

## MINI- REVIEW

Minireviews provides an opportunity to summarize existing knowledge of selected ecological areas, with special emphasis on current topics where rapid and significant advances are occurring. Reviews should be concise and not too wide-ranging. All key references should be cited. A summary is required.

# The additive partitioning of species diversity: recent revival of an old idea

Joseph A. Veech, Keith S. Summerville, Thomas O. Crist and Jon C. Gering

Veech, J. A., Summerville, K. S., Crist, T. O. and Gering, J. C. 2002. The additive partitioning of species diversity: recent revival of an old idea. *Oikos* 99: 3–9.

Ecologists have traditionally viewed the total species diversity within a set of communities as the *product* of the average diversity within a community (alpha) and the diversity among the communities (beta). This multiplicative concept of species diversity contrasts with the lesser known idea that  $\alpha$ - and  $\beta$ -diversities sum to give the total diversity. This *additive partitioning of species diversity* is nearly as old as the multiplicative concept, yet ecologists are just now beginning to use additive partitioning to examine patterns of species diversity. In this review we discuss why additive partitioning remained “hidden” until just a few years ago. The rediscovery of additive partitioning has expanded the way in which ecologists define and measure  $\beta$ -diversity. Beta diversity is no longer relegated to describing change only along an environmental gradient. Through additive partitioning,  $\beta$ -diversity is explicitly an average amount of diversity just as is  $\alpha$ -diversity. We believe that the additive partitioning of diversity into  $\alpha$  and  $\beta$  components will continue to become more widely used because it allows for a direct comparison of  $\alpha$ - and  $\beta$ -diversities. It also has particular relevance for testing ecological theory concerned with the determinants of species diversity at multiple spatial scales and potential applications in conservation biology.

J. A. Veech, K. S. Summerville and T. O. Crist, Dept of Zoology, Miami Univ., Oxford, OH 45056-1400, USA (veechja@muohio.edu). – J. C. Gering, Div. of Science, Truman State Univ., Kirksville, MO 63501, USA.

Ecologists often revive old ideas by giving them new purpose. A recent example is the rediscovery of additive diversity partitioning. Lande (1996) demonstrated analytically that total species diversity in a region ( $\gamma$ ) could be partitioned into additive components representing within-community diversity ( $\alpha$ ) and among-community diversity ( $\beta$ ), where diversity is measured as species richness, or by using either the Simpson [ $1 - \sum p_i^2$ ] or

Shannon index [ $-\sum p_i \ln(p_i)$ ] where  $p_i$  is the proportional abundance of species  $i$  for  $i = 1$  to  $n$  total number of species in the sample. Lande (1996) appears to have been the first to cast the additive partitioning of diversity in terms of Whittaker's (1960, 1972) familiar  $\alpha$ -,  $\beta$ -, and  $\gamma$ -diversities. However, the idea that diversity can be partitioned into additive components is not new. MacArthur et al. (1966) and Levins (1968) indepen-

Accepted 23 April 2002

Copyright © OIKOS 2002  
ISSN 0030-1299

OIKOS 99:1 (2002)

dently developed simple equations for additively partitioning diversity a few years after Whittaker (1960) and decades before Lande (1996), but their equations did not use Whittaker's terms. Because of this, ecologists have traditionally followed Whittaker (1960) and viewed  $\gamma$ -diversity as being the product, not the sum, of  $\alpha$ - and  $\beta$ -diversities.

Of much greater importance, strict adherence to the multiplicative relationship has unduly influenced how ecologists define and measure  $\beta$ -diversity. In this review, we suggest that viewing  $\gamma$ -diversity as the sum of  $\alpha$ - and  $\beta$ -diversities leads to the most operational definition of  $\beta$ -diversity and quantifies it in a manner commensurate with the measurement of  $\alpha$ - and  $\gamma$ -diversities. In effect, the revival of additive diversity partitioning has given new meaning to  $\beta$ -diversity, which we discuss later in the review. Our first task, however, is to understand why the additive partitioning of species diversity went relatively unnoticed by ecologists for three decades. We begin with a brief history of  $\beta$ -diversity.

