Comments

ANALYZING OR EXPLAINING BETA DIVERSITY? COMMENT

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In a recent paper, Tuomisto and Ruokolainen (2006, hereafter referred to as TR) discussed the domains of application of the so-called "raw-data approach" compared to the "distance (Mantel) approach" for studying and testing hypotheses about patterns and determinants of beta diversity. Following Legendre et al. (2005, hereafter referred to as LBP), they addressed the dilemma of an either/or approach in reference to a conceptual framework made of three different "levels of abstraction" depending upon the ecological question to be addressed and thus on the response variable to be studied: (1) community composition data; (2) variation in community composition data or beta diversity; or (3) variation in beta diversity, i.e., variation in variation in community composition data.

TR contradicted LBP, however, by claiming that only the third level of abstraction is relevant to address ecological hypotheses involving geographic distance such as the dispersal limitation underlying the neutral theory of biodiversity (Hubbell 2001). More specifically, they considered that submitting matrices of distances/dissimilarities in community composition to multiple regression along with Mantel tests is the only way to test such hypotheses (TR: p. 2700).

We disagree with such a restrictive vision and the main purpose of our comment is to show that spatially explicit, distance-based analyses of beta diversity do not necessarily belong to the so-called third level of abstraction, let alone to multiple regression on distance matrices and can, moreover, be viewed as a prolongation of the raw-data approach, in accordance with the overall concept of variance partition. This emerges from

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a general definition of alpha and beta diversity components as functions of variance in species identity among individuals within and among communities, which is homologous to the definitions of diversity adopted in various other domains and especially in population genetics (e.g., Lewontin 1972, Nei, 1973, Rao 1982). In the sequel, we will show that such a definition leads naturally to an additive relationship between the portions of species diversity explained and unexplained by external environmental variables. We believe, just like Lande (1996), that this partitioning model is fully consistent with the well-rooted ecological notions of alpha, beta, and gamma diversity, even though Whittaker (1960, 1972), who introduced them, initially referred to an analytical multiplicative relationship (see Veech et al. 2002 for a recent review of the two approaches). We will then demonstrate that this additive framework based on well-mastered techniques of variance/covariance decomposition is also encompassing the double variance-partitioning scheme with respect to explanatory variables and principal components of the canonical analysis advocated by both LBP and TR in their second-level raw-data approach. Finally, we will show how, based on a rewriting of the beta component as a measure of dissimilarity, the concept of variogram leads to a direct distance-based additive apportionment of beta diversity, which doesn't require the invocation of a third level of abstraction nor of a Mantel tests approach. We shall finally discuss the goals of potential methods for third-level analyses of the variance among intersite dissimilarities, which is a variance of a variance as correctly presented by LBP. Throughout the text, our arguments are supported by specific references to and commentaries of LBP and TR.

First level, within-community diversity

On the argumentation that basically in ecology "the raw-data tables […] consist of the observations of the abundances of one or more species […] in more than one study site […]", TR (p. 2698) defined community composition as first-level data. By that, they diverged from the proposition of LBP (p. 436) that a first-level analysis consists in "studying variation in species identity of individuals at a given site [which] is studying alpha diversity," an idea brought from genetics to ecology by Lande (1996). This opposition is all the more surprising given that TR say a little farther (p. 2702) "it is important to notice that species composition is not an entity that has ecological behavior of its own, but it is a result of how individuals belonging to different species behave." Indeed, from this last statement, which has our full support, the basic response variable of diversity analyses appears unambiguously to be the taxonomic

identities of the n individual organisms recorded according to a reference nomenclature during a given field survey, i.e., a taxonomic relevé, considered as representative of a given study area or region. For the purpose of data analysis, a straightforward translation of such a list is a binary random variable, say Y_{ij}, which indicates whether an arbitrary individual ($1 \leq i \leq n$) belongs to a particular species ($1 \leq j \leq s$). This can be written in matrix form as follows:

$$\mathbf{Y}[y_{ij}] = \begin{cases} 1 & \text{if the } i\text{th observation belongs to species } j \\ 0 & \text{otherwise} \end{cases}.$$

