Independence of alpha and beta diversities

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Introduction

Though Veech and Crist’s paper (Veech and Crist 2010) deals primarily with species richness, ecologists partitioning diversity generally use multiple diversity measures and compare the beta values among them (e.g., Gering et al. 2003, Summerville et al. 2003, 2006, Couteron and Pelissier 2004, Stendera and Johnson 2005, Ribiero et al. 2008). This paper therefore takes a more general perspective and treats all standard measures, not just species richness.


Statistical independence between alpha and beta is primarily an empirical question; it depends on nature and on our sampling scheme. In some kinds of ecosystems, it is conceivable that high differentiation is associated with high within-group diversity. The reverse is also conceivable. If nature has these regularities, we would want our measures of alpha and beta to be able to reflect them. We would not want a definition of beta that predetermined the kind of regularities we could observe.

The meaning of “independence”

Veech and Crist (2010) take the experimenter’s view; they regard gamma and alpha as the fundamental quantities, and beta as the derived quantity. Conceptually, however, gamma is the compound or derived quantity, produced by the interplay of the two more fundamental quantities, the mean within-group diversity and the between-group diversity. This observation is at the root of all attempts to partition gamma diversity into alpha and beta components.

Many partitioning schemes have been proposed, and all agree that the within-group or alpha component of diversity depends only on the diversities of each group, not on between-group relationships. Alpha is blind to any sharing of species between the groups. If we measure alpha diversity of a set of samples that all share the same species, and then we rename the species so that none are shared across samples, alpha does not change at all. Alpha is logically and mathematically unrelated to the way that species frequencies are connected across groups. This is what I mean by “independence” in Jost (2007).

A complete partitioning of gamma diversity would divide gamma into one component that describes this within-group or alpha diversity, and another logically unrelated component that describes how the groups are related to each other. Because these components measure completely different things, they should be defined so that each is free to vary independently of the other. My partitioning theorem (Jost 2007) shows how to find just the component due to the relations between groups, and it identifies the conditions under which this can be identified with beta diversity (or relative differentiation between groups). Sometimes this partitioning is additive (e.g., Shannon and Renyi entropies), sometimes it is multiplicative (all true diversities sensu
Jost 2007), and sometimes it is neither (Gini-Simpson index).

The resulting beta component is not mathematically constrained by alpha. Fig. 1 compares this kind of partitioning with additive partitioning of the three most common indices. In the partitioning formulas produced by my theorem, the value of alpha puts no mathematical constraints on the possible values of beta. For a fixed number of groups, any value in the domain of alpha is compatible with any value in the domain of beta, and vice versa. Alpha and beta form a Cartesian product parameter space. The partitioning scheme does not pre-determine the kind of relationship that will be observed in nature between alpha and beta.

The mathematical independence of alpha and beta is not the same thing as statistical independence, which depends on the particular sampling scheme used and the joint probability distributions of the species. An analogy with vector decomposition may help illustrate the difference. If we knew nothing about the universe except the value of the \( x \) component of a vector, we would have absolutely no clue about the value of its \( y \) or \( z \) components. This shows that the components are logically and mathematically independent (orthogonal). Yet if geologists were using vectors to describe the topography of a mountain, they would observe correlations between the \( x \), \( y \), and \( z \) values. The correlations would accurately reflect characteristics of the real topography, and this is what makes vectors useful. Because there are no forced mathematical relations between \( x \), \( y \), and \( z \), we can easily infer the actual topography from these numbers. The same is true of the alpha and beta produced by my partitioning scheme. It might well happen that in some parts of the world, high values of alpha are correlated with high (or low) values of beta. The goal is not to eliminate the possibility of these empirical correlations, but rather to ensure that beta is not confounded mathematically with alpha. Then, if correlations between alpha and beta are observed in the real world, we can confidently attribute this to nature and not to artifacts of our measures.