### A brief history of defining and measuring $\beta$ -diversity

Beta diversity as an ecological term was originally introduced by Whittaker to describe changes in species composition and abundance across environmental continua such as gradients of elevation and moisture. Whittaker (1956) adopted the Gleasonian idea of the individualistic distribution of plant species after finding gradual continuity in the vegetation of the Great Smoky Mountains of the eastern United States. According to Whittaker (1956, 1960), each plant species exhibited an individualistic response to environmental conditions (Westman and Peet 1982) (Fig. 1). Whittaker (1956) defined the diversity within a "community" as "alpha diversity" given that Fisher's alpha parameter of the log-series species-abundance distribution was a useful way of measuring the diversity.  $\beta$ -diversity was then taken as the change in the number of species from one place to another along the gradient (Whittaker 1956, 1960), and later defined as "species turnover" or changes in species composition from one community to another (Whittaker 1972) (Fig. 1). Beginning with the first time Whittaker coined the term "beta diversity", the concept of  $\beta$ -diversity was intimately linked to the notion of change along a gradient.  $\beta$ -diversity as species turnover became widely accepted among ecologists. Today, many ecologists continue to use the two terms synonymously (Harrison et al. 1992, Blackburn and Gaston 1996, Mourelle and Ezcurra 1997, Sweeney and Cook 2001, Summerville and Crist 2001, and many others); see Vellend (2001) for a convincing argument against this practice.

Whittaker (1960, 1972, 1977) recommended several different metrics for measuring  $\beta$ -diversity; most of

these were based on percent similarity or the ratio of the number of species shared by two communities (or samples) to the total number of species found in both communities. For example, Whittaker (1956, 1960) suggested that  $\beta$ -diversity could be measured as the number of "half-changes" along an environmental gradient. A "half-change" was defined as a decrease of 50% or more in the percent similarity between two samples (not necessarily adjacent) as measured by the Jaccard coefficient (Fig. 2). Since Whittaker, other metrics have been developed; most notable among these are the metrics based on species gain and loss along a gradient (Cody 1975, Bratton 1975, Routledge 1977, Wilson and Mohler 1983, Wilson and Shmida 1984, Shmida and Wilson 1985, Magurran 1988).  $\beta$ -diversity is derived from the difference between the rate at which species are gained from a sample at one end of the gradient to successive samples along the gradient and the rate at which they are lost (Fig. 3). The half-change and the gain-loss metrics reinforce the idea that  $\beta$ -diversity is change along a gradient, though the gradient need not be spatially explicit (Cody 1975). Other researchers (Connor and McCoy 1979, Caswell and Cohen 1993, Rosenzweig 1995) have defined  $\beta$ -diversity as the slope of the species-area relation. Few researchers have put this definition to use in measuring  $\beta$ -diversity perhaps because it requires knowing the true area of the community being sampled and because it assumes that species-area curves in island systems are nested (Wilson and Shmida 1984).

Interestingly, Whittaker (1960, 1972, 1977) recognized and used another definition of  $\beta$ -diversity that was quite different from his gradient-based definition in

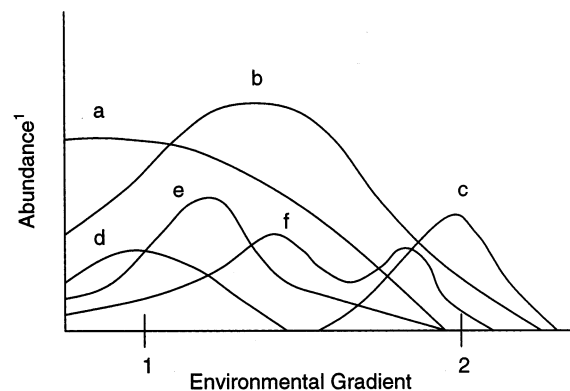


Fig. 1. Species abundances plotted along an environmental gradient as in Whittaker (1956, 1960). At point 1, there are five species (all except c) while at point 2 there are only three species (b, c, and f). The species diversity at points 1 and 2 each could represent the  $\alpha$ -diversity of a "community" or sample plot on the gradient. Diversity could be measured as species richness or by metrics (e.g. Shannon or Simpson indices) based on proportional abundances of species. <sup>1</sup>Whittaker often plotted abundance as percent cover in a plot, but in this diagram it can also represent the number of individuals or density.

