

center of the French Ministry of Foreign Affairs (MAE). The authors are indebted to D. Chessel for important insights into the relationship between diversity indices and multivariate analyses, and to E. G. Leigh, Jr., H. Tuomisto, and an anonymous reviewer for their insightful comments on an earlier version.

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Ecology, 89(11), 2008, pp. 3232–3237
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ANALYZING OR EXPLAINING BETA DIVERSITY? COMMENT

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Tuomisto and Ruokolainen (2006; hereafter referred to as TR) have recently argued that there has been confusion about what statistical approaches, “raw data” or “distance,” are more appropriate when testing hypotheses about the origin and maintenance of beta diversity. They also argued that “inconsistencies and errors in [the] recommendations” of Legendre et al. (2005; hereafter referred to as LBP) gave way to more confusion on this issue. Essentially, TR stated that both the raw-data and distance approaches were appropriate, but targeted different predictions and should therefore be seen as complementary. However, TR’s method of variation partitioning on distance matrices is based on an inaccurate definition of spatial autocorrelation, which makes the “spatial” fraction meaningless. Consequently, that method is unable to quantify the relative contribution of neutral processes to beta diversity. In any case, TR have provided no answer to the doubts expressed by LBP over the mathematical validity of variation partitioning on distance matrices, and simply claimed that as their method targeted a “different

Manuscript received 5 February 2007; revised 5 July 2007; accepted 2 August 2007. Corresponding Editor: N. C. Kenkel.

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response variable” than the raw-data approach, its use was justified. Finally, the recommendation of TR that the distance approach is the only appropriate approach for testing Hubbell’s (2001) neutral theory is incorrect. Here I will discuss these issues in more detail.

What is spatial autocorrelation?

In their *Ecological vs. statistical hypotheses* section (p. 2703), TR describe the predictions of the neutral model as follows:

Community composition is heterogeneous over the landscape at all spatial scales as a result of the cumulative effects of spatially autocorrelated random walk in species abundances. This spatial structure is entirely due to autocorrelation, and spatial dependence on underlying environmental variables is not present.

While their description of the neutral model is accurate, the statistical prediction they derive from it is that (p. 2703):

From [the neutral] hypothesis (...) it follows that two nearby sites should share more species in more similar abundances than two sites further apart.

That statistical prediction is inaccurate because spatial autocorrelation is not defined as the tendency of two nearby sites to be more similar than faraway sites (which would imply a simple monotonic decrease of similarity with increasing geographic distance), but is instead defined as “the property of random variables taking values, at pairs of locations a certain distance apart, that are more similar (positive autocorrelation) or less similar (negative autocorrelation) than expected for randomly associated pairs of observations” (Legendre 1993). A more formal and mathematically satisfying definition of spatial autocorrelation is “the lack of independence [...] among the error components of field data, due to geographic proximity” (Legendre and Legendre 1998:9).

This distinction may appear trivial, yet it has important implications in the present debate. Even though random neutral processes may create spatial autocorrelation in the vegetation data and lead to a monotonic decrease in similarity (or conversely, to an increase in dissimilarity) with increasing geographic distance when there is species turnover (i.e., replacement) across a sampled transect or surface, this is not necessarily so, for instance, in the case of ubiquitous species. Simply put, there is no clear and unambiguous link between spatial autocorrelation and similarity decay with distance. Consequently, regressing community composition dissimilarity on geographical distances (log-transformed or not) to quantify the contribution (using R^2) of neutral processes to variation of beta diversity between pairs of sites, which is the goal of TR’s method of variation partitioning on distance matrices, is fundamentally incorrect. While such a regression is often

used in similarity decay plots to fit a particular model (Nekola and White 1999), the coefficient of determination (R^2) should be interpreted as nothing more than a simple measure of the adjustment of that model to the data.

It is important here to distinguish two research questions: The objective of variation partitioning (either in the raw-data approach or in TR’s variation partitioning on distance matrices) is not to quantify the strength of spatial autocorrelation in the data (which can be calculated through Mantel correlograms), but to quantify its relative contribution to the overall pattern. There is no link between the strength of spatial autocorrelation and its relative contribution to beta diversity. For example, spatial autocorrelation can be small (i.e., low Mantel r in an autocorrelogram) yet explain most of the variation of community composition if all of this variation is spatially structured and there is no dependence on environmental variables. In any case, the R^2 of a logarithmic similarity-decay curve is neither related to the strength or relative contribution of spatial autocorrelation to beta diversity.

