right] \Big/\right.$$

$$\left[(0.5)\sum_{i=1}^{S} p_{i1}^{2} + (0.5)\sum_{i=1}^{S} p_{i2}^{2}\right] - 0.5\Bigg\}/\{0.5\}$$

$$= \left[\sum_{i=1}^{S}(p_{i1} + p_{i2})^{2}\right] \Bigg/ \left[\sum_{i=1}^{S} p_{i1}^{2} + \sum_{i=1}^{S} p_{i2}^{2}\right] - 1$$

$$= \left[\sum_{i=1}^{S}(p_{i1}^{2} + p_{i2}^{2} + 2\ p_{i1}p_{i2}) - \sum_{i=1}^{S} p_{i1}^{2} - \sum_{i=1}^{S} p_{i2}^{2}\right] \Bigg/$$

$$\left[\sum_{i=1}^{S} p_{i1}^{2} + \sum_{i=1}^{S} p_{i2}^{2}\right]$$

$$= \left[\sum_{i=1}^{S} 2\ p_{i1}p_{i2}\right] \Bigg/ \left[\sum_{i=1}^{S} p_{i1}^{2} + \sum_{i=1}^{S} p_{i2}^{2}\right]$$

which is the Morisita–Horn index for two equally-weighted communities.

Proof 6

If each community has S equally-common species and they share C species, ${}^{q}D_{\gamma}$ equals

$$[(2S - 2C)(1/2S)^{q} + C(1/S)^{q}]^{1/(1-q)}$$

and ${}^{q}D_{\alpha}$ equals

$$= \left[(0.5)\sum_{i=1}^{S} p_{i1}^{q} + (0.5)\sum_{i=1}^{S} p_{i2}^{q}\right]^{1/(1-q)}$$

$$= [(0.5)\ S(1/S)^{q} + (0.5)\ S(1/S)^{q}]^{1/(1-q)}$$

$$= [S(1/S)^{q}]^{1/(1-q)} = S.$$

Then the similarity measures is

$$[({}^{q}D_{\alpha}/{}^{q}D_{\gamma})^{q-1} - (1/2)^{q-1}]/[1 - (1/2)^{q-1}]$$

$$= \{[(2S - 2C)(1/2S))^{q} + C(1/S)^{q}]/$$

$$[S^{1-q}] - 2^{1-q}\}/\{1 - 2^{1-q}\}$$

$$= \{[(2S - 2C)(1/2)^{q}(1/S) + C/S)] - 2^{1-q}\}/\{1 - 2^{1-q}\}$$

$$= \{[(2S(1/2)^{q}(1/S) - 2C(1/2)^{q}(1/S)) + C/S] - 2^{1-q}\}$$

$$/\{1 - 2^{1-q}\}$$

$$= \{[2^{1-q} - 2^{1-q}(C/S) + C/S)] - 2^{1-q}\}/\{1 - 2^{1-q}\}$$

$$= \{C/S\ (1 - 2^{1-q})\}/\{1 - 2^{1-q}\}$$

$$= C/S.$$

Proof 7

For q = 0 the measure is

$$\left\{\left[\sum_{i=1}^{S}(0.5\ p_{i1} + 0.5\ p_{i2})^{0}\right] \Bigg/ \left[(0.5)\sum_{i=1}^{S} p_{i1}^{0} + (0.5)\sum_{i=1}^{S} p_{i2}^{0}\right]\right.$$

$$\left. - 2\right\}/\{1 - 2\}$$

$$= -\{\{N_{tot}\}/\{[N_1 + N_2]/[2]\} - 2\}$$

$$= -[N_{tot} - (N_1 + N_2)]/[(N_1 + N_2)/2]$$

$$= [(N_1 + N_2) - N_{tot}]/[(N_1 + N_2)/2]$$

$$= [N_{shared}]/[(N_1 + N_2)/2]$$

which is the Sørensen index.

For the Shannon case it is necessary to take the limit of the measure as q approaches unity:

$$\left\{\left[\sum_{i=1}^{S}(0.5\ p_{i1} + 0.5\ p_{i2})^{q}\right] \Bigg/ \left[0.5\sum_{i=1}^{S} p_{i1}^{q}\right.\right.$$

$$\left.\left. +0.5\sum_{i=1}^{S} p_{i2}^{q}\right] - 2^{1-q}\right\} \Bigg/ \{1 - 2^{1-q}\}.$$

