

FORUM

Beta diversity metrics and the estimation of niche width via species co-occurrence data: reply to Zeleny

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Summary

1. Zeleny (2008) demonstrated that the co-occurrence based assessment of species habitat specialization (introduced by Fridley *et al.* 2007) depends on the size of the species pool. To correct for the effect of the species pool on the estimation of species niche width, Zeleny suggested a modification of the original algorithm by replacing additive partitioning as a measure of beta diversity with Whittaker's beta.
2. We used simulated data to show that the alternative index proposed by Zeleny (2008) will poorly represent the niche widths of species inhabiting a set of plots with a highly skewed distribution of local richness values. We therefore expand on Zeleny's (2008) analysis by considering two additional metrics of beta diversity based on compositional similarity and by testing the performance of these indices under different local-regional richness relationships.
3. *Synthesis.* None of the four tested metrics of beta diversity produced unbiased estimates of niche width under curvilinear local-regional richness relationships. In this context, we provide additional guidance to potential users of co-occurrence based niche width estimates by specifying the conditions under which certain indices of beta diversity best represent niche width information.

Key-words: additive partitioning, beta diversity, ecoinformatics, Jaccard similarity, multiple-site similarity, niche breadth estimation, Whittaker's beta

Zeleny (2008) has shown that the co-occurrence based estimation of species specialization introduced by Fridley *et al.* (2007) is influenced by variation in the size of the species pool along an environmental or compositional gradient. To correct for this sensitivity to species pool variation, he suggests replacing the original measure of beta diversity that is based on additive partitioning of diversity components (e.g. Lande 1996; Veech *et al.* 2002) with Whittaker's beta (Whittaker 1960). Zeleny's observation is an important one that we have independently uncovered in recent cross-continental comparisons of realized niche widths of temperate trees (Manthey 2007). Because variation in species pool size is a common characteristic in community data that cover a wide variety of habitats, and co-occurrence based estimation of species specialization should be independent of species pool attributes, we here briefly expand on Zeleny's (2008) analysis to provide additional guidance to potential users of co-occurrence based niche width estimates.

Alternative measures of beta diversity

The calculation of the generalist-specialist metric proposed by Fridley *et al.* (2007), originally expressed as 'theta', is based on a measure of beta diversity calculated from a fixed number of randomly chosen plots in which a focal species occurs. Since the origin of the concept (Whittaker 1960) ecologists have used a large number of different measures to investigate the variation in beta diversity (Wilson & Shmida 1984; Koleff *et al.* 2003). This variety reflects differences in the basic properties of each statistic and researchers have repeatedly warned that the relevance of any metric depends on the research objective as well as properties of the community data (Koleff *et al.* 2003). Fridley *et al.* (2007) applied additive partitioning as a measure of beta diversity (Lande 1996):

$$\beta_a = \gamma - \mu(\alpha)$$

where γ is the total number of species encountered in a random sample of plots and $\mu(\alpha)$ is mean alpha diversity (mean plot richness). Zeleny (2008) replaced this measure by Whittaker's beta (Whittaker 1960):

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$$\beta_w = \gamma/\mu(\alpha)$$

Zeleny showed that Whittaker's approach of multiplicative partitioning is independent of variation in species pool size under the condition that plot richness is a linear function of the species pool. Although we agree that there are circumstances where β_w is a better generalist-specialist metric than β_a , we demonstrate here that use of β_w is not appropriate in some cases. In particular, β_w will poorly represent the niche widths of species inhabiting plots with a highly skewed distribution of local richness values. For example, in the data set from the south-eastern US used in Fridley *et al.* (2007), the flooded-habitat specialist *Taxodium ascendens* was unrealistically highly ranked in the habitat generalist-specialist list when β_w was used. The species is common to the south-eastern Coastal Plain, where it typically grows in species-poor swamp forests (Christensen 2000). In most of the plots that contain *T. ascendens* the species co-occurs with a few other specialized trees adapted to continuous high water levels. Additionally, it occurs rarely in low abundance in nearby species-rich floodplain forests that are flooded only periodically. Thus, the plot richness distribution of the species is strongly positively skewed. Without these scattered occurrences in adjacent habitats, γ and $\mu(\alpha)$, as well as the resulting β_w , would be very low. The few occurrences in the rich floodplain forests, however, contribute strongly to γ , whereas mean alpha is hardly affected by the few rich species plots, which leads to a strong increase in β_w . Because we expect that specialists from species-poor habitats will often have positive skewness in plot richness distribution, the resulting correlation between plot richness and a generalist-specialist metric based on β_w in empirical data can be negative and decouple the beta diversity metric from actual niche width.