Neutral theory and similarity decay plots

TR’s statistical prediction to test the neutral model in the context of variation partitioning on distance matrices appears to stem from a direct, yet unfounded, extension of Hubbell’s (2001) use of similarity decay plots (Nekola and White 1999) to test neutral theory. In chapter seven of his seminal monograph, Hubbell predicted that under neutral ecological drift community composition similarity across the landscape will decrease logarithmically with geographical distance, because at such scales dispersal limitation leads to clumped species distributions, and therefore to high species turnover.

The similarity decay with distance is greatly influenced by grain size (i.e., resolution) and spatial extent (i.e., area), with the best relationships observed with large grain sizes and spatial extents (Nekola and White 1999). Indeed, a decay of similarity will be detected only if the variation due to grain size is smaller than the variation due to spatial extent (Nekola and White 1999), a condition rarely met from censuses conducted at local scales. As such, Hubbell used similarity decay plots to make predictions about the importance of neutrality on beta diversity only at broad spatial scales (i.e., biogeographical scales), and these predictions are based on the functional form of the decay curve, not through variation partitioning between geographical and environmental distances. Hubbell argued that, since neutral theory predicts that similarity decay happens on environmentally homogeneous landscapes, the decay curve should be smooth (i.e., logarithmic) and only depend on the fundamental biodiversity number θ and dispersal rate m (Hubbell 2001). On the other hand, under niche-assembly theory, similarity decay results from species

