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Toward a unified view of diversity partitioning

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The debate on the properties and use of additive and multiplicative partitioning of species diversity exemplified in this forum reflects the broader challenge of quantifying and interpreting alpha, beta, and gamma diversity at multiple scales of sampling. As noted by Wilsey and Ricotta in their contributions, ecologists use a wide range of measures of beta diversity, partly because of differences in study questions of the investigators and partly because of the differences in their statistical properties. The lack of agreement on the numerous dimensionless measures of community turnover and dissimilarity is a longstanding problem in community ecology (Vellend 2001, Koleff et al. 2003, Magurran 2004, Ricotta 2007). So, too, there has been

some disagreement on the statistical properties and applicability of the alpha and beta components of diversity partitioning.

The popularity of Whittaker's (1960) multiplicative partition of diversity, and subsequent additive partitions by MacArthur et al. (1966), Allan (1975), and Lande (1996), is that they provide a single set of values of alpha and beta diversity for a given sampling scale and therefore give a simple, intuitive measure of species diversity and composition. For this reason, we believe that partitioning methods are a powerful tool for quantifying spatial and temporal variation in biodiversity in a manner that is accessible to ecologists, managers, and non-scientists. The cost of simplicity is that partitioning methods discard information on site-specific composition retained in pairwise dissimilarity and ordination that may be important to the underlying biophysical or land-use gradients that produce beta diversity (but see Hofer et al. 2008). Thus, as an

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TABLE 1. Comparison of the simulation procedures used by Baselga (2010) and Veech and Crist (2010).

Procedure	Simulation of alpha	Simulation of gamma	Additive beta independent of		Multiplicative beta independent of	
			Alpha	Gamma	Alpha	Gamma
Baselga 1	RND (gamma/ N to gamma)	RND (10 to 1000)	no	no	no	yes
Baselga 2	RND (1 to 100)	RND (alpha to alpha $\times N$)	no	no	yes	no
Veech and Crist	RND (1 to gamma)	RND (10 to 1000)	no	no	no	yes

Note: RND represents a random variable selected from a uniform distribution with the given limits; N = number of samples in the data set (5, 50, or 500).

aggregate decomposition of diversity, both additive and multiplicative diversity partitions share the same strengths and limitations. As is clear from the foregoing contributions, however, additive and multiplicative partitions differ in their properties, expression, and interpretation of beta diversity. Here, we address several key points raised in the forum papers including the independence of alpha, beta, and gamma components of diversity, the randomization procedures used to evaluate independence, the use of entropies vs. true diversities, and the relationships between diversity partitioning and other community analyses. We conclude with a set of recommendations on the use of diversity partitioning.

In the past 5–10 years, diversity partitioning has become an increasingly common way of analyzing patterns of alpha and beta diversity. In addition to the contributions of this Forum, there have been other critiques of additive diversity partitioning. A common feature of some of these critiques (and some of the forum contributions) is to criticize additive partitioning because the beta component derived from additive partitioning (for some indices, notably species richness) is not independent of alpha. At the same time, the critics emphasize the “independence” of beta and alpha as derived from multiplicative partitioning (e.g., Baselga 2010, Jost 2010, Ricotta 2010). Jost (2006, 2007) referred to “independence” of multiplicative beta and alpha several times, without explicitly using the term “statistical independence.” In our opening paper of this forum, we explicitly evaluated the statistical independence of beta (multiplicative and additive) and alpha. We don’t agree with Jost that “Statistical independence of alpha and beta is neither necessary nor desirable,” and “Therefore, Veech and Crist’s discussion of statistical independence, and their simulations, are not closely related to the real issues underlying partitioning.” Statistical independence (or the lack thereof) of alpha and beta is the main issue with respect to evaluating the potential benefits of additive and multiplicative partitioning. A researcher’s ability to recognize and account for the non-independence of two or more variables is crucial for proper statistical practice.

In his contribution to this forum series, Jost now refers to multiplicative beta and alpha as being “mathematically independent.” However, “mathematical independence” does not exist as a property of two empirical variables. We conducted a keyword abstract search in ISI

Web of Science on “mathematical independence” and “mathematically independent” and obtained 3 and 32 citations respectively, as of 1 June 2009. Virtually all of these papers were using “mathematically independent” as a synonym for “statistically independent.” By comparison, “statistical independence” and “statistically independent” returned 470 and 1243 citations, respectively. Contrary to Jost, mathematical independence is not a synonym for orthogonality. Two variables (\mathbf{X} and \mathbf{Y} , portrayed as matrices) are orthogonal if and only if $\mathbf{X}'\mathbf{Y} = 0$ (Rodgers et al. 1984). Moreover, orthogonality of two variables is a separate condition from whether the variables are statistically independent (uncorrelated); that is, two variables can be orthogonal and either correlated or not correlated (Rodgers et al. 1984). If two variables are each represented as elements in a one-dimensional matrix or vector then the vectors must be perpendicular in order to be orthogonal; alpha and beta are not orthogonal.