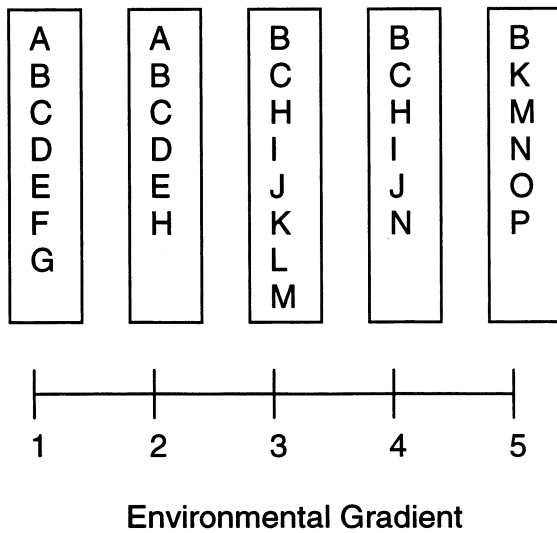


Fig. 2.  $\beta$ -diversity measured by the number of half-changes along an environmental gradient (Whittaker 1956). There are five samples or communities along the gradient with species A–P distributed among the samples. The percent similarity between two samples can be measured by the Jaccard Index [ $C_j = [j/(a + b - j)] \times 100$ ; where  $j$  = number of species in both samples,  $a$  = number of species in the first sample, and  $b$  = number of species in the second sample]. A half-change occurs when percent similarity between two samples declines to  $\leq 50\%$ . For instance, a half-change does not occur between samples 1 and 2 because  $C_j(1,2) = 0.625$ , but  $C_j(1,3) = 0.15$  which does represent a half-change.  $C_j(3,4) = 0.56$ , but  $C_j(3,5) = 0.27$  which represents another half-change. Therefore,  $\beta$ -diversity among the five samples is recorded as two half-changes.

that it was not necessarily bound to a coenocline. Whittaker (1960) reasoned that if one knew the average diversity within a set of communities or samples (i.e.  $\alpha$ -diversity), then one could obtain the total diversity represented by all samples (i.e.  $\gamma$ -diversity), by multiply-

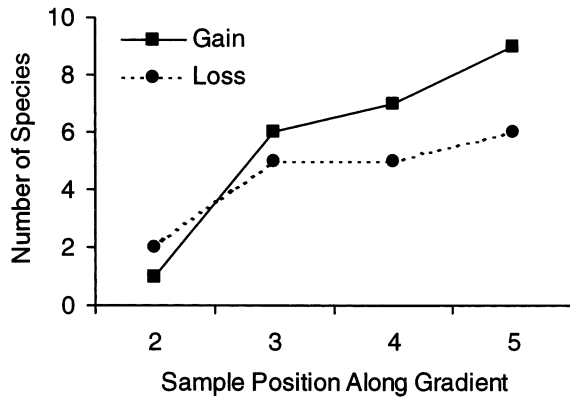


Fig. 3. Species gain and loss along the gradient depicted in Fig. 2. Most  $\beta$ -diversity metrics based on species gain and loss are derived from the difference between the two curves, though the different metrics vary in whether the gradient is spatially explicit and whether the metric is standardized to  $\alpha$ -diversity and corrected for sample size.

ing the average diversity by the number of communities. In such a way, he was implicitly recognizing the number of communities as a measure of  $\beta$ -diversity (Routledge 1977). Of course, using  $\gamma = \alpha \cdot \beta$ , overestimated  $\gamma$ -diversity when communities or samples shared species. This problem was averted in practice, however, because Whittaker and other ecologists of the day usually had estimates for  $\alpha$ - and  $\gamma$ -diversities, and so the task was to measure  $\beta$ -diversity. One way of measuring  $\beta$ -diversity was to rearrange the multiplicative relationship to get  $\beta = \gamma/\alpha$ , which Whittaker (1960, 1972) called the “simplest definition” of  $\beta$ -diversity. Generally, Whittaker and other ecologists measured  $\beta$ -diversity using metrics based on species turnover much more often than they used  $\beta = \gamma/\alpha$ . Nonetheless,  $\gamma$ -diversity as the product of  $\alpha$ - and  $\beta$ -diversities became firmly entrenched in ecology and it remains so today (Haydon et al. 1993, Schluter and Ricklefs 1993, Brown and Lomolino 1998, Gaston and Blackburn 2000, Stiling 2002).