**Practical importance of this kind of independence**

The practical importance of mathematical independence is best illustrated using the Gini-Simpson index. In the additive scheme, for any given value of alpha, beta is constrained to be less than \((1 - 1/N)(1 - \text{alpha})\), where \( N \) is the number of groups or samples. Therefore, when Gini-Simpson alpha is high (close to unity), the additive Gini-Simpson beta is necessarily close to zero, even when all samples are completely different from each other. Additive Gini-Simpson beta values close to zero may therefore mean either that the samples are nearly identical or completely different. Since ecologists use beta to quantify differentiation between sites or samples, they can be misled by this ambiguity.

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**Fig. 1.** Permitted values of alpha and beta for \( N \) equally large samples or communities. The top row shows additively defined values. The bottom row shows multiplicative values for the same indices, converted to true diversities as in Jost (2007).
Table 1 shows how additive Gini-Simpson beta and alpha/gamma misranks data sets. Beetles are more differentiated between sites than butterflies, but additive beta is higher for the butterflies. Beetle communities are less similar to each other than the butterfly communities, yet the additive similarity measure alpha/gamma is higher for beetles than for butterflies.

Table 2 shows replication invariance of Jost’s beta. Values are number of individuals of four taxonomic groups sampled from three sites. On the left, species group 2 is a duplicate of species group 1, but with different species. When Gini-Simpson beta is calculated as in Eq. 15d of Jost (2007), using unweighted species relative abundances in the calculation of alpha and gamma, the beta of the combined set is the same as the beta of the subsets. This is replication invariance. This beta also obeys the stronger property demonstrated at right. When any two subsets of species with the same beta are pooled, the beta of the pooled set is the same as the beta of the subsets. This is replication invariance. It is tempting to conclude that these problems are the fault of the Gini-Simpson index itself, perhaps because of its sensitivity to widespread dominant species. Yet the problems just mentioned have nothing to do with dominance; they arise also for completely even communities with no dominance. What these problems really prove is that additive partitioning is not a generally valid framework for producing measures of compositional differentiation. When the Gini-Simpson index is properly partitioned into mathematically independent alpha and beta components, the problems disappear. For the case of N equally weighted communities, the beta component of the Gini-Simpson index is then constrained between 0 and \((1 - 1/N)\). These constraints do not contain alpha. Values close to \((1 - 1/N)\) unambiguously indicate high relative compositional differentiation among groups, regardless of the value of alpha.

As Veech and Crist (2010) noted in their paper, mathematical independence of alpha and beta makes beta “replication invariant.” Merging of distinct copies of a population, each copy with different species but with the same relative abundances and hence the same amount of relative differentiation, increases alpha without changing beta. This principle, and a stronger version which holds when all samples are given equal weights, is illustrated in Table 2. While Veech and Crist (2010) mention it in the context of species richness, replication invariance is a property of the pure between-group component of any measure of diversity or
compositional complexity derived from my partitioning theorem. For example, the between-group component of the correctly-partitioned Gini-Simpson index is replication-invariant, as shown in Table 2.

For these measures, lumping two nonoverlapping sets of species (e.g., Set 1 is made up of Morpho butterfly species and Set 2 is made up of Caligo butterfly species) with the same degree of differentiation among sites results in a new group with the same value of differentiation among sites. Pooling per se does not change the value of beta. This property is essential if ecologists want to compare the beta diversity of a subset of species to the beta diversity of the whole, or to the complement of the subset. Otherwise such comparisons make no sense. The beta of Jost (2007) has this property when all samples are given equal weights, but additive Gini-Simpson beta lacks it.

Discussion of partitioning schemes usually revolves around the definition of beta. However, we must also consider whether a scheme’s alpha, beta, and gamma work together coherently. This is important, since partitioning studies often combine alpha, beta, and gamma into the ratios beta/gamma and alpha/gamma, to facilitate interpretation (Nei 1973, Lande 1996, Veech et al. 2002). Even in studies which do not use these ratios explicitly, results are often expressed as bar graphs displaying alpha and beta as proportions of gamma (Gering et al. 2003, Summerville et al. 2003, 2006, Stendera and Johnson 2005). Unfortunately, for Shannon entropy and the Gini-Simpson index the ratio alpha/gamma (which is supposed to reflect community similarity) is constrained by the value of alpha. It necessarily approaches unity when alpha diversity is high, even if samples or communities share no species (Jost 2006, 2007). Likewise, for these measures the ratio beta/gamma necessarily approaches zero when alpha diversity is high (Jost 2008).