The numerator and denominator approach zero as q approaches 1, so L'Hospital's rule applies and the quotient of derivatives is

$$\left\{\left[\sum_{i=1}^{S}(0.5\ p_{i1} + 0.5\ p_{i2})^{q}\ \ln\ (0.5\ p_{i1} + 0.5\ p_{i2})\right]\right.$$

$$\times \left[0.5\sum_{i=1}^{S} p_{i1}^{q} + 0.5\sum_{i=1}^{S} p_{i2}^{q}\right]^{-1}$$

$$+(-1)\left[0.5\sum_{i=1}^{S} p_{i1}^{q} + 0.5\sum_{i=1}^{S} p_{i2}^{q}\right]^{-2}$$

$$\times \left[0.5\sum_{i=1}^{S} p_{i1}^{q}\ \ln\ p_{i1} + 0.5\sum_{i=1}^{S} p_{i2}^{q}\ \ln\ p_{i2}\right]$$

$$\times \left[\sum_{i=1}^{S}(0.5\ p_{i1} + 0.5\ p_{i2})^{q}\right]$$

$$\left. +[2^{1-q}\ \ln\ 2]\right\} \Bigg/ \{2^{1-q}\ \ln\ 2\}$$

which, in the limit as q approaches 1, equals

$$\left[\sum_{i=1}^{S}(0.5\ p_{i1} + 0.5\ p_{i2})\ \ln\ (0.5\ p_{i1} + 0.5\ p_{i2})\right.$$

$$\left. -0.5\sum_{i=1}^{S} p_{i1}\ \ln\ p_{i1} - 0.5\sum_{i=1}^{S} p_{i2}\ \ln\ p_{i2} + \ln\ 2\right] \Bigg/ [\ln\ 2]$$

which is the Horn index of overlap for equally-weighted communities.

The result for q = 2 follows from Proof 5 since, for q = 2,

$$[({}^{q}D_{\gamma}/{}^{q}D_{\alpha})^{q-1} - (1/2)^{q-1}]/[1 - (1/2)q - 1]$$

$$= [({}^{q}D_{\alpha}/{}^{q}D_{\gamma})^{1/(1-q)} - 0.5]/[0.5].$$

Appendix 2. Definitions of alpha and beta

The alpha and beta components of Shannon entropy are well-understood; their analogues are widely used in many disciplines and backed up by an immense amount of mathematical theory. They possess the following important properties:

1) Alpha and beta both use the same metric.
2) Alpha can never exceed gamma.
3) If all the communities in a region have the same Shannon entropy, say H_0, then the alpha entropy of the region is H_0.
4) Alpha and beta are independent.

The importance of Properties 1 and 2 has been emphasized by Lande (1996) and Lewontin (1972). Property 3 expresses, in the most noncommital and general way possible, the notion that alpha is in some sense an average of the diversity indices of the individual communities. Property 4 is implicit in all uses of the concepts of alpha and beta; a low value of alpha should not, by itself, force beta to be high, and vice versa.

In biology the definitions of alpha and beta for Shannon entropy,

$$H_\alpha = w_1H_1 + w_2H_2 + \ldots \tag{A1}$$

$$H_\alpha + H_\beta = H_\gamma, \tag{A2}$$

are often carried over directly to the Gini–Simpson index (Lande 1996, Veech et al. 2002). However, there is an essential difference between the Shannon entropy and the Gini–Simpson index; the Shannon entropy is not bounded above, while the Gini–Simpson index always lies between zero and one. This means that both the alpha and gamma Gini–Simpson indices have values very close to unity when communities are highly diverse. Therefore whenever alpha is high, beta defined through Eq. A2 must always be close to zero. Alpha and beta defined by this equation are not independent but inversely related. This violation of property 4 is graphically demonstrated in Fig. A1, which contrasts the behavior of the Shannon and Gini–Simpson beta components defined by Eq. A2.

Property 1 is also violated when beta is defined by Eq. A2. To understand what it means for alpha and beta to have the same metric, consider how Shannon entropy works. When there are two equally likely alternatives, Shannon entropy (using natural logarithms) is always 0.6931; whether this number comes from a calculation of alpha or of beta makes no difference in its interpretation. If there are two distinct equally-likely species in each community, alpha will be 0.6931, and if there are two completely distinct equally likely comunities in the region, beta will be 0.6931. Alpha and beta share the same metric and so their contributions to total diversity can be reasonably compared (by converting them to true diversities as shown in the main text). When the Gini–Simpson index is applied to a system with two equally-likely alternatives, it gives a value of 0.5. Yet if beta is defined through Eq. A2, when there are two equally-likely completely distinct communities beta does not usually equal 0.5. In fact beta has no fixed value in this situation; its value depends on alpha and cannot be interpreted without knowledge of alpha.

