Partitioning diversity[1]

Contemporary ecologists work with three measures of diversity: alpha, beta, and gamma diversity. Alpha diversity is *local diversity*, and it is measured *within* a place, such as a single plot, an individual forest stand, or a single stream. Gamma diversity is *regional diversity*, and it is the total diversity measured for *a group of* places—all plots in the study, all streams in a watershed, all Costa Rican dry forest stands. Beta diversity links alpha and gamma, or local and regional, diversities and is defined as "the extent of differentiation of communities along habitat gradients" (Whittaker, R. H. 1972. "Evolution and measurement of species diversity." *Taxon* 21:213–251; the quotation is from p. 214). Alpha and gamma diversity *can be measured directly*, either as numbers of species (*species richness*) or as numbers of species weighted by their relative abundance in the sample. There are many versions of these latter *species diversity measures*; familiar ones include the Shannon-Weiner and Simpson's index, among others.

Beta diversity, on the other hand, is a *derived quantity*, but how to best derive this quantity from measurements of alpha and gamma diversities, and how to interpret beta, has been a vexing and at times contentious problem for ecologists since Robert H. Whittaker first presented the concept in 1960 ("Vegetation of the Siskiyou Mountains, Oregon and California." *Ecological Monographs* 30:279–338; see especially pp. 319–323). Whittaker himself asserted that gamma equals the product of alpha and beta (and hence beta can be calculated by dividing gamma by alpha), but Russell Lande asserted that an additive "partition" of diversity (alpha + beta = gamma) provides a more natural measure of beta diversity (Lande, R. 1996. "Statistics and partitioning of species diversity, and similarity among multiple communities." *Oikos* 76:5–13). The sparks have been flying ever since.

This Forum was prompted by the submission of the lead paper (by Veech and Crist) as a Comment on a paper published two years ago by Lou Jost (2007. "Partitioning diversity into independent alpha and beta components." *Ecology* 88:2427–2439). Jost provided a unified mathematical framework for computation and use of *numbers equivalents* of classical diversity measures (the latter are referred to as *entropies*). The numbers equivalent of any diversity index is the number of equally likely elements (individuals, species, etc.) needed to produce the observed value of the diversity index (the entropy). The idea of a numbers equivalent originated in economics and was first introduced to ecologists by Mark O. Hill (1973. "Diversity and evenness: a unifying notation and its consequences." *Ecology* 54:427–432). All of the authors in this Forum agree that using numbers equivalents instead of the classical diversity indices (entropies) such as H' should be used in any diversity partitioning. One could go further and suggest that, even if the interest is only in describing the diversity of a single assemblage, the numbers equivalent, not the entropy, should be the diversity measure of choice. But my goal in organizing this Forum was to move beyond this easy point of agreement and to look for additional common ground. The resulting papers provide some of that and, I hope, illuminate some ways forward.

In their opening contribution, Veech and Crist address the importance of the independence of alpha and beta diversity and use simulations to show that if gamma is set a priori, and alpha drawn as a random proportion of gamma, then there is some association between alpha and beta (because of their common dependence on gamma) but not a lot of statistical dependence of alpha and beta, regardless of whether an additive or multiplicative partition is used to derive beta from (fixed) gamma and (random) alpha. In his contribution, Besalga shows that Veech and Crist's simulation is only one of several reasonable choices. First, the total number of samples N was not fixed by Veech and Crist, but it should be if gamma is fixed (or the first to be determined) and alpha is sampled second. Alternatively, alpha could be simulated first and gamma then determined from the simulated alphas (and fixed N). Besalga shows that the order of simulation matters; one could argue that the primary value (and correctness) of Jost's derivations is that they were analytical and based on first principles, not on the order of simulation.

Jost, while focusing on the theory, indirectly highlights the empiricist's dilemma. We can measure alpha, we would like to measure beta, and gamma should be the derived quantity. If we are to do

---

[1] Reprints of this 31-page Forum are available for $10.00 each, either as PDF files or as hard copy. Prepayment is required. Order reprints from the Ecological Society of America, Attention: Reprint Department, 1990 M Street, N.W., Suite 700, Washington, D.C. 20036 (esaHQ@esa.org).

this, then alpha and beta should be independent entities. But empirically, we measure alpha, estimate gamma from alpha, and then derive beta from our measured alpha and estimated gamma. Statistically, we treat gamma as a known, fixed quantity (as in Veech and Crist's simulation), but in reality, gamma, like alpha, is a random variable. Furthermore, Jost's theory, and analyses by Besalga and Ricotta in this Forum, insist on equal sample sizes (N) when comparing among assemblages. But rarely do ecologists actually have equal or fixed sample sizes (imagine, for example, comparing beta diversity, however derived, of ants living in 30 bogs with beta diversity of ants living in 80 forest stands). Even in Wilsey's careful empirical comparison—the one touchstone of realism in this Forum—in which the sample sizes were intended to be identical, one plot had to be dropped due to an "accidental mowing event." Rarefaction methods, used widely to compare species richness among sites or samples of different sizes, has yet to achieve much penetrance in the beta diversity literature (but see Olszewski, T. D. 2004. "A unified mathematical framework for the measurement of richness and evenness within and among multiple communities." *Oikos* 104:377–387).

Jost's 2007 paper provided perhaps the most important theoretical advance in measuring diversity since Whittaker introduced the concept of beta diversity into ecology. But as illustrated by the contributions to this Forum, challenges remain. Reaching consensus on how to partition diversity measures will be harder than agreeing on the measures themselves. Application of the theory places difficult demands on the sampling done in the field. Assumptions about the world (e.g., gamma as a fixed quantity, whether known or unknown) continue to shape our analysis and conclusions. And a real breakthrough would require a method to measure beta diversity independently of either alpha or gamma diversity. This Forum illustrates that there is much yet to be done to identify and characterize patterns of biological diversity.

—AARON M. ELLISON
Associate Editor-in-Chief

Key words: alpha diversity; beta diversity; diversity partition; gamma diversity; numbers equivalents; simulation modeling; species diversity.