Because neither β_a nor β_w are universal solutions to estimating niche widths from co-occurrence data, we consider here two additional metrics of beta diversity based on compositional similarity. The simplest such approach involves the average of pairwise similarities (e.g., Lennon *et al.* 2001; Condit *et al.* 2002) of plots containing a focal species. Here we evaluate the suitability of Jaccard's similarity index, noting that results using the Sørensen index are qualitatively identical. In addition, we use the more recent advance of 'multiple-site' similarity measures that take into account species shared by more than two sites and avoid the problem of covariance between pairwise similarities (Diserud & Ødegaard 2007). Of two recent suggestions of multiple-site similarity measures, we consider only the multiple Simpson index (Baselga *et al.* 2007), as the multiple Sørensen index is a simple linear function of β_w (Diserud & Ødegaard 2007).

Performance of different beta diversity metrics under simulated species pool variation

We simulated a gradient in species pool size by constructing a coenocline of 300 species whose optimum locations followed an exponential distribution along a single dimension of 5000 units (Fig. 1a–c). Niche shapes were constructed

randomly using a Beta function as in Fridley *et al.* (2007). To focus on the sensitivity of the co-occurrence based estimation of species specialization to local richness gradients we used fixed niche widths of 1000 gradient units and restricted species optimum locations between 500 and 4500 gradient units. Species whose curves were truncated by gradient ends were excluded from further analysis. We randomly located 1000 plots along the gradient and 'sampled' species from each plot according to either a linear or curvilinear relationship between local and regional richness (Fig. 1d). While a linear relationship might be more common (e.g. Cornell & Lawton 1992; Caswell & Cohen 1993; Cornell & Karlson 1996), a curvilinear relationship may arise simply from small sampling scales or if per-species stochastic extinction rates are higher than colonization rates (He *et al.* 2005). For the linear local-regional relationship we randomly sampled 50% of the species pool based on the simulated probability of occurrences; for the curvilinear relationship we fixed the random sample at 50 individuals.

To demonstrate the effect of strongly skewed plot richness distributions on the estimation of niche width, we added five species with symmetrical, bimodal response curves to the gradient. While the total niche widths are equal to the other species, the parameters for the two modes vary regularly to produce different plot richness distributions (Table 1, Fig. 1c). For each sampling design we applied the four selected measures of beta diversity (β_a , β_w , multiple Simpson and Jaccard's similarity), expressing the two similarity indices as dissimilarities. All calculations were performed in the R statistical environment (R Development Core Team 2008). The modified algorithm for the simulation and the estimation of habitat specialization including all measures of beta diversity can be found in Supporting Appendices S1 and S2.

Figure 2 presents the correlation between mean plot richness and estimated niche widths, expressed by the scores of the respective measures of beta diversity, for the two sampling designs. Because niche widths are fixed in the simulated coenocline there should be no correlation between niche widths and mean plot richness. None of the four selected measures of beta diversity could reproduce such a pattern under the condition of a curvilinear local-regional species richness relationship (Fig. 2b,d,f,h). The lowest correlation coefficients, as well as the flattest slopes, are realized with β_w and multiple Simpson (Fig. 2b,f). However, for β_w , the distortion of the bimodal species from the regression line is relatively high (Fig. 2b). With a linear local-regional richness relationship the correlation coefficients are low for the relation between mean plot richness and scores for β_w , multiple Simpson, and Jaccard (Fig. 2a,e,g), while additive partitioning (β_a) is strongly affected by the richness of plots (Fig. 2c). With increasing positive skewness of the plot richness distribution and decreasing mean plot richness, the β_w scores of the bimodal species rise strongly (Fig. 2a, Table 1).