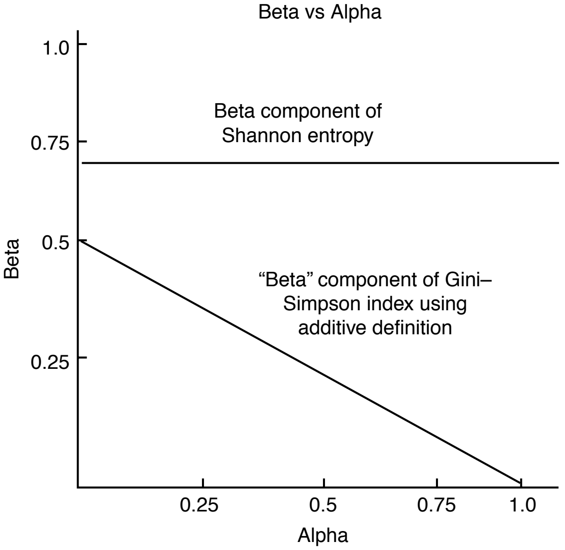

Fig. A1. Beta versus alpha for two equally-weighted communities with no species in common. The definition $H_\beta = H_\gamma - H_\alpha$ yields a beta component which is independent of the alpha component when it is applied to the Shannon entropy, but not when it is applied to the Gini–Simpson index.

Consider any two distinct communities with no species in common, such as communities A and B in Table A1. Suppose a region consists of communities A and B with equal statistical weights. The alpha Shannon entropy is 0.9764 and the beta Shannon entropy is 0.6931; the true beta diversity is therefore exp (0.6931) which is 2.00, correctly indicating that there are two distinct communities. One could do the same calculation for communities A and C, obtaining a different alpha Shannon entropy, 1.488, but the same beta Shannon entropy, 0.6931 since these are also two distinct communities. The same could be done for communities B and C, or any other pair of completely distinct communities; regardless of their alpha, their beta Shannon entropy will always be 0.6931. Beta is independent of alpha and characterizes the degree of overlap of the communities, using the same metric as alpha. (Had there been two equally-common species in each community, alpha would have been 0.6931; the same metric applies to both.)

Doing the same calculations with the Gini–Simpson index gives a "beta" (as defined by Eq. A2) of 0.2050 for communities A and B, but 0.1550 for communities A and C, and 0.1000 for communities B and C. The degree of overlap is confounded with the alpha diversity. Converting the "beta" values to true diversities yields 1.258, 1.183, and 1.111, which do not have obvious interpretations.

It can be proven that the proper way to combine two independent components of a Gini–Simpson index is not through Eq. A2 but through

$$H_\alpha - H_\alpha H_\beta + H_\beta = H_\gamma \tag{A3}$$

Table A1. Alpha, beta, and gamma indices for various hypothetical regions each consisting of two equally-weighted completely distinct communities. Alpha differs between pairs of communities, but beta Shannon entropy is independent of alpha and is identical for any pair of equally-weighted completely distinct communities; Shannon beta diversity always equals 2.00 for such pairs. The Gini–Simpson index behaves irregularly when beta is defined by Eq. A2 but behaves like Shannon entropy when beta is properly defined by Eq. A3.

Species:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Community A:	0.6	0.4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Community B:	0	0	0.3	0.2	0.4	0.1	0	0	0	0	0	0	0	0	0	0
Community C:	0	0	0	0	0	0	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1

	A+B	A+C	B+C
Shannon H_α	0.9764	1.487	1.791
Shannon H_γ	1.6696	2.181	2.484
Gini–Simpson H_α	0.5900	0.6900	0.8000
Gini–Simpson H_γ	0.7950	0.8450	0.9000
Shannon $H_\beta = H_\gamma - H_\alpha$	0.6931	0.6931	0.6931
${}^1D(H_\beta) = \exp(H_\beta)$	**2.000**	**2.000**	**2.000**
Gini–Simpson "H_β" from $H_\gamma - H_\alpha$	0.2050	0.1550	0.1000
${}^2D(\text{“}H_\beta\text{”}) = 1/(1\text{-“}H_\beta\text{”})$	**1.258**	**1.183**	**1.111**
Gini–Simpson H_β from Eq. A3	0.5000	0.5000	0.5000
${}^2D(H_\beta) = 1/(1-H_\beta)$	**2.000**	**2.000**	**2.000**

(Aczel and Daroczy 1975, Tsallis 2001, Keylock 2005). This expression not only allows alpha and beta to be independent, but also ensures that alpha and beta use the same metric, as demonstrated below. Comparison of Eq. A2 and A3 shows that the "H_β" calculated by Eq. A2 is really not H_β but $H_\beta - H_\beta H_\alpha$, explaining the shape of the graph of Gini–Simpson "H_β" in Fig. A1 (its y-intercept is H_β and its slope is $-H_\beta$).