Matrix $\mathbf{Y}$ ($n \times s$) is called an individual $\times$ species-occurrence table, from Gimaret-Carpentier et al. (1998). When the list is comprised of individuals encountered in a set of m sampling sites (but this is, from our perspective, already and blatantly a second-level problem; see next section), summing per site the individual rows of $\mathbf{Y}$ yields a usual site $\times$ species abundance matrix, say $\mathbf{A}[a_{kj}]$ with size ($m \times s$), which is a "shrunken" version of $\mathbf{Y}$ ($n \times s$). From either $\mathbf{Y}$ or $\mathbf{A}$ table, the relative frequency of species j in the taxonomic relevé is given as

$$p_{+j} = \frac{1}{n}\sum_{i=1}^{n} y_{ij} = \frac{1}{n}\sum_{k=1}^{m} a_{kj} \qquad (1)$$

and its (uncorrected) variance (Lande 1996) as

$$\text{SV}_j = \frac{1}{n}\sum_{i=1}^{n} (y_{ij} - p_{+j})^2 = p_{+j}(1 - p_{+j}). \qquad (2)$$

Furthermore, the most popular diversity indices can be directly computed as a weighted sum of the SV_j values over the s observed number of species:

$$\text{TD} = \sum_{j=1}^{s} w_j \text{SV}_j. \qquad (3)$$

Indeed, taking the weighting function w_j equal to one, whatever the species, means quantifying the total diversity of the taxonomic relevé via the Simpson index, whereas taking $w_j = 1/p_{+j}$ or $w_j = \log(1/p_{+j})/(1 - p_{+j})$ means relying on total species richness (minus 1, i.e., $s - 1$) or on the Shannon index, respectively (Pélissier et al. 2003). In the following discussion we refer to these three measures of species diversity as the usual diversity metrics, while additional metrics are thinkable from other definitions of w_j.

Lessons learned.—(1) Contrary to TR, but in accordance with LBP, we believe that a first-level analysis consists in characterizing the within-site/community diversity, regardless at this point whether there is or not overlap in species composition (i.e., shared species) between different sites or communities. (2) A simple general expression of the within-community diversity, which encompasses the most popular diversity indices, is

the generalized, multivariate variance given by TD (Eq. 3). (3) When the taxonomic relevé is limited to a single sampling site, TD measures alpha diversity of that site; when the taxonomic relevé is comprised of individuals encountered in a set of sampling sites distributed over an ecological region, TD measures gamma diversity.

Second level, explaining among-communities variation

Can the spatial variation in the abundance of a given species or the variation in community composition, i.e., in the abundances of all the species that form a community at a time, be explained by variation in environmental characteristics and/or geographical location? These ecological questions raised by TR (pp. 2698–2699) are, with respect to both theirs and LBP nomenclature, level-two questions to be addressed via the raw-data approach, i.e., using canonical analysis sensu Legendre and Legendre (1998). While we fully agree with this idea, we have to remember that canonical analysis is a two-step process, which involves a multiple linear regression, followed by principal component decomposition (Legendre and Legendre 1998). Hence, the above ecological questions are first and foremost specified as a general multivariate linear model equation (the first step of the canonical analysis [Pélissier et al. 2003, Pélissier and Couteron 2007]), for which we believe that our first-level individual $\times$ species-occurrence matrix, $\mathbf{Y}$, introduced in the previous section, is a much more appropriate "response variable" than the classical site $\times$ species abundance matrix, $\mathbf{A}$, as in TR and LBP. Associated to any form of linear model is of course an additive scheme of variance partitioning (Lebart et al. 1997:228), advocated in a spatially explicit context by LBP (pp. 440–441).

Taking matrix $\mathbf{Y}$ ($n \times s$) as the response variable and introducing $\mathbf{X}$ ($n \times q$) a matrix of dummy variables coding for habitat types as the "explanatory variable," it can be demonstrated that TD, the total variance in species identity among the n individuals of the community (Eq. 3) partitions into an explained or among-habitat component (TDA) and an unexplained residual or within-habitat component (TDW) (Couteron and Pélissier 2004), so that our first-step linear model enters within the additive diversity partitioning framework proposed by Lande (1996). This establishes a clear analytical relationship between our first and second levels of abstractions, which is holding for any usual diversity metric provided that the appropriate choice of the weighting function w_j is made:

$$\text{TD} = \text{TDW} + \text{TDA} = \sum_{j=1}^{s} w_j \text{SVW}_j + \sum_{j=1}^{s} w_j \text{SVA}_j. \qquad (4)$$