Table 1 illustrates this for the Gini-Simpson index; the completely distinct beetle communities have a “similarity” (alpha/gamma) of 90%, suggesting high similarity even though the beetle communities share no species. The butterfly communities, which are more similar to each other than the beetle communities, have a lower similarity, 64%. Alpha, beta, and gamma based on Shannon entropy and the Gini-Simpson index lack the mathematical properties needed for these ratios to be informative about the similarity or differentiation among communities.

The misleading behavior of these ratios is more extreme for the Gini-Simpson index than in Shannon entropy. This is why the bar graphs in additive partitioning studies of high-diversity ecosystems generally show much smaller beta contributions for the Gini-Simpson index than for Shannon entropy (e.g., Gering et al. 2003, Summerville et al. 2003). This is also why bar graphs of Shannon entropy or the Gini-Simpson index for high-diversity systems will generally show smaller beta contributions than the corresponding bar graphs of low-diversity systems, even if differentiation is greater for the high-diversity system. This occurs for example in Fig. 3 of Summerville et al. (2003) for the Gini-Simpson index. The similarity measure alpha/gamma for early-season moths (92%) is lower than for late-season moths (98%), seemingly indicating more differentiation between sites in the early season. This is just a mathematical artifact due to the greater alpha diversity of late-season moths. For the observed late-season alpha diversity of 0.972, the “similarity” measure alpha/gamma is mathematically constrained to be between 97.2% and 100%, no matter how differentiated the samples. Biological conclusions should not be drawn from such bar graphs.

If the ratio alpha/gamma is to be interpretable as a similarity measure, for a given set of N communities or samples, it must vary over a fixed range that does not depend on the species frequencies of the samples. Only then will it be a useful stand-alone descriptive statistic for the samples. The ratio alpha/gamma will have fixed upper and lower limits, independent of species frequencies, if alpha is defined as in Jost (2007) and the diversity measure possesses the “doubling” property first discussed by Hill (1973). The slightly stronger version of this property used by Jost (2007) states that if we pool N equally diverse, equally large, completely distinct samples, each with diversity X, then the diversity of the pooled samples must be N × X. The ratio alpha/gamma for these samples would be X/(N × X) = 1/N, independent of alpha. This sets the minimum possible value of the ratio for N equally large communities. The maximum value of unity occurs when all communities are identical. Thus if the diversity measure has the special property just mentioned, the ratio alpha/gamma varies over a fixed range that depends only on the number and sizes of the samples, not on the species frequencies of the samples. For any given set of samples, we can easily judge whether its ratio alpha/gamma is near to one or the other of these limits, and from this we can judge the relative similarity of the samples.

This same “doubling” property also makes diversity measures behave intuitively in other contexts. Measures without this property lead to logical contradictions when used in conservation biology (Appendix, Jost 2009). Shannon entropy and the Gini-Simpson index lack this property, so conclusions based on these measures are often invalid. This is why I call measures that possess this property “true diversities.” Shannon entropy and the Gini-Simpson index should be called something else. I suggest the umbrella term “measures of compositional complexity” (Jost 2009) to encompass true diversities (as just defined), entropies, and other such measures.

The use of true diversities brings order to the chaotic partitioning results always reported in studies that additively partition species richness, Shannon entropy or the Gini-Simpson index. The early-season and late-
season moth data in Summerville et al. (2003) gives additive “beta” values of [316, 0.62, 0.07] for species richness, Shannon entropy, and the Gini-Simpson index respectively, for early-season moths, and [356, 0.89, 0.016] for late-season moths in the same landscape. These values are all in different units (species, bits, and probabilities) and cannot be compared. When these indices are converted to true diversities, the beta values (all in units of effective number of distinct communities) are [3.41, 1.85, 1.53] for early-season moths and [4.04, 2.44, 2.33] for late-season moths. Since these are now in the same units, they can be compared with each other, and valid conclusions can be drawn about the differentiation of rare vs. common moth species, or between early and late moth differentiation. (My correction to the published data is only approximate, since it assumes all sites have equal statistical weights.) Note the close agreement between Shannon and Simpson beta in the corrected versions. The species richness differentiation is greater than the other two because there were many singleton species in the data. This correction can alter conclusions; the uncorrected Gini-Simpson beta drops from early to late season, while in the corrected Gini-Simpson beta increases from early to late season. This latter behavior agrees with the behavior of the beta values of the other indices from early to late season. By inventing numerical examples where the right answer is obvious, the reader can easily convince himself that when conclusions differ based on additive and multiplicative Shannon or Simpson beta values, the multiplicative scheme always gives the biologically sensible and mathematically consistent conclusion about relative differentiation.