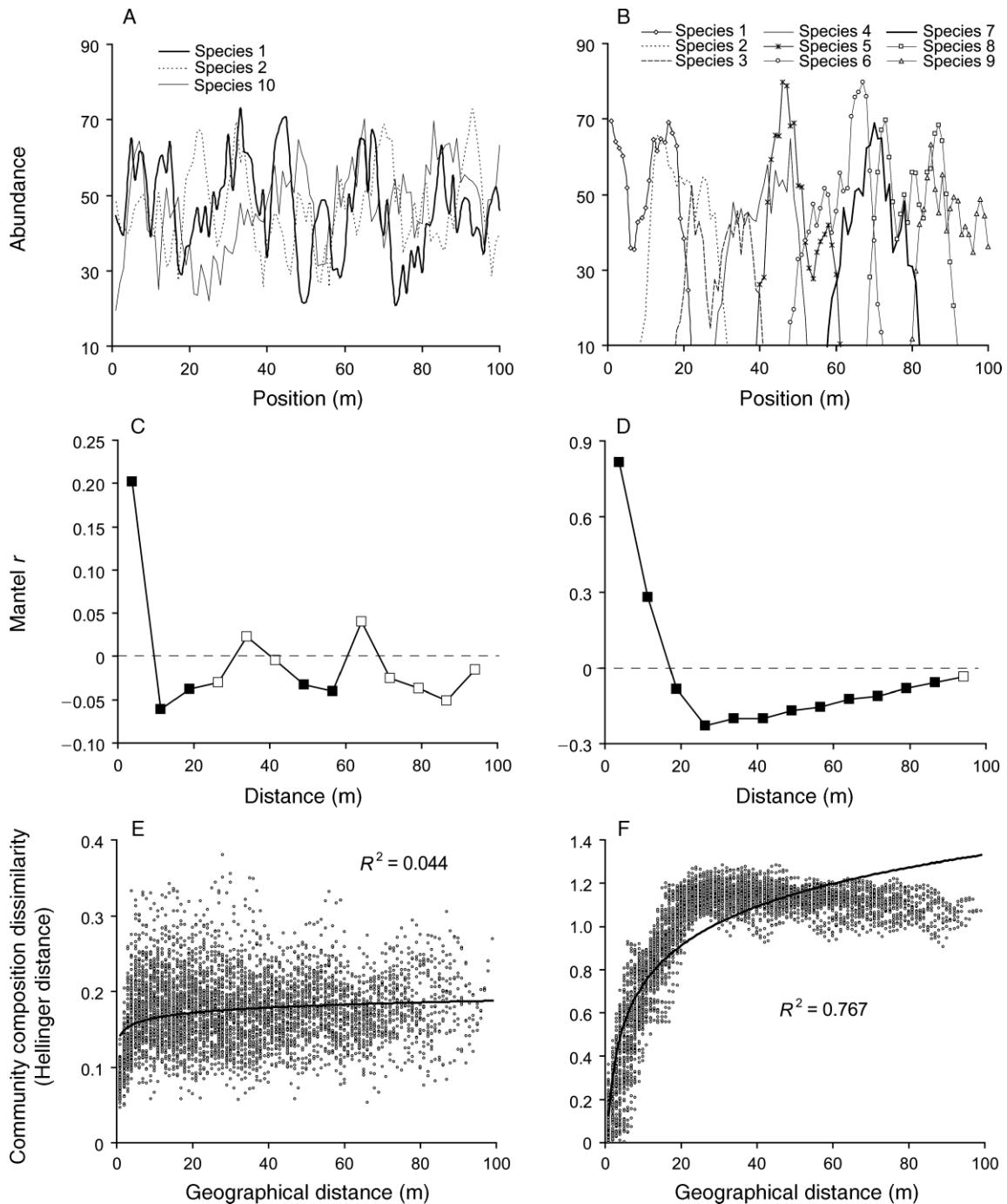


FIG. 1. Two cases of neutral communities. (A) Abundances of 10 species along a 100-m transect; only three species are shown on the graph for clarity. Data for each species were generated from a series of random numbers (one every meter) between 0 and 100 taken from a standard normal distribution, to which spatial autocorrelation was added by computing moving averages (window width = 5, i.e., the value plus the two neighbors on either side). (B) Abundances of 10 species along a 100-m transect; only the first nine species are shown. Data for each species were generated the same way as in panel (A), with the exception that species turnover along the transect was added by restricting the first nine species to limited but overlapping parts of the transect. (C) Mantel correlogram associated with panel (A). Hellinger distance was used for calculating community composition dissimilarity. Black squares indicate significant spatial autocorrelation after progressive Bonferroni correction ($\alpha = 0.05$, 999 permutations). Positive Mantel r values express positive spatial autocorrelation. (D) Mantel correlogram associated with panel (B); see description of panel (C) for explanation. (E) Relationship between community composition dissimilarity (Hellinger distance) and geographical

turnover along environmental gradients or habitats; the associated similarity decay will not be smooth because habitats are typically patchy, recurrent, and have sharp boundaries (Hubbell 2001).

This neutral prediction should be restricted to the interpretation of broad-scale patterns in similarity decay plots, yet TR erroneously extend it to all spatial scales and use a matrix of log-transformed geographical distances to quantify the contribution of neutral processes in variation partitioning on distance matrices from any sampling design, regardless of grain size and spatial extent. Such a method, on top of being mathematically doubtful, can greatly underestimate the importance of neutral processes when many or all species are ubiquitous, which can often happen at local spatial scales or in species-poor systems. Again, this is because there is no clear link between spatial autocorrelation and distance decay of similarity. I will show this through the simple following numerical example.

A simple numerical example

Let us imagine a transect where environmental conditions are completely homogeneous throughout, so that no variation in community composition can be attributed to environmental control. Ten species are found along the 100-m transect (note that it could very well be 100 mm, cm, or km), but in two different arrangements (Fig. 1A, B; for clarity, not all species are shown on the graphs). In Fig. 1A, abundance data were generated from a series of 100 random numbers between 0 and 100 taken from a standard normal distribution, from which spatial autocorrelation was added by computing moving averages (window width = 5, i.e., the value plus the two neighbors on either side). In Fig. 1B, the exact same procedure was followed, with the exception that species turnover was added by restricting the first nine species to limited but overlapping parts of the transect. Thus, in both cases, variation of community composition is entirely due to random but spatially autocorrelated walks in species abundances, a purely neutral process. As it can be seen from Mantel correlograms (Fig. 1C, D), there is significant spatial autocorrelation in community composition at several distance classes in both cases.

This simple numerical example shows that when spatial autocorrelation leads to gradual species turnover (Fig. 1B), which is frequently observed at broader spatial scales, a good relationship between community composition dissimilarity and geographical distance (the inverse of a similarity decay plot) can be found (Fig. 1F).

Conversely, when species are ubiquitous (Fig. 1A), such a relationship is very much weaker (Fig. 1E).