To be more specific, we can denote by n_k the number of observations in habitat k, with

$$n = \sum_{k=1}^{m} n_k$$

and by $p_{kj} = a_{kj}/n_k$ the relative frequency of species j in habitat k, a_{kj} being as above the abundance of species j in habitat k. The approximation of $\mathbf{Y}$ by multiple linear regression on the variables contained in $\mathbf{X}$ is $\hat{y}_{ij}(k) = p_{kj}$ (Pélissier et al. 2003), from which we can derive explicit formulas for SVW$_j$, the contribution of a given species j to TDW, the mean within-habitat diversity (or alpha diversity as defined in the previous section), and for SVA$_j$, which is the contribution of j to TDA, the among-habitat diversity (or "between-habitat" diversity, an expression used as a synonymous for beta diversity by Whittaker [1972:230]). Namely

$$SVW_j = \sum_{k=1}^{m} \frac{n_k}{n} \cdot p_{kj}(1 - p_{kj}) \tag{5}$$

$$SVA_j = \sum_{k=1}^{m} \frac{n_k}{n} \cdot (p_{kj} - p_{+j})^2. \tag{6}$$

Couteron and Pélissier (2004) also provided explicit formulas for SVW$_j$ and SVA$_j$ for nested partitions (i.e., for subsequent partitions of SVA$_j$ among habitat types and sampling locations), as well as guidelines on the nonparametric testing of statistical significance based on randomization procedures. The decomposition framework lends itself to tests based on random shifting procedures (as introduced by Harms et al. 2001), which upon availability of fully mapped or regularly sampled data are preferable for distinguishing between habitat effects and clumping effects unrelated to habitat. Moreover, in this well-established framework, which is encompassed by multivariate analysis of variance (MANOVA sensu Anderson 2001), multilevel hierarchical analyses are more straightforward than the approach proposed by Crist et al. (2003). MANOVA is indeed very general and applies either to questions about individual species' habitat preferences (testable via SV$_j$) or to variation in community composition (analyzable through TD).

Lessons learned.—(1) Contrary to TR statement, a direct relationship between alpha and beta diversity can be expressed through a simple general linear model that leads from the first to the second level of abstraction; consequently, it is only when gamma diversity is ignored that alpha diversity tells nothing about beta diversity. (2) The complementary nature of alpha and beta components of diversity established by Whittaker's work has long been hidden because authors have quantified alpha diversity by indices (e.g., Fisher's alpha, Shannon and Simpson indices) that have no direct connection with dissimilarity measures used to quantify beta diversity (e.g., Jaccard, Sorensen, and Steinhaus indices). (3) Our model is closely related to the linear model that underlies

classical canonical analysis; but using as the response variable, the individual species-occurrence matrix, $\mathbf{Y}$, in lieu of the site species abundance matrix, $\mathbf{A}$, is the only way to relate the raw-data approach to gamma diversity, via its natural, additive apportionment into a part explained (beta diversity) and a part unexplained (alpha diversity) by variation in environmental conditions (second level of abstraction). (3) Standard routines derived from MANOVA as well as nonparametric tests of statistical significance, which can be based either on randomization or random shifting procedures, are available to conduct these analyses.

Second level, the "raw-data" approach

In the previous section, we focused on the variance (diversity) partitioning scheme associated to the generalized linear models. We now turn to the one associated to the principal component decomposition, which is the core subject of multivariate analysis, including the canonical raw-data approach as referred to by LBP and TR. One can indeed recognize in

$$TDA = \sum_{j=1}^{s} w_j \cdot \sum_{k=1}^{m} \frac{n_k}{n} \cdot (p_{kj} - p_{+j})^2$$

(Eq. 4 and 6) an expression of the total inertia or total variance (i.e., the sum of all eigenvalues) of the correspondence analysis (CA; Legendre and Legendre 1998) of the site × species abundance matrix $\mathbf{A}$ when $w_j = 1/p_{+j}$, and non-symmetric correspondence analysis (NSCA; Gimaret-Carpentier et al. 1998) of $\mathbf{A}$ when $w_j = 1$. Taking $w_j = \log(1/p_{+j})/(1 - p_{+j})$ also leads to a form of column weighted correspondence analysis whose inertia is consistent with Shannon diversity (see the proofs in Pélissier et al. 2003). Total inertia demonstrated by the site × species abundance matrix, $\mathbf{A}$, is therefore the part of total community diversity (TD) explained by the dummy variables that partition the individual × species-occurrence matrix, $\mathbf{Y}$, into sampling sites. This quantifies between-site beta diversity, expressed consistently with any of the three usual diversity metrics using the species weighting function, w_j.