### The additive partitioning of species diversity: first 30 years

The additive partitioning of species diversity is nearly as old as the multiplicative concept of Whittaker (1960). MacArthur et al. (1966) proposed that the diversity between two samples (i.e. bird censuses from two habitats) was equal to the combined diversity of the two samples minus the average within-sample diversity. In effect, MacArthur et al. (1966) proposed  $\beta = \gamma - \alpha$  (or  $\gamma = \alpha + \beta$ ) though they did not express this additive relationship in terms of  $\alpha$ ,  $\beta$ , and  $\gamma$  nor did they refer to their formula as an “additive partition of diversity”. They also did not generalize their formula beyond the case of two samples. MacArthur’s seminal work on the structure of bird communities is widely cited and has a prominent role in the history of community ecology (MacArthur and MacArthur 1961, MacArthur 1964). However, none of this published work fully develops additive partitioning as an analytical method for examining the multiple determinants of species diversity.

Not long after MacArthur et al. (1966), Levins (1968) used additive partitioning to examine the diversity of *Drosophila* communities. Levins (1968), like MacArthur, was primarily interested in examining the multidimensional niche breadth of species as it pertained to competition and coexistence. Perhaps, because of this focus on the niche, an additive partition of diversity in terms of  $\alpha$ -,  $\beta$ -, and  $\gamma$ -diversities did not emerge from the work of Levins, MacArthur, or anyone else in the late 1960’s. Nonetheless, Levins (1968) deserves credit for being one of the first to conduct an additive partition of diversity.

Table 1. Studies that have partitioned species diversity. List was mostly compiled by conducting a cited reference search [on Allan (1975a) and Lande (1996)] using the Institute of Scientific Information database. The list is probably not exhaustive.

Study	Type of diversity partitioned	Organism(s)
Allan (1975b)	Spatial	Aquatic invertebrates
Holland and Jain (1981)	Spatial	Vernal pool plants
Lynch (1981)	Spatial and Temporal	Ants
Barker et al. (1983)	Spatial and Temporal	Yeast in cactuses
DeVries et al. (1997)	Spatial and Temporal	Butterflies
Gimaret-Carpentier et al. (1998)	Spatial	Plants
DeVries et al. (1999a)	Spatial and Temporal	Butterflies
DeVries et al. (1999b)	Spatial and Temporal	Butterflies
Taylor and Bruns (1999)	Spatial	Mycorrhizal fungus on orchids
Wagner et al. (2000)	Spatial	Plants
Fournier and Loreau (2001)	Spatial	Beetles
DeVries and Walla (2001)	Spatial and Temporal	Butterflies
Gering et al., in press	Spatial	Beetles

For the next 30 years, additive partitioning of diversity went unnoticed by ecologists, save a few exceptions (Table 1). The most notable of these exceptions was Allan's (1975a) review of Pielou's (1969) "hierarchical partitioning" method and Lewontin's (1972) "pooling samples" method. For a given community, the hierarchical partitioning method of Pielou (1969) determines a diversity component based on the diversity of species (as measured by the Shannon index) in a genus. Such a component is determined for each genus and then the mean is taken as the "species-level" diversity. A single component representing the "genus-level" diversity is also measured by the Shannon index in which proportional abundances of genera (not species) are used. The "species-level" and "genus-level" diversities so obtained do sum to the diversity that would be obtained by  $\sum p_i \ln(p_i)$  using all species without regard for genus affiliation. Hence, Pielou's method is an additive decomposition of "total" diversity, though it is very different from Lewontin's "pooling samples" method.

Allan (1975a, b) clearly recognized how Lewontin's method could be used to compare the relative contributions of different "dimensions" or factors to a total amount of species diversity (see also Alatalo and Alatalo 1977, Lynch 1981). Indeed, Lewontin's method arose through his demonstration that genetic diversity was greater within human races than between races. In the "pooling samples" method, the total diversity within a community (measured by species richness, Shannon, or Simpson index) derives from the diversity within pooled samples of the community. Most importantly, the total diversity within the community is greater than the average diversity within samples, and the difference between total and average is taken as the between-sample diversity. Hence, total diversity equals the sum of average within-sample diversity and between-sample diversity. Unfortunately, neither Lewontin, Pielou, nor Allan, expressly linked additive partitioning to Whittaker's concepts of  $\alpha$ -,  $\beta$ -, and  $\gamma$ -diversities.