By extending this to the context of variation partitioning, as TR suggest, one would partition the variation of beta diversity between pairs of sites (i.e., the response matrix) between a matrix of environmental distances (representing the environmental control model) and a matrix of log-transformed geographical distances (representing the neutral model). I must stress that I do not support the use of this method given that serious doubts have been expressed over its mathematical validity. Indeed, perhaps the main problem with variation partitioning on distances matrices is that the isolated fractions are not additive. Surprisingly, TR appear to be aware of this fact, as they mention (p. 2707) that in this method, “ R^2 values will change depending on [...] whether all environmental variables are combined into a single distance matrix or used in separate matrices.” This seriously undermines the credibility of the method itself, as it is very much unclear how the R^2 coefficients should be interpreted if the fractions themselves are not additive. Another problem concerns the potential, albeit unknown, effects of the lack of independence among the distances on the coefficients themselves (Legendre et al. 2005:442). Still, I will assume here that the method is valid (which clearly remains to be shown) and use it nonetheless to illustrate that on top of being doubtful, this method also greatly underestimates the contribution of neutral processes.

In that numerical example, environmental conditions are identical throughout the transect, so the environmental matrix would be filled with constant values and would explain none of the variation of beta diversity. Therefore, the contribution of neutral processes to variation of beta diversity, as suggested by TR, would then simply be expressed by the coefficients of determination of the logarithmic relationships shown in Fig. 1E, F. This would lead one to conclude that in Fig. 1A, <5% (taken from the R^2 of the logarithmic model) of the observed pattern was due to neutrality, whereas in Fig. 1B, ~77% of the pattern would be attributed to neutral processes. Such conclusions are obviously inaccurate given that, in both cases, patterns were entirely due to random, spatially autocorrelated walks in abundances, a purely neutral process. Here it is clear that using a matrix of log-transformed geographical distances to quantify the contribution of neutral processes can greatly underestimate their actual importance, particularly when most or all species are ubiquitous (e.g., Fig. 1A). Again, this is because spatial autocorrelation does not necessarily imply, for multi-species data, that two

← distance (i.e., inverse of a similarity-decay plot) from the data of panel (A). The curve shows the logarithmic relationship with its R^2 value. (F) Relationship between community composition dissimilarity (Hellinger distance) and geographical distance from the data of panel (B); see description of panel (E) for explanation.

nearby sites will be more similar (multivariate similarity) than two faraway sites, as suggested by TR's statistical prediction. In other words, TR use an inaccurate statistical prediction to quantify the contribution of neutral processes to variation of beta diversity, and to test that prediction they propose and use a doubtful and unvalidated statistical method.

*Variation of beta diversity between pairs
of sites vs. between regions*

TR argued that the distance approach targeted different kinds of questions about beta diversity than the raw-data approach, which they referred to as different "levels of abstraction." LBP had also used this "level of abstraction" concept and mentioned that one could either be interested in studying the variation of community composition among sites within a given region (i.e., beta diversity), or in studying the variation of beta diversity among groups of sites or regions. However, variation partitioning on distance matrices, as proposed by TR, focuses strictly on the variation of dissimilarities *between pairs of sites*. Individual pairs of dissimilarities taken alone do not give a measure of beta diversity of a large area (Anderson et al. 2006). Therefore, this method could not answer such questions as: "Does beta diversity differ between different groups of sites (i.e., that contain more than two sites) or regions?" And, more importantly, "Why does beta diversity vary between these groups of sites or regions?" Hence, even if variation partitioning on distance matrices could accurately quantify the contribution of spatial autocorrelation to the variation of beta diversity among pairs of sites (which, as I have shown earlier, is not the case), and even if its mathematical validity were demonstrated (which remains to be done), it would still be of limited practical use: Indeed, most ecologists that are truly interested in studying the variation of beta diversity among groups of sites or regions would likely want to compare regions in which more than two sites have been observed. A more appropriate way of answering questions related to the variation of beta diversity among groups of sites or regions would be to use multivariate dispersion on distance matrices, a method described by Anderson et al. (2006) to specifically answer such questions.

Testing neutral theory: raw data or distances?

One of the main conclusions of TR was that Hubbell's (2001) neutral theory can only be tested using the distance approach since its testable predictions are stated in terms of distances and not raw data. Their main argument against the use of the raw-data approach to test neutral theory was that the detection of a particular spatial pattern in community composition through spatial modeling techniques such as principal coordinate analysis of neighbor matrices (PCNM;

Borcard and Legendre 2002) does not support neutral theory because neutral theory does not predict that this was the expected spatial pattern, and that any specific spatial pattern is just as much in accordance with the neutral model as long as the degree of spatial autocorrelation is similar. I see no contradiction here. I argue that the detection of a significant *residual spatial structure* (i.e., after controlling for variation due to the environmental variables) provides support for the theory. This detection is quite easy using the raw-data approach, unless TR can demonstrate that the neutral model specifies a type of spatial autocorrelation that cannot be modelled by PCNM analysis. Given that previous simulation work has shown that PCNM analysis could accurately model a wide range of spatial structures, including spatially autocorrelated data (Borcard and Legendre 2002), such a demonstration appears unlikely.