It remains to find the correct expression for Gini–Simpson alpha, given its independence from beta. The alpha Gini-Simpson index can be written $1-\lambda_\alpha$, beta can be written $1-\lambda_\beta$, and gamma can be written $1-\lambda_\gamma$. Then Eq. A3 can be written:

$$(1-\lambda_\alpha) - (1-\lambda_\alpha)(1-\lambda_\beta) + (1-\lambda_\beta) = (1-\lambda_\gamma) \tag{A4}$$

which simplifies to

$$\lambda_\alpha = \lambda_\gamma/\lambda_\beta. \tag{A5}$$

The gamma component H_γ is by definition the Gini–Simpson index applied to the pooled communities, so that

$$\lambda_\gamma = \sum_{i=1}^{S}[(w_1 p_{i1} + w_2 p_{i2} + \ldots)^2]. \tag{A6}$$

When all communities are completely distinct (no shared species), this reduces to

$$\lambda_{\gamma\ \mathrm{distinct}} = \sum_{j=1}^{N} w_j^2 \lambda_j \tag{A7}$$

where λ_j is p_{ij}^2 for the jth community. Inserting this result into Eq. A5 gives an expression for λ_α when all communities are distinct:

$$\lambda_{\alpha\ \mathrm{distinct}} = (w_1^2\lambda_1 + w_2^2\lambda_2 + \ldots)/\lambda_{\beta\ \mathrm{distinct}}. \tag{A8}$$

When all communities have identical values of λ, so that $\lambda_j = \lambda$ for all j, $\lambda_{\alpha\ \mathrm{distinct}}$ must also equal λ by property 3 (the requirement that the alpha component is some kind of "average" of the diversities of the individual communities). Therefore for this case

$$\lambda = (w_1^2\lambda + w_2^2\lambda + \ldots)/\lambda_{\beta\ \mathrm{distinct}} \tag{A9}$$

and by factoring out λ, the value of $\lambda_{b\ \mathrm{distinct}}$ is determined:

$$\lambda_{\beta\ \mathrm{distinct}} = (w_1^2 + w_2^2 + \ldots) \tag{A10}$$

Equation A10 can be substituted into Eq. A8 to yield an expression for ${}^q\lambda_\alpha$:

$$\lambda_\alpha = (w_1^2\lambda_1 + w_2^2\lambda_2 + \ldots)/(w_1^2 + w_2^2 + \ldots). \tag{A11}$$

Because λ_α is by assumption independent of the beta component (which measures the distinctness of the communities), this result cannot depend on the beta component and must therefore apply even when the communities are not distinct. The alpha component of the Gini–Simpson index is therefore:

$$H_\alpha = 1 - [(w_1^2\lambda_1 + w_2^2\lambda_2 + \ldots)/(w_1^2 + w_2^2 + \ldots)]. \tag{A12}$$

or, in terms of H_j,

$$H_\alpha = (w_1^2 H_1 + w_2^2 H_2 + \ldots)/(w_1^2 + w_2^2 + \ldots). \tag{A13}$$

This turns out to be the same definition of alpha (conditional) entropy recently proposed for this index in physics (Abe and Rajagopal 2001). Note that when community weights are all equal, this reduces to the normal biological definition of the alpha Gini–Simpson index.

These new results can be applied to the communities in Table A1. For all pairs of distinct communities, regardless of the value of H_α, H_β is now 0.500, as expected. Converting this to a true diversity gives 2.00 in each case, just as with the Shannon entropy, correctly indicating that there are two distinct communities in each region. Alpha and beta are now truly measured in the same metric, and alpha is independent of beta, so beta can be interpreted on its own. In addition, the numbers equivalents of H_{α}, H_{β}, and H_{γ} now follow Whittaker's law, alpha diversity times beta diversity equals gamma diversity, just as in the Shannon case. (This follows at once from Eq. A5 and the transformation function $D(H_{\text{Gini}-\text{Simpson}}) = 1/\lambda$.)

When weights are equal, therefore, Properties 1–4 are all satisfied by the components of the Gini–Simpson index, as long as its H_{β} is defined by Eq. A3. In this case the alpha component is the same as that traditionally used in biology. However, when community weights are unequal, the alpha component defined by Eq. A12 (the only definition that makes alpha and beta independent) is sometimes greater than the gamma component. For example, let community A, with weight 0.7, contain three species with frequencies {0.5, 0.2, 0.3} and community B, with weight 0.3, contain the same species with frequencies {0.9, 0.05, 0.05}. Alpha is 0.55 while gamma is 0.54. This violates property 2. Olszewski (2004), using a very different approach, has also noted counterintuitive behavior in this index when community weights are unequal (see his Fig. 6). The unavoidable conclusion of the present derivation is that the Gini–Simpson index cannot be decomposed into meaningful alpha and beta components (i.e. components that possess Properties 1–4) when the community weights are unequal. A paper in preparation will generalize the above considerations to most non-Shannon diversity indices.

For additional explanation and worked examples, see the author's website, www.loujust.com.