It follows that two-table variants of ordination methods such as CCA (canonical correspondence analysis) or RDA (redundancy analysis), whose particular forms can be made compatible with the usual diversity metrics (see Couteron and Ollier 2005), realize a first-stage additive partition of TDA into "explained" and residual "unexplained" portions by a set of environmental descriptors, before permitting a subsequent additive decomposition of either the explained or the residual fraction into canonical ordination axes (constrained vs. unconstrained ordinations, respectively).

Lessons learned.—(1) The so-called "raw-data approach" is directly related to the additive partitioning

framework of species diversity proposed by Lande (1996), a fact which is completely absent in LBP and TR. (2) It follows that ordination techniques provide subsequent apportionment of *TDA* according to principal axes, in a way that can be made consistent with the usual diversity metrics. (3) Thus, canonical partitioning in the classical sense of Legendre and Legendre (1998) refers to total inertia (or variance) of the site × species abundance table, **A**, i.e., to the among-site beta diversity (TDA), which is the only part of community total diversity, TD, accounted for by the sampling design. (4) Explained or unexplained portions of TDA relative to a set of environmental descriptors can subsequently be additively partitioned into canonical vs. partial canonical ordination axes.

From the "raw-data" approach to distance-based analyses

According to TR (p. 2697, 2703, 2705), the fact that beta diversity can be viewed as a distance (or more generally a dissimilarity) is the main justification for using the Mantel approach and to move from second to third level of abstraction, where the response variable is a dissimilarity matrix between pairs of sites. That beta diversity is usually quantified via dissimilarity indices, is used however to instill the misleading idea that it is not conceivable to consider "the variation in community composition, i.e. beta diversity" in the light of the geographic locations of the sites or of the inter-site distances. Though it is not blatantly stated as such, this idea is conveyed in many places of the paper, by rhetoric tricks or omissions. For instance, in Fig. 2, it is as if an analysis of inter-community or inter-site geographic distance, could not be used to explain variation in community composition. Why should using the inter-site geographic distance as an explanatory variable automatically mean skipping to an analysis of the variation in variation in community composition, i.e., to a third-level question? There is absolutely no compelling reason to do so, since several alternatives are possible.

In fact, TDA, which is a variance according to our definition, can be rewritten as a sum of intersite dissimilarities, and directly broken down into additive portions relating to classes of inter-site distance. Indeed, a classical result of variance decomposition (in its broader meaning) is that averaging squared departures around a mean value is equivalent to averaging squared differences (i.e., distances) between individual observations (see for instance Anderson 2001). It follows that the contribution of species j to the among-site beta diversity, SVA_j (Eq. 6), can be rewritten as

$$\mathrm{SVA}_j = \sum_{k=1}^{m}\sum_{k'=1}^{m}\mathrm{SVA}_j(k,k') = \frac{1}{2n^2}\sum_{k=1}^{m}\sum_{k'=1}^{m}n_k n_{k'}(p_{kj}-p_{k'j})^2.$$

(7)

At the multispecies level,

$$\mathrm{SVA}(k,k') = \sum_{j=1}^{s}w_j\mathrm{SVA}_j(k,k')$$

is a measure of dissimilarity between composition in sites k and k' (it is in fact a mathematical distance), which may be made fully consistent, through w_j, with any of the three usual diversity indices. Summing $\mathrm{SVA}(k, k')$ values for all (k, k') pairs of sites yields the among-site beta diversity:

$$\mathrm{TDA} = \sum_{k=1}^{m}\sum_{k'=1}^{m}\mathrm{SVA}(k,k').$$

A distance-dependent partition of TDA follows from the dissimilarity measure defined above. As soon as a set $\{H_h\}$ of nonoverlapping distance classes is defined, the portion of the total among-site beta diversity relating to a given distance class centered on h is

$$\mathrm{TDA}(h) = \sum_{d(k,k')\in H_h}\mathrm{SVA}(k,k')$$

$$= \sum_{d(k,k')\in H_h}\sum_{j=1}^{s}w_j\mathrm{SVA}_j(k,k'). \quad (8)$$

When the union of H_h contains the range of intersample distances, we logically derive the following from the above expression:

$$\mathrm{TDA} = \sum_{h}\mathrm{TDA}(h).$$

Alternatively, standardizing TDA(h) for the number of plots and individuals (see Couteron and Pélissier [2004] for details) in each distance class provides a dissimilarity variogram or, equivalently, a generalized, multivariate variogram, which can be plotted as a function of the intersite geographical distance and tested against the null hypothesis of an absence of spatial structure by randomly reallocating the taxonomic compositions among the sampling sites (Wagner 2004).