The PCNM approach is closely related to spatial autocorrelation structure functions, and essentially consists in extracting from a predetermined spatial matrix the eigenvectors that maximize Moran's index of spatial autocorrelation (I); the resulting eigenvectors describe global to local spatial structures and can thus be used in regression to model spatial structures at all spatial scales (Dray et al. 2006). Therefore, the raw-data approach with PCNM uses explanatory variables that can model spatially autocorrelated patterns across a range of scales, and thus allows an accurate quantitative assessment of the contribution of spatial autocorrelation to variation in community composition. This is the exact opposite conclusion of TR, who argued that "the raw-data approach fails to address the neutral model in a relevant way, and is unable either to falsify the neutral hypothesis or to quantify its relative contribution to the observed spatial pattern" (p. 2704).

Although both the raw-data and the distance approach can be used to test neutral theory, they both have their respective domains of application. The raw-data approach with PCNM has promising applications, since it allows one to dissect the spatial structures of community composition at different scales (Borcard and Legendre 2002) and estimate the relative influence of niche and neutral processes at each of these scales. Such tests offer great opportunities for future tests of neutral theory (McGill et al. 2006), especially considering that spatial scale has been suggested as a way to reconcile empirical ecology with neutral models (Holyoak and Loreau 2006).

Still, as TR pointed out, a drawback of the raw-data approach is that it can sometimes be hard to distinguish between the relative importance of niche and neutral processes on community patterns because spatial and environmental variables often covary. The resulting "space-environment" fraction can either be interpreted as a spatially structured environmental influence con-

trolling abundance patterns or as neutral processes acting within a heterogeneous environment (Bell et al. 2006). One way of minimizing that problem is to use a sampling design that decouples the environmental and geographical distances (Gilbert and Lechowicz 2004). The “pure spatial” fraction may often be due to some spatially structured unmeasured environmental variables, which can then lead to an overestimation of the contribution of neutral processes. Hence, to use the raw-data approach to test neutral theory, one must have access to relevant, extensive, and accurately quantified environmental data.

As for the distance approach, the use of similarity decay plots is appropriate for identifying the best functional form of a decay curve in a similarity-decay plot: A smooth similarity-decay curve provides greater support for neutral theory, whereas a “bumpy” curve suggests that the environment exerts stronger control over beta diversity (Hubbell 2001). A drawback of this approach is that it only allows a qualitative assessment of the dominant process (i.e., niche or neutrality), yet does not allow one to quantify their relative importance. Still, as this method does not require environmental data, it can be particularly interesting when these are not available.

Conclusion

Research on the origin and maintenance of beta diversity has regained great attention since the publication of Hubbell’s theory. Much theoretical and empirical work is currently under way to assess the relative importance of niche and neutral processes on community patterns. On the applied side, understanding the origin and maintenance of beta diversity has important implications for ecosystem management, such as the design of nature reserves. Therefore, it is crucial that researchers master the concepts and methods required for testing hypotheses about how beta diversity is maintained in ecosystems.

Throughout this comment I have stressed that an abusive interpretation of the relationship between the decay of similarity and spatial autocorrelation, as well as an unfounded use of Mantel R^2 values in the context of variation partitioning, both proposed by TR, should be avoided. Variation partitioning on distance matrices, in addition to being mathematically doubtful and yet unvalidated, is based on an inaccurate statistical prediction to quantify the contribution of neutral processes to variation of beta diversity.

The distance approach is appropriate for identifying the best functional form of the similarity decay curve in similarity decay plots. The raw-data approach, on the

other hand, is appropriate to partition the variation of community composition between environmental and spatial factors and can accurately quantify the contribution of spatial autocorrelation to variation of community composition among sites. In summary, contrary to TR, who argued that only the distance approach could be used to test neutral theory, both the raw-data and the distance approaches are useful in testing different neutral predictions about the origin and maintenance of beta diversity. Yet, they both have their domains of application and can thus be seen as complementary.

Acknowledgments

Thanks to A. Paquette for comments on a previous version of the manuscript. This work was supported by an International Doctoral Scholarship from University of Canterbury and a Ph.D. Research Scholarship from the Fonds Québécois de la Recherche sur la Nature et les Technologies (FQRNT).

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