The remainder of the paper is mostly focused on further evaluating the statistical independence of alpha and beta, particularly in the light of Baselga’s contribution. Baselga (2010) presents a thorough and insightful examination of statistical independence of beta and alpha. Baselga simulated pairs of alpha and gamma values and then derived additive and multiplicative beta from these paired values. This general approach follows our approach but the simulations differ (Table 1). Procedure 1 of Baselga and our simulation procedure do not demonstrate statistical independence of multiplicative beta and alpha; however, Procedure 2 of Baselga does (Table 1). In Procedure 2, the constraints on gamma are set directly by alpha and N (the number of samples in the data set). In Procedure 1 and our procedure, gamma is constrained to be between 10 and 1000 (or some other predefined limits); alpha does not constrain gamma. Rather gamma constrains alpha in Procedure 1 and in our procedure. In Procedure 2, gamma does not constrain alpha (except that alpha cannot be greater than gamma); alpha is constrained between 1 and 100 (or some other predefined limits) (Table 1). In Procedure 2, gamma is selected from all possible values for a given alpha (and N) whereas in Procedure 1 (and our procedure) alpha is selected from all possible values for a given gamma. Most applications of diversity partitioning (additive and multiplicative) assume that gamma is set (a given value for a data set)

with alpha being a variable confined to the limit set by gamma (i.e., Procedure 1). Gamma is not assumed to be a variable whose upper limit must always increase with alpha and N (i.e., Procedure 2).

Previous studies by Jost (2006, 2007) and the contributions to this forum by Baselga and Jost suggest that multiplicative beta is measuring some aspect of gamma diversity that is completely separate from the aspect measured by alpha diversity. This may be correct, but this view needs clarification. One assumption of this view is that completely different ecological and evolutionary processes produce alpha and beta-diversity. Baselga (2010) states: "As previously reported by Wilson and Shmida (1984), alpha and beta diversity patterns are the result of different ecological and biogeographical processes." Our own perspective on alpha and beta diversity is that some of the same ecological and evolutionary processes affect both alpha and beta, and that alpha and beta together determine gamma-diversity, whether the partitioning is additive or multiplicative. The lack of complete statistical independence is not problematic as there are ways to account for the dependence between alpha and beta (as we explain in the lead forum paper; also see Wilsey 2010).

In his forum paper, Jost (2010) disputes or misunderstands our explanation of statistical independence. He states: "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." Although this statement is true for many variables that scientists measure, it is not true for gamma diversity. Gamma diversity is *completely* determined by the combined effect of just *two* variables. Moreover, the two variables (alpha and beta) combine in a known and constant way (either $\alpha + \beta$ or $\alpha \times \beta$) in determining gamma. A third variable is not in the equation for gamma. Because alpha, beta, and gamma are random variables with a non-zero covariance, they are not conditionally independent. Knowing the values of any two of them allows for the *exact* determination of the third. This is true for additive and multiplicative beta. Jost states: "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." This is indeed true, for both additive and multiplicative beta. In fact, if we only know alpha and nothing else, we cannot even calculate beta. Our main point here is that in the additive and multiplicative partitioning schemes, beta can *only* be determined by first determining alpha and gamma (which are directly measured). Moreover, as with most species responses measured at multiple sampling scales, these three quantities will generally have a non-zero covariance, which indicates that the variables are linearly correlated (Rodgers et al. 1984).

Contrary to Jost (2010), we have not confused the functional relationships among alpha, beta, and gamma. Continuing with the coin toss analogy, Jost correctly

states that the outcomes of flipping two coins are statistically independent of each other. This is their functional relationship (actually the absence of a relationship): the outcome of one toss in no way affects the outcome of the other toss. If we flip two coins (or flip one coin two times) then we could determine the frequency of heads (or tails) solely based on knowing the frequency of tails (or heads). The complete set of possible values are [(0, 2), (1, 1), and (2, 0)]; these are relationships between empirical values. However, alpha and beta do not have this type of functional or empirical relationship. The frequency of heads (or tails) could be directly determined by counting the number of times that the event occurs; that is, the value of each variable can be determined with direct observation and without knowledge of the value of the other variable. In diversity partitioning, beta is not and cannot be determined by direct observation or measurement; it can only be determined by knowing alpha and gamma. Many other (but not all) metrics for measuring beta also require that alpha be calculated (Wilson and Shmida 1984, Vellend 2001, Koleff et al. 2003). Thus, alpha and beta may not have an underlying functional relationship: beta as a property or characteristic of a set of samples (data set) may only exist with reference to an observed and measured alpha.