We note that TR (p. 2701) mention the variogram in a way that seems to involve the computation of a variance of intersite dissimilarity, i.e., in this case a variance of variance, and thus a third-level object. But according to the usual definition, the variogram expresses how intersite dissimilarity changes with distance by directly apportioning the overall variance of the response variable with respect to distance classes and dividing by the number of pairs of sites in each class. This does not involve the computation of a variance of intersite dissimilarity, and it is therefore not at all congruent with their definition of third-level analysis.

The principle of multivariate variography (sensu Wackernagel 1998) can be applied not only to TDA, but also to any partition of TDA into principal/canonical axes yielded by a given single- or two-table

ordination method (see Couteron and Ollier 2005 for an illustration). Hence, combining these different principles constitutes a very rich and flexible yet largely unexplored framework for comparing the effect of environmental variables on the observed relationship between beta diversity and intersite distance. Moreover, in our model, the part of total community diversity explained by external explanatory variables, ordination axes, or distance classes is quantified in the same measurement unit (one of the three usual diversity metrics, albeit this is not an absolute restriction), so that their relative proportions of explained total community diversity can be directly compared. This ultimately allows one to measure the respective influence of environment and space on diversity variation.

Lessons learned.—(1) TR seems to have missed that the among-site beta diversity can be seen as a sum of dissimilarities between all pairs of sites; such dissimilarities can be expressed in any of the three usual diversity metrics. (2) TDA is therefore amenable to an additive apportionment with respect to classes of intersite geographical distance, which can be combined in many ways using the potential of ordination methods, thereby reviving the concept of multiscale ordination (MSO; sensu Ver Hoef and Glenn-Lewin 1989, Wagner 2003, 2004); MSO is a straightforward extension of the raw-data approach. (3) Statistical tests of significance for the existence of nonrandom spatial structure exist and can also be applied to residual patterns after factoring out the effect of environmental descriptors; for instance, the absence of any significant residual spatial pattern would mean that dispersal limitation is probably not a pervasive factor in the communities under study.

Third-level analyses: for what and how?

In the previous points, we have gradually shifted from a raw-data to a distance-based analysis framework. The transition has been smooth because both frameworks rely on additive partitions of variance and covariance (used here in their generalized meaning; see Couteron and Ollier [2005]). Our method of carrying out distance-based analyses nevertheless does not pertain to the third level of abstraction as defined by TR.

We have not considered the variance among intersite beta-diversity values, which is a variance of variance, whereas TDA is simply a generalized variance that allows weighting of either sites or species. Nor have we tried to model individual intersite beta-diversity values from either environmental or spatial variables, which is the goal of multiple regression on distance matrices as presented by Duivenvoorden et al. (2002) and Tuomisto et al. (2003). This clearly demonstrates that reference to third level analyses is not a prerequisite for investigations into how beta diversity may be influenced by environment discrepancies and/or intersite distance.

There is thus no reason to share the opinion of TR that distance-dependent ecological hypotheses, such as the neutral theory of biodiversity, can only be tested using the Mantel approach, although we agree that canonical partitioning, which is the core of what is usually meant by the raw-data approach, is by itself not sufficient to address such hypotheses. In fact, the framework for distance-based analyses, which we have briefly summarized above, permits one to investigate and test any distance-based ecological hypothesis, including the neutral ones. For instance, based on theoretical results borrowed from population genetics, Chave and Leigh (2002) and Etienne (2005) featured explicit predictions under neutrality with respect to Simpson's intersite beta diversity (or to the closely related intersite similarity function), which may be used in the near future to derive analytical expectations of the multivariate variogram under neutral assumptions. It is hence not yet established that reference to the third level of abstraction will, by itself, permit more efficient testing of distance-based ecological hypotheses than the framework described in *From the "raw-data" approach to distance-based analyses.*

The first level of abstraction basically computes alpha diversity from a vector of species abundances. The second level deals with variation in abundances observed by a particular survey, which means comparing the abundance vectors making the site × species table or, equivalently, submitting this table to eigenanalysis and/or canonical partitioning (the raw-data approach). The objective of the third level should not be defined only from comparison of distance matrices via a Mantel test, since its broader objective is ultimately to compare diversity patterns found in distinct surveys, hence to compare the structures present in several site × species tables. Indeed, if surveys share either sites (e.g., diachronic relevés) or species (at least most of them), there are appealing alternatives to distance-matrix comparisons (Dray et al. 2003, Thioulouse et al. 2004), which probably use more of the available initial information of the set of site × species tables. It is only when surveys share neither sites nor species (e.g., different ecological regions) that comparisons of distance matrices and Mantel tests may justify themselves. Compared to the broad panel of aims and data types characterizing ecological investigations, these are in fact far more restrictive circumstances for using the Mantel approach than it may appear from reading TR.