### Recent advances in the additive partitioning of species diversity

Lande (1996) appears to have been the first to place the additive partitioning of species diversity in the context of Whittaker's concepts of  $\alpha$ -,  $\beta$ -, and  $\gamma$ -diversities. Most recently, Loreau (2000), Wagner et al. (2000), and Fournier and Loreau (2001) explicitly demonstrated how  $\gamma$ -diversity is partitioned into  $\alpha$ - and  $\beta$ -diversities at multiple spatial scales (Fig. 4). Given that Whittaker's concepts are familiar to many ecologists, such a link as established by Lande (1996) and extended by Wagner et al. (2000) should lead to greater awareness of additive partitioning among ecologists.

Since Lande's (1996) review, ecologists have been steadily using additive partitioning of diversity to examine landscape patterns of diversity (DeVries et al. 1999b, Wagner et al. 2000, Fournier and Loreau 2001), habitat-level patterns (DeVries et al. 1997, 1999a, DeVries and Walla 2001, Fournier and Loreau 2001), and temporal patterns of diversity (DeVries and Walla 2001) (Table 1). This increased use of additive diversity partitioning may be partly due to Lande's (1996) use of the terms "alpha", "beta", and "gamma" diversities as well as a growing acceptance among ecologists for defining  $\beta$ -diversity as the diversity among samples, regardless of whether the samples occur along an environmental gradient and whether they are spatial or temporal.

As with other diversity partitioning schemes, Lande's (1996) additive version treats  $\alpha$ -diversity as the *average* within-sample diversity, regardless of whether diversity is measured by species richness, the Shannon index, or the Simpson index. Likewise,  $\beta$ -diversity is also an average; it is the average amount of diversity not found in a single, randomly-chosen sample. For instance, imagine that we have five samples each taken from a plot in which the abundance of each plant species has been recorded. We estimate the diversity of each and take the average as  $\alpha$ -diversity. For each of the five, there is also a complement that consists of the other

four samples combined. By additive partitioning,  $\beta$ -diversity is simply the average diversity within the complements. Therefore, both  $\alpha$ -diversity and  $\beta$ -diversity are averages, which makes it easier to compare one to another. For instance, if  $\alpha = 25$  species and  $\beta = 75$  species, then the average amount of diversity not found in one of the samples is three times greater than the average amount found within one of the five samples. This concept of  $\beta$ -diversity explicitly recognizes that  $\beta$ -diversity can be measured and defined relative to  $\alpha$ -diversity.  $\beta$ -diversity and  $\alpha$ -diversity are commensurate.

In contrast, traditional metrics for  $\beta$ -diversity (such as  $\gamma/\alpha$  and those based on species turnover and species gain and loss) provide estimates of  $\beta$  that are not commensurate with  $\alpha$ . This is because the units of  $\beta$  and  $\alpha$  are not the same; for richness, species are the units of  $\alpha$  but  $\beta$  is unitless. Additionally,  $\beta$  and  $\alpha$  are not commensurate because  $\beta$  is derived from pairwise