There are several limitations of diversity partitioning. As Wilsey demonstrates with empirical data, additive beta richness must be corrected when comparing beta values that derive from two different partitions (data sets) that differ in either alpha or gamma (Ricotta 2008). An outright misuse of diversity partitioning is the use of entropies to calculate beta as α/γ ; there are serious mathematical problems in doing this and these problems can lead to erroneous inferences (Jost 2006, 2007, 2010, Ricotta 2010). The α/γ ratio has much better mathematical properties when alpha and gamma are expressed as true diversities or numbers equivalent (Jost 2007). For any set of species abundance data, alpha, beta, and gamma can be calculated as true diversities of any order q (Jost 2006, 2007, Ricotta 2008). However, the units for alpha and beta are not the same when using true diversities. Alpha is measured or interpreted as the number of equally common species whereas beta is interpreted as the effective number of distinct communities (Jost 2007, 2010). We agree with Ricotta (2010) that a "statistically well behaved" metric for beta diversity is desirable but not at the expense that it measures (or interprets) a quantity in a way that is not useful or is nonsensical. For instance, a multiplicative partition of species richness ($q = 0$) from data of the North American Breeding Bird Survey revealed that in one ecoregion of 700 000 km² there were only 2.85 distinct bird communities, even though the data set consisted of 263 spatially distinct survey routes scattered throughout the ecoregion. Lastly, the beta derived from diversity partitioning does not directly measure differences in species composition among individual samples

or communities, but instead is an overall average of the diversity not found in any one sample (Veech et al. 2002, Crist and Veech 2006).

We believe that both additive and multiplicative partitioning can be very useful for studies of species diversity, despite their limitations. Perhaps their greatest value is that, as an overall decomposition of beta diversity, additive and multiplicative partitioning can be applied to multiple scales of sampling (Wagner et al. 2000, Crist et al. 2003, Crist and Veech 2006). Similarly, studies on the local–regional relationships of species have benefited from multi-scale perspectives of diversity partitioning (Loreau 2000, Gering and Crist 2003, Cornell et al. 2007). Diversity partitioning can also decompose the alpha and beta components of the species–area relationship, additively or multiplicatively, and determine the fraction of the total beta component of richness that is due to changes in habitat area (Crist and Veech 2006). Lastly, diversity partitioning has been used to determine the contributions of different habitats to overall landscape diversity (Wagner and Edwards 2001, Lu et al. 2007).

To some extent, additive vs. multiplicative partitioning is a false dichotomy. Ricotta (2005) showed that there is substantial similarity between the two approaches and Jost (2007) further demonstrated that when some entropies are converted into true diversities the resulting mathematical relationship between alpha, beta, and gamma is additive. The greatest value of diversity partitioning is in simultaneously analyzing alpha and beta, and not in solely measuring beta diversity. As Ricotta (2010) notes there is no perfect and completely satisfactory metric for measuring beta. The measurement of beta has received much attention in the past five years. Ecologists have and continue to develop methods that also measure differences in species composition, take into account differences in sampling effort, and differences in species detectability.

We suggest the following recommendations for researchers using diversity partitioning. Use either additive or multiplicative species richness ($q = 0$) to measure beta (alpha at $q = 0$ is the same in the additive and multiplicative framework). If there is a benefit or desire to weigh the alpha and beta values by species abundances, favoring either common or rare species, then also calculate q -diversity metrics. The latest release of our software (PARTITION 3.0) partitions additive and multiplicative species richness as well as any q metric (program *available online*).⁴ Do not use entropies in diversity partitioning; true diversities are superior alternatives for many reasons. Avoid the labels “additive” and “multiplicative” when referring to diversity partitioning. Be aware of the de facto but relatively minor statistical dependence between alpha and beta that exists simply because beta must be calculated from

alpha and gamma. Use appropriate statistical adjustments to remove the dependence (as demonstrated in Veech and Crist 2010, Wilsey 2010). As Wilsey notes, the general approach and metric used in analyzing a diversity pattern will depend on the goals of the investigation. Diversity partitioning is particularly well suited for analyzing multi-scale patterns of species diversity; it will continue to play an important role in this active area of research in the future.