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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

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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
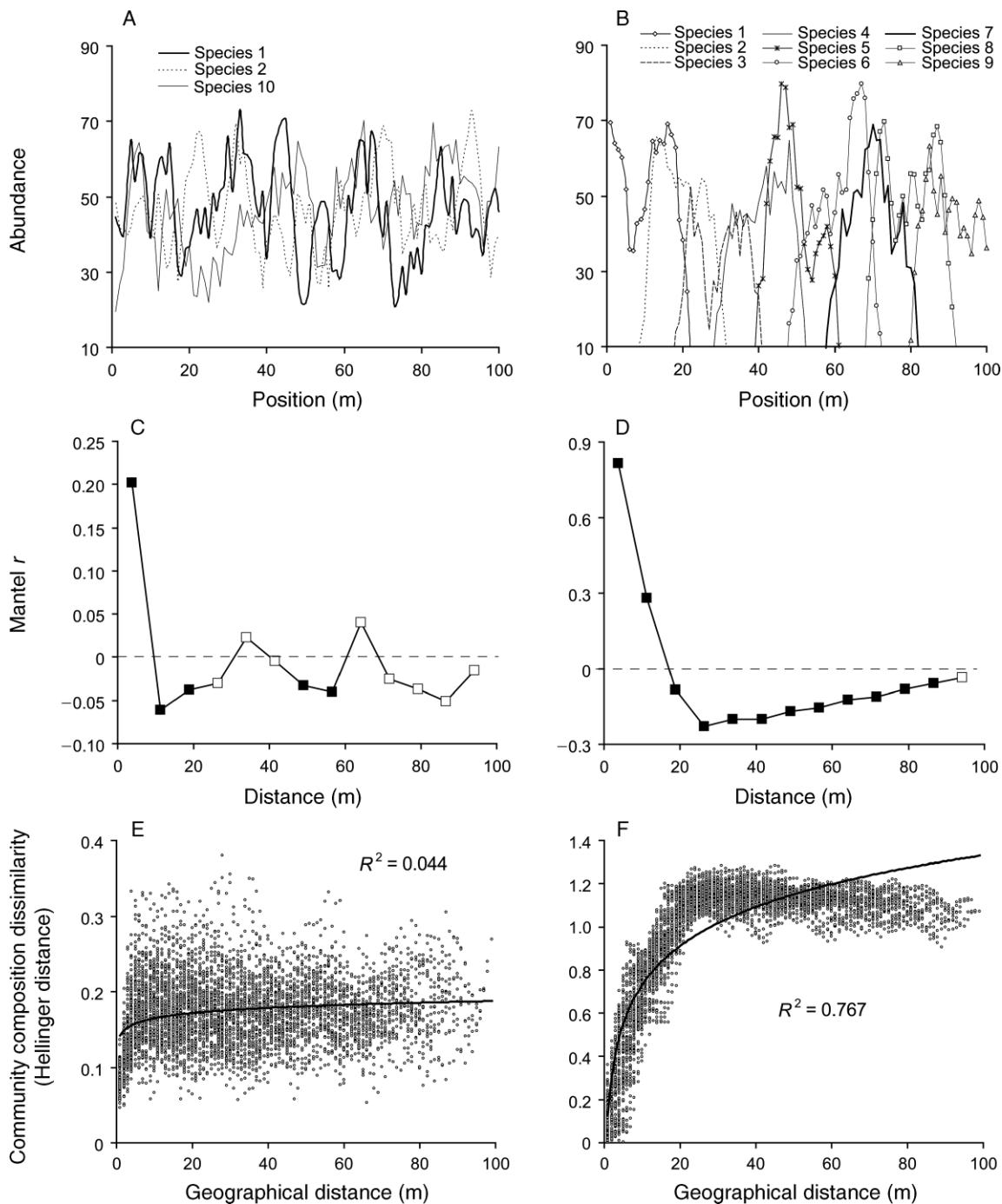
FIG. 1. Two cases of neutral communities. (A) Abundances of 10 species along a 100-m transect; only three species are shown on the graph for clarity. Data for each species were generated from a series of random numbers (one every meter) between 0 and 100 taken from a standard normal distribution, to 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 a 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

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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.

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