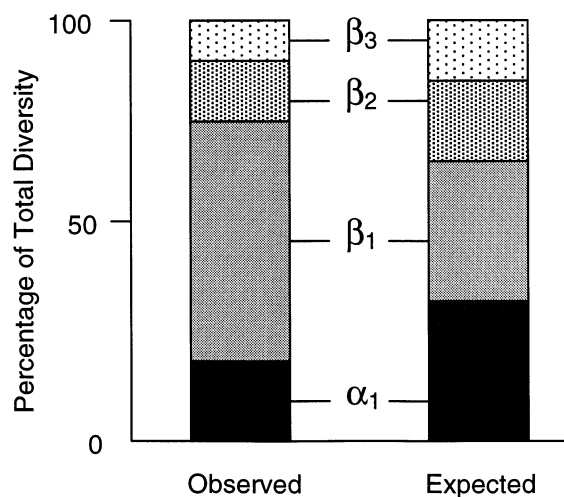


Fig. 4. The additive partitioning of  $\gamma$ -diversity into  $\alpha$  and  $\beta$  components at three nested spatial scales. Mean diversity within samples at each scale ( $\alpha_1$ ,  $\alpha_2$ , and  $\alpha_3$ ) can be obtained based on species richness or proportional abundances of species in each sample. From these values,  $\beta$ -diversity at any scale is determined by subtracting the  $\alpha$ -diversity at that scale from the  $\alpha$ -diversity at the next highest scale (e.g.  $\beta_1 = \alpha_2 - \alpha_1$ ). When there are three sampling scales,  $\gamma = \alpha_1 + \beta_1 + \beta_2 + \beta_3$ ; in a like way additive diversity partitioning can be extended to any number of scales. Converting each diversity component into a percentage is a convenient way of expressing their relative contributions to  $\gamma$ -diversity. Randomization routines can be used to obtain an expected partition of diversity based on a random distribution of individuals among samples and then the observed partition can be compared to the expected, visually or by comparison with null statistical distributions in which many randomized partitions are created (Crist et al., *subm.*). Note that, in this hypothetical example, the observed partition differs from the expected, mostly due to differences in  $\alpha$ - and  $\beta$ -diversities at the lowest scale. Presumably, the difference between the observed and expected diversity components could be due to ecological processes that lead to a non-random dispersion of individuals (e.g. intraspecific aggregation, habitat selection, and limited dispersal capacity).

comparisons of samples (i.e. species turnover) and  $\alpha$  is calculated from all samples simultaneously. In addition, many of the metrics based on species gain and loss provide estimates of  $\beta$ -diversity that depend on how the environmental gradient is defined. That is, the same set of samples could be “arranged” differently on a gradient of moisture compared to one defined by temperature, soil type, spatial location. In each case, the estimates of  $\beta$ -diversity along the gradient might be different.  $\beta$ -diversity as measured by additive partitioning avoids these gradient-related shortcomings of the traditional metrics.

We are not suggesting, however, that additive partitioning provides a metric of  $\beta$ -diversity that should replace all previous metrics; we are promoting  $\beta = \gamma - \alpha$  only as an alternative that may be very useful for some purposes (see below). Moreover, we agree with Lande (1996) that a good comprehensive measure of community similarity is  $1 - \beta/\gamma$ . Defining  $\beta$ -diversity as the average amount of diversity not found in a sample (as we did previously) does not explicitly recognize differences among samples or communities, which, after all, is the original intent of  $\beta$ -diversity. However, sample similarity (measured as  $1 - \beta/\gamma$ ) does directly assess sample differentiation, and it can only be derived from the additive relationship,  $\gamma = \alpha + \beta$ .

We predict a steady increase in the use of additive diversity partitioning, particularly as methods for evaluating the statistical significance of diversity components (Crist et al., *subm.*) become more widely known. One potential method involves producing partitions that would be expected from randomized data and comparing those expected partitions to the actual partitions (Fig. 4). In addition, we think ecologists should continue to define  $\beta$ -diversity in very general terms, and not just as change along an environmental gradient. Conservation biologists have recently recognized applications for diversity partitioning in survey design (DeVries et al. 1997, Gimaret-Carpentier et al. 1998, DeVries and Walla 2001) and nature reserve placement and design (Fournier and Loreau 2001, Gering et al., *in press*). Diversity partitioning can improve biological surveys by identifying the primary source(s) of the total species diversity of a region. For example, DeVries et al. (1997) found that the diversity of tropical butterflies in a “region” was due largely to differences between sampling months (or a  $\beta_{\text{month}}$  component). In a similar way, partitioning of spatially explicit diversity can identify the most important source of diversity and target conservation efforts accordingly.

Ecologists, both theoretical and empirical, should begin to use diversity partitioning as a conceptual framework and an analytic method to address questions pertaining to the relationship between local and regional species diversity (Loreau 2000, Godfray and Lawton 2001). The difference between the average species diversity of local communities and the diversity

within their region is  $\beta$ -diversity (Loreau 2000, Crist et al., *subm.*). Therefore, any factors that affect  $\beta$ -diversity will also determine if local ecological communities are saturated with some constant number of species or whether the species richness of communities varies in proportion to the regional species richness.

Additive diversity partitioning is flexible in that  $\gamma$ -diversity can be partitioned on the basis of any categorical factor (e.g. habitat, feeding guild, host or resource use); therefore, it can potentially be used to analyze any postulated determinant of species diversity. Likewise, any research question that calls for a comparative analysis of the diversity within a set of “samples” and that among the samples is a potential candidate for using diversity partitioning. We suggest that the use of diversity partitioning may eventually lead ecologists to a greater understanding of the factors controlling the spatial and temporal distribution of biodiversity on our planet and help us design effective strategies for saving it.

*Acknowledgements* – We thank an anonymous reviewer for comments on the manuscript. This research was partially supported by funding from The Nature Conservancy (USA) and the Ohio Board of Regents Research Challenge Program (USA).