Veech and Crist’s notions of statistical independence

As discussed above, the kind of independence that underlies my partitioning scheme is not the same thing as statistical independence. Therefore Veech and Crist’s (2010) discussion of statistical independence, and their simulations, are not closely related to the real issues underlying partitioning. Nevertheless it is necessary to comment briefly on some of their statements about statistical independence.

First, Veech and Crist point out that for any particular data set and any particular partitioning scheme, the values of alpha, beta, and gamma are all completely determined if we know the true values of any two of them. Veech and Crist use this to claim that beta is necessarily mathematically constrained by alpha even under my partitioning scheme. This statement confuses functional relationships with a particular set of function values. Many aspects of nature are the result of the combined effects of multiple independent variables. The existence of a formula for the combined effect has no bearing on the independence of the underlying variables. Using their example of flipping two fair coins, we could find the total number of heads for each experiment (an experiment being a flip of the two coins). For any instance of the experiment, if someone told us the outcome of one of the flipped coins and also told us the total number of heads, we could determine if the other coin gave a head or a tail. This does not change the fact that the outcomes of flipping the two coins were statistically and logically independent of each other.

The authors also claim that alpha, beta, and gamma are pairwise independent. Gamma is not independent of alpha or beta. If one knows nothing else about the world, except that alpha = 50, this lets us infer that gamma is greater than or equal to 50. Likewise, in additive partitioning of species richness, if one knows that beta is 10, then gamma is necessarily greater than 10. Note how different this is from the relation between alpha and beta using either additive partitioning of Shannon entropy, or multiplicative partitioning of any true diversity. If someone tells us the value of alpha, and nothing else, this knowledge by itself tells us absolutely nothing additional about the value of beta.

Most of the authors’ article is devoted to a simulation intended to test the independence of alpha and beta. However, Veech and Crist use a simulation procedure that does not fix the number of communities N. In multiplicative partitioning, the value of N explicitly determines the range of beta. The authors’ simulation therefore confounds two effects: the known effect of N on beta, and the influence of alpha on beta. Had they used a fixed N (which is the normal situation in a real ecological investigation), they would have found that multiplicative beta was independent of alpha. This is explained in detail by Baselga (2010) in this Forum. In any case, statistical relations between alpha and beta are empirical issues, which depend on the nature of the ecosystems under study and the sampling scheme. They are irrelevant to investigating the mathematical relationships between alpha and beta. The mathematical independence of within- and between-group diversity is shown by proofs and algebra (e.g., Jost 2007), not simulations.

Conclusion

When the additive partitioning framework is applied to Shannon entropy and the Gini-Simpson index, mathematical artifacts often masquerade as ecologically meaningful results. The complete partitioning of true diversities into mathematically independent alpha and beta components lets us study within- and between-group diversity without distortion, in a mathematically rigorous and self-consistent framework. This same mathematics resolves problems created by additive partitioning of diversity in other sciences, such as population genetic (Jost 2008).

Practical applications of this approach need to account for biases caused by small samples. Chao et al. (2008) recently generalized some of the similarity measures in Jost (2007) and developed nearly unbiased small-sample estimators for some of them. Anne Chao
and her collaborators continue to develop new estimators for true alpha, beta, and gamma diversity; these and the unbiased similarity estimators are implemented in the freely-downloadable program, SPADE (Chao and Shen 2009).

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LITERATURE CITED


APPENDIX

Logical consistency of diversity measures (Ecological Archives E091-134-A1).