Conclusion

As shown by Zeleny (2008), additive partitioning is strongly affected by species pool variation (resulting in local richness

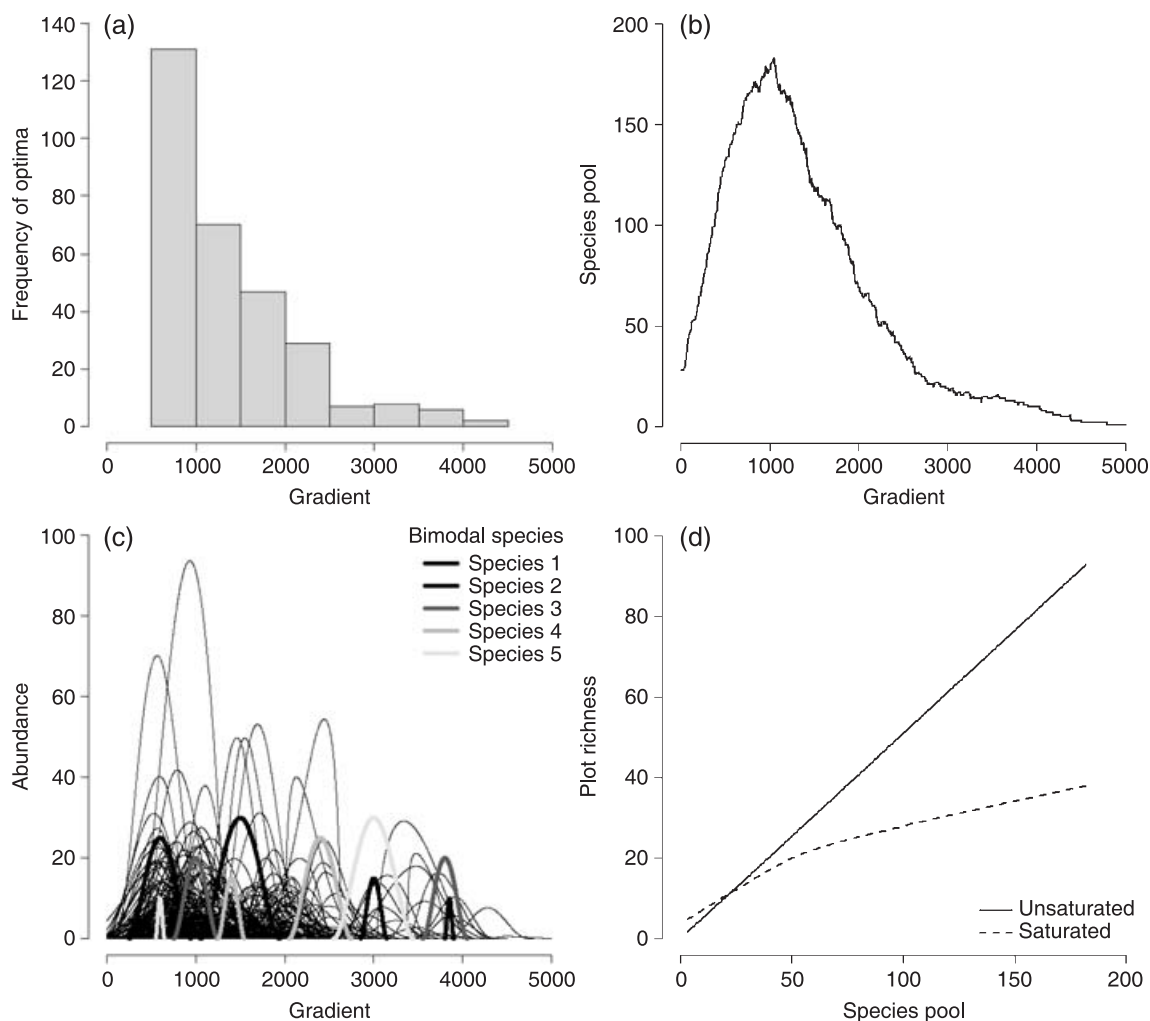


Fig. 1. Characteristics of the simulation scenario with fixed niche widths (i.e., all niche widths are identical) and exponential distribution of species optima along the gradient: distribution of species optima (a), resulting changes in the size of species pool (b), location of response curves of five bimodal species (c), and local-regional species richness relationships for two sampling designs (d).

Table 1. Parameters of response curves of five bimodal species, skewness of plot richness distribution and mean plot richness resulting from two sampling designs with different local-regional species richness relationship. Skewness was calculated with the R package 'e1071'

Species	Response curve parameters				Local-regional richness relationship			
	Left mode		Right mode		Linear		Curvilinear	
	Width	Amplitude	Width	Amplitude	Skewness of richness distribution	Mean plot richness	Skewness of richness distribution	Mean plot richness
1	900	30	100	10	-0.784	61.7	-1.125	28.0
2	700	25	300	15	-0.203	47.1	-0.030	23.4
3	500	20	500	20	0.141	45.0	1.004	16.5
4	300	15	700	25	0.839	34.9	0.742	21.0
5	100	10	900	30	2.485	14.1	1.343	12.2

gradients) under both linear and curvilinear local-regional richness relationships and should generally be replaced by other measures of beta diversity when using co-occurrences to estimate niche widths. Zeleny's (2008) proposed alternative, β_w , performs well with continuous species richness gradients

but is sensitive to species from species-poor habitats that have strongly skewed plot richness distributions (filled dots in Fig. 2a), consistent with our experience of using β_w to describe the niche widths of south-eastern US tree species of well-known habitat affinities. In contrast, co-occurrence metrics