## References

- Alatalo, R. and Alatalo, R. 1977. Components of diversity: multivariate analysis with interaction. – *Ecology* 58: 900–906.
- Allan, J. D. 1975a. Components of diversity. – *Oecologia* 18: 359–367.
- Allan, J. D. 1975b. The distributional ecology and diversity of benthic insects in Cement Creek, Colorado. – *Ecology* 56: 1040–1053.
- Barker, J. S. F., Toll, G. L., East, P. D. et al. 1983. Heterogeneity of the yeast flora in the breeding sites of cactophilic *Drosophila*. – *Can. J. Microbiol.* 29: 6–14.
- Blackburn, T. M. and Gaston, K. J. 1996. The distribution of bird species in the New World: patterns in species turnover. – *Oikos* 77: 146–152.
- Bratton, S. P. 1975. A comparison of the beta diversity functions of the overstory and herbaceous understory of a deciduous forest. – *Bull. Torrey Bot. Club* 102: 55–60.
- Brown, J. H. and Lomolino, M. V. 1998. *Biogeography*, 2nd ed. – Sinauer Associates Publishing.
- Caswell, H. and Cohen, J. E. 1993. Local and regional regulation of species-area relations: a patch-occupancy model. – In: Ricklefs, R. E. and Schluter, D. (eds), *Species diversity in ecological communities*. Univ. of Chicago Press, pp. 99–107.
- Cody, M. L. 1975. Towards a theory of continental species diversities: bird distributions over Mediterranean habitat gradients. – In: Cody, M. L. and Diamond, J. M. (eds), *Ecology and evolution of communities*. Harvard Univ. Press, pp. 214–257.
- Connor, E. F. and McCoy, E. D. 1979. The statistics and biology of the species-area relationship. – *Am. Nat.* 113: 791–833.
- DeVries, P. J., Murray, D. and Lande, R. 1997. Species diversity in vertical, horizontal, and temporal dimensions of a fruit-feeding butterfly community in an Ecuadorian rainforest. – *Biol. J. Linn. Soc.* 62: 343–364.
- DeVries, P. J., Lande, R. and Murray, D. 1999a. Associations of co-mimetic ithomiine butterflies on small spatial and temporal scales in a neotropical rainforest. – *Biol. J. Linn. Soc.* 67: 73–85.
- DeVries, P. J., Walla, T. and Greeney, H. 1999b. Species diversity in spatial and temporal dimensions of fruit-feeding butterflies from two Ecuadorian rainforests. – *Biol. J. Linn. Soc.* 68: 333–353.
- DeVries, P. J. and Walla, T. R. 2001. Species diversity and community structure in neotropical fruit-feeding butterflies. – *Biol. J. Linn. Soc.* 74: 1–15.
- Fournier, E. and Loreau, M. 2001. Respective roles of recent hedges and forest patch remnants in the maintenance of ground-beetle (Coleoptera: Carabidae) diversity in an agricultural landscape. – *Lands. Ecol.* 16: 17–32.
- Gaston, K. J. and Blackburn, T. M. 2000. *Pattern and process in macroecology*. – Blackwell Science.
- Gering, J. C., Crist, T. O. and Veech, J. A. 2002. Additive partitioning of species diversity across multiple spatial scales: implications for regional conservation of biodiversity. *Conserv. Biol.* in press.
- Gimaret-Carpentier, C., Pelissier, R., Pascal, J. and Houllier, F. 1998. Sampling strategies for the assessment of tree species diversity. – *J. Veg. Sci.* 9: 161–172.
- Godfray, H. C. J. and Lawton, J. H. 2001. Scale and species numbers. – *Trends Ecol. Evol.* 16: 400–404.
- Harrison, S., Ross, S. J. and Lawton, J. H. 1992. Beta-diversity on geographic gradients in Britain. – *J. Anim. Ecol.* 61: 151–158.
- Haydon, D., Radtkey, R. R. and Pianka, E. R. 1993. Experimental biogeography: interactions between stochastic, historical, and ecological processes in a model archipelago. – In: Ricklefs, R. E. and Schluter, D. (eds), *Species diversity in ecological communities*. Univ. of Chicago Press, pp. 117–130.
- Holland, R. F. and Jain, S. K. 1981. Insular biogeography of vernal pools in the central valley of California. – *Am. Nat.* 117: 24–37.
- Lande, R. 1996. Statistics and partitioning of species diversity, and similarity among multiple communities. – *Oikos* 76: 5–13.
- Levins, R. 1968. *Evolution in changing environments, some theoretical explorations*. – Princeton Univ. Press.
- Lewontin, R. C. 1972. The apportionment of human diversity. – In: Dobzhansky, T. (ed.), *Evolutionary biology*. Vol. 6. Appleton-Century-Crofts Publishing, pp. 381–398.
- Loreau, M. 2000. Are communities saturated? On the relationship between alpha, beta, and gamma diversity. – *Ecol. Lett.* 3: 73–76.
- Lynch, J. F. 1981. Seasonal, successional, and vertical segregation in a Maryland ant community. – *Oikos* 37: 183–198.
- MacArthur, R. H. 1964. Environmental factors affecting bird species diversity. – *Am. Nat.* 98: 387–397.
- MacArthur, R. H. and MacArthur, J. W. 1961. On bird species diversity. – *Ecology* 42: 594–598.
- MacArthur, R., Recher, H. and Cody, M. 1966. On the relation between habitat selection and species diversity. – *Am. Nat.* 100: 319–332.
- Magurran, A. E. 1988. *Ecological diversity and its measurement*. – Princeton Univ. Press.
- Mourelle, C. and Ezcurra, E. 1997. Differentiation diversity of Argentine cacti and its relationship to environmental factors. – *J. Veg. Sci.* 8: 547–558.
- Pielou, E. C. 1969. *An introduction to mathematical ecology*. – Wiley Interscience.
- Rosenzweig, M. L. 1995. *Species diversity in space and time*. – Cambridge Univ. Press.
- Routledge, R. D. 1977. On Whittaker’s components of diversity. – *Ecology* 58: 1120–1127.
- Schluter, D. and Ricklefs, R. E. 1993. *Species diversity: an introduction to the problem*. – In: Ricklefs, R. E. and Schluter, D. (eds), *Species diversity in ecological communities*. Univ. of Chicago Press, pp. 1–10.