LITERATURE CITED

- Allan, J. D. 1975. Components of diversity. *Oecologia* 18:359–367.
- Baselga, A. 2010. Multiplicative partition of true diversity yields independent alpha and beta components, additive partition does not. *Ecology* 91:1974–1981.
- Cornell, H. V., R. H. Karlson, and T. P. Hughes. 2007. Scale-dependent variation in coral community similarity across sites, islands, and island groups. *Ecology* 88:1707–1715.
- Crist, T. O., and J. A. Veech. 2006. Additive partitioning of rarefaction curves and species–area relationships: unifying alpha-, beta-, and gamma-diversity with sample size and habitat area. *Ecology Letters* 9:923–932.
- Crist, T. O., J. A. Veech, J. C. Gering, and K. S. Summerville. 2003. Partitioning species diversity across landscapes and regions: a hierarchical analysis of alpha, beta, and gamma diversity. *American Naturalist* 162:734–743.
- Gering, J. C., and T. O. Crist. 2002. The alpha-beta-regional relationship: providing new insights into local-regional patterns of species richness and scale dependence of species diversity components. *Ecology Letters* 5:433–444.
- Hofer, G., H. H. Wagner, F. Herzog, and P. J. Edwards. 2008. Effects of topographic variability on the scaling of plant species richness in gradient dominated landscapes. *Ecography* 31:131–139.
- Jost, L. 2006. Entropy and diversity. *Oikos* 113:363–375.
- Jost, L. 2007. Partitioning diversity into independent alpha and beta components. *Ecology* 88:2427–2439.
- Jost, L. 2010. Independence of alpha and beta diversities. *Ecology* 91:1969–1974.
- Koleff, P., K. J. Gaston, and J. J. Lennon. 2003. Measuring beta diversity for presence–absence data. *Journal of Animal Ecology* 72:367–382.
- Lande, R. 1996. Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos* 76:5–13.
- Loreau, M. 2000. Are communities saturated? On the relationship between alpha, beta, and gamma diversity. *Ecology Letters* 3:73–76.
- Lu, H. P., H. H. Wagner, and X. Y. Chen. 2007. A contribution diversity approach to evaluate species diversity. *Basic and Applied Ecology* 8:1–12.
- MacArthur, R., H. Recher, and M. Cody. 1966. On the relation between habitat selection and species diversity. *American Naturalist* 100:319–332.
- Magurran, A. E. 2004. *Measuring biological diversity*. Blackwell Publishing, Oxford, UK.
- Ricotta, C. 2005. On hierarchical diversity decomposition. *Journal of Vegetation Science* 16:223–226.
- Ricotta, C. 2007. A semantic taxonomy for diversity measures. *Acta Biotheoretica* 55:23–33.
- Ricotta, C. 2008. Computing additive beta-diversity from presence and absence scores: a critique and alternative parameters. *Theoretical Population Biology* 73:244–249.
- Ricotta, C. 2010. On beta diversity decomposition: trouble shared is not trouble halved. *Ecology* 91:1981–1983.
- Rodgers, J. L., W. A. Nicewander, and L. Toothaker. 1984. Linearly independent, orthogonal, and uncorrelated variables. *American Statistician* 38:133–134.

⁴ <http://www.users.muohio.edu/cristto/partition.htm>

- Veech, J. A., and T. O. Crist. 2010. Diversity partitioning without statistical independence of alpha and beta. *Ecology* 91:1964–1969.
- Veech, J. A., K. S. Summerville, T. O. Crist, and J. C. Gering. 2002. The additive partitioning of species diversity: recent revival of an old idea. *Oikos* 99:3–9.
- Vellend, M. 2001. Do commonly used indices of beta-diversity measure species turnover? *Journal of Vegetation Science* 12: 545–552.
- Wagner, H. H., and P. J. Edwards. 2001. Quantifying habitat specificity to assess the contribution of a patch to species richness at a landscape scale. *Landscape Ecology* 16:121–131.
- Wagner, H. H., O. Wildi, and K. C. Ewald. 2000. Additive partitioning of plant species diversity in an agricultural landscape mosaic. *Landscape Ecology* 15:219–227.
- Whittaker, R. H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs* 30:279–338.
- Wilsey, B. J. 2010. An empirical comparison of beta diversity indices in establishing prairies. *Ecology* 91:1984–1988.
- Wilson, M. V., and A. Shmida. 1984. Measuring beta diversity with presence–absence data. *Journal of Ecology* 72:1055–1064.