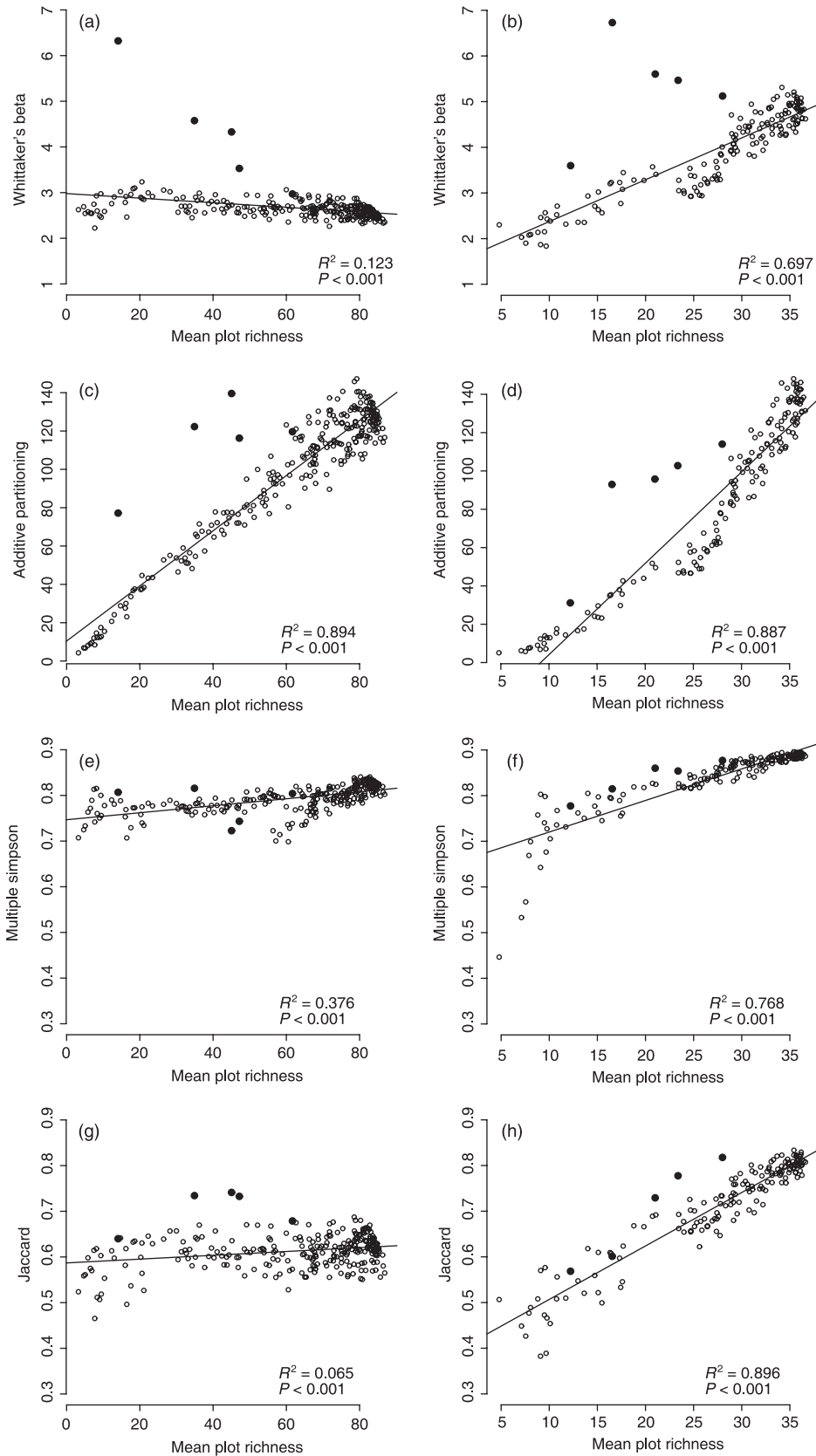


Fig. 2. Results of the application of four measures of β -diversity to the simulation scenario with two contrasting sampling designs. All figures display the correlation between mean plot richness and calculated generalist-specialist scores. Figures in the left column display results for the sampling design with linear local-regional species richness relationship and figures in the right column show results for the curvilinear relationship. Measures of beta diversity: β_w (a, b), β_a (c, d), multiple Simpson (e, f), Jaccard (g, h). The large filled dots in each figure represent the respective scores for five bimodal species.

based on compositional similarity were robust to richness gradients and species of strongly skewed or bimodal distribution (Fig. 2e,g).

Our recommendations for choosing an appropriate beta diversity index in the estimation of relative niche widths from co-occurrence data can be summarized as follows. First, no beta diversity metric is immune to problems that arise when a community is either highly saturated ecologically (e.g., when competition strongly decouples realized and fundamental niches) or ‘appears’ saturated due to a very small sample of individuals (see Fridley *et al.* 2006; Palmer *et al.*, in press). In such cases co-occurrence data are a poor descriptor of habitat affinities, and experimental data are required to delimit niche widths. Second, where plot richness distributions among species are non-skewed, β_w , along with similarity indices, provide a more robust description of relative niche widths than the original β_a used by Fridley *et al.* (2007). A more usual case, however, is that at least some species will exhibit strongly skewed richness distributions (see the example of *T. ascendens* mentioned above) that β_w cannot handle but are relatively inconsequential to metrics based on similarity. We therefore advocate that the original formulation of co-occurrence based estimates of niche widths based on β_a be replaced with similarity indices like pairwise Jaccard or more recent multi-site similarity techniques. Like the original Simpson index the multiple Simpson approach ignores complete nestedness as a difference between sites (Lennon *et al.* 2001; Koleff *et al.* 2003, Baselga *et al.* 2007). Thus, the choice of similarity index will depend in part on whether researchers choose to interpret nestedness patterns as ‘turnover’ in the sense of habitat variation.

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. R code implementing the generalist-specialist metric with five alternative measures of beta diversity.

Appendix S2. R code for simulated coenocline for testing different beta-diversity measures in the generalist-specialist metric.

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