- Shmida, A. and Wilson, M. V. 1985. Biological determinants of species diversity. – *J. Biogeogr* 2: 1–20.
- Sweeney, B. A. and Cook, J. E. 2001. A landscape-level assessment of understory diversity in upland forests of north-central Wisconsin, USA. – *Lands. Ecol.* 16: 55–69.
- Stiling, P. 2002. *Ecology, theories and applications*, 4th ed. – Prentice-Hall Publishing.
- Summerville, K. S. and Crist, T. O. 2001. Effects of experimental habitat fragmentation on patch use by butterflies and skippers (Lepidoptera). – *Ecology* 82: 1360–1370.
- Taylor, D. L. and Bruns, T. D. 1999. Population, habitat and genetic correlates of mycorrhizal specialization in the 'cheating' orchids *Corallorhiza maculata* and *C. mertensiana*. – *Mol. Ecol.* 8: 1719–1732.
- Vellend, M. 2001. Do commonly used indices of  $\beta$ -diversity measure species turnover? – *J. Veg. Sci.* 12: 545–552.
- Wagner, H. H., Wildi, O. and Ewald, K. C. 2000. Additive partitioning of plant species diversity in an agricultural mosaic landscape. – *Lands. Ecol.* 15: 219–227.
- Westman, W. E. and Peet, R. K. 1982. Robert H. Whittaker (1920–1980): the man and his work. – *Vegetatio* 48: 97–122.
- Whittaker, R. H. 1956. Vegetation of the Great Smoky Mountains. – *Ecol. Monogr.* 26: 1–80.
- Whittaker, R. H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. – *Ecol. Monogr.* 30: 279–338.
- Whittaker, R. H. 1972. Evolution and measurement of species diversity. – *Taxon* 21: 213–251.
- Whittaker, R. H. 1977. Evolution of species diversity in land communities. – In: Hecht, M. K., Steere, W. C. and Wallace, B. (eds), *Evolutionary biology*. Vol. 10. Plenum Press, pp. 1–67.
- Wilson, M. V. and Mohler, C. L. 1983. Measuring compositional change along gradients. – *Vegetatio* 54: 129–141.
- Wilson, M. V. and Shmida, A. 1984. Measuring beta diversity with presence-absence data. – *J. Ecol.* 72: 1055–1064.