

# Reply to Chen and Schmera: Partitioning beta diversity into replacement and nestedness-resultant components is not controversial

With reference to our recent paper addressing the global biogeography of human infectious diseases (1), Chen and Schmera (2) suggest that our method for evaluating beta diversity and its components is controversial. We used the method developed by Baselga (3) (hereafter, BAS framework) for partitioning compositional dissimilarity into replacement (turnover) and nestedness-resultant components. Chen and Schmera advance an alternative approach developed by Podani and Schmera (4) (hereafter, POD framework), which partitions beta diversity into replacement and richness-difference components. Chen and Schmera suggest that the BAS framework is inappropriate because (i) BAS nestedness ( $\beta_{nes}$ ) is not related to other nestedness measures, (ii) BAS replacement ( $\beta_{sim}$ ) overrepresents true replacement due to scaling differences, and (iii) interpretability of BAS components of beta diversity ( $\beta_{sor}$ ) is problematic. Although Chen and Schmera raise some interesting concerns, we reject their suggestion of a comparative analysis using the POD framework for the following reasons:

i)  $\beta_{nes}$  is not a measure of nestedness itself but a measure of how dissimilar two communities are because of nestedness (5). It has, however, clear connections with nestedness measures, because:

$$\beta_{nes} = \frac{|b-c|}{2a+b+c} * \frac{a}{a + \min(b,c)}$$

The second component is Simpson similarity, a pairwise measure of nestedness (6). The first component (before the product) quantifies richness difference, so  $\beta_{nes}$  quantifies dissimilarity due to richness difference provided the assemblages are nested. Legendre (7) shows that the BAS nestedness-resultant component and the POD richness-difference component

( $Rich_s$ ) reflect different concepts, where  $Rich_s$  quantifies how dissimilar two assemblages are because of richness differences, these being nested or not.

ii)  $\beta_{sim}$  does not overestimate replacement (5). In fact, the BAS replacement component of dissimilarity ( $\beta_{sim}$  or  $\beta_{jtu}$  for Sørensen and Jaccard indices, respectively) effectively removes the effect of richness difference. In contrast, the POD replacement component remains dependent on richness difference, which therefore affects both components of dissimilarity (8). Therefore, the partition of dissimilarity in the POD framework is not effective—the replacement component does not account for an unequivocal ecological concept but rather jointly reflects antithetic phenomena (replacement and richness difference), blurring its meaning. The fact that denominators of turnover and nestedness-resultant components are different does not imply a “scaling difference.” Assemblage dissimilarity indices are dimensionless, and account for the degree of difference from none (0) to total dissimilarity (1).

iii) Almeida-Neto et al. (6), Baselga (5), and Legendre (7) resolved any controversy regarding the meaning of the BAS nestedness-resultant component of dissimilarity and its relationship with the concept of nestedness itself. Baselga (5), Legendre (7), and Baselga and Leprieur (8) clarified the respective concepts in the BAS and POD frameworks.

To conclude, only the BAS framework yields a replacement component that is mathematically independent of richness difference. Thus, any relationship between replacement and richness difference can be interpreted as an empirical phenomenon, and not an

unavoidable outcome of mathematically dependent measures. In our view, the primary objective of partitioning dissimilarity is to remove the pervasive effects of richness patterns from replacement patterns. Hence, the BAS framework is the more effective way to analyze dissimilarity in our application.

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