

Separating the two components of abundance-based dissimilarity: balanced changes in abundance vs. abundance gradients

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Summary

1. Dissimilarity measures can be formulated using matching components that can be defined as the intersection in terms of species composition of both sets (a) and the relative complements of each set (b and c respectively). Previous work has extended these matching components to abundance-based measures of dissimilarity.
2. Using these matching components in terms of species abundances I provide a novel partition separating two components of abundance-based dissimilarity: (i) balanced variation in abundance, whereby the individuals of some species in one site are substituted by the same number of individuals of different species in another site; and (ii) abundance gradients, whereby some individuals are lost from one site to the other.
3. New indices deriving from the additive partition of Bray-Curtis dissimilarity are presented, each one accounting separately for these two antithetic components of assemblage variation.
4. An example comparing the patterns of increase of assemblage dissimilarity with spatial distance in two tropical forests is provided to illustrate the usefulness of the novel partition to discern the different sources of assemblage variation.
5. The widely used Bray-Curtis index of dissimilarity is the result of summing these two sources of dissimilarity, and therefore might consider equivalent patterns that are markedly different. Therefore, the novel partition may be useful to assess biodiversity patterns and to explore their causes, as substitution and loss of individuals are patterns that can derive from completely different processes.

Key-words: abundance, beta diversity, Bray-Curtis, distance decay, replacement, subset, turnover

Introduction

The dissimilarity in species composition between two assemblages is a basic parameter for the assessment of biodiversity patterns (Legendre & Legendre 1998). However, despite its apparent simplicity, dissimilarity is a concept that has proven elusive because (i) assemblage composition can be defined in several ways; and (ii) differences in assemblage composition can also be defined in several ways. Regarding the definition of assemblage composition, the most important criterion is whether composition is defined qualitatively (i.e. species presence or absence in each site) or quantitatively (i.e. species abundance in each site). In relation to the second issue, even once the definition of composition is set, a myriad of definitions of dissimilarity are possible (Legendre & Legendre 1998; Koleff, Gaston & Lennon 2003), each one accounting for different facets of dissimilarity.

In previous papers I have shown that incidence-based measures of dissimilarity can be partitioned into turnover and nestedness-resultant dissimilarity components (Baselga 2010,

2012). In short, the rationale is that in nested assemblages the poorest site is a subset of the richest site. Such nested assemblages are obviously dissimilar, a fact properly accounted by Whittaker's beta diversity (i.e. gamma/alpha) or the derived Sørensen or Jaccard indices. However, in that case no species is replaced by other. Therefore, species replacement and nestedness are markedly different ways of generating dissimilarity. These two components of incidence-based dissimilarity can be derived from different underlying processes (speciation vs. extinction, for example). For this reason, separating both components of incidence-based dissimilarity has proven useful to assess empirical patterns of variation in species composition and their potential underlying determinants (e.g. Hortal *et al.* 2011; Leprieur *et al.* 2011; Baselga, Gómez-Rodríguez & Lobo 2012).

Incidence-based pairwise dissimilarity indices are usually formulated using the matching components a , b and c , which stand for the species present in both sites, the species present in the first site but not in the second, and the species present in the second site but not in the first respectively. Using set theory terminology, the matching components can also be defined as the intersection in terms of species composition of both sets (a) and the relative complements of each set (b and c respectively).

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The advantage of this terminology is that it makes intuitively obvious that incidence-based indices can be extended to account for other facets of biological diversity just considering the intersection and relative complements of sets in terms of such different attributes, i.e. phylogenetic diversity (Leprieur *et al.* 2012) or functional diversity (Villegger, Grenouillet & Brosse 2013).

Even previously, but using a different reasoning and point of view, this procedure was used to extend incidence-based dissimilarity (or similarity) indices to account for species abundances (Tamas, Podani & Csontos 2001). Using this procedure, it remains clear that the widely used Bray-Curtis coefficient is an abundance-based extension of the Sørensen index (a fact already known, e.g. Legendre & Legendre 1998). In short, the explanation for this relationship between both measures relies in the fact that the intersection (A component) and the relative complements (B and C components) in terms of species abundances can be formulated as:

$$A = \sum_i \min(x_{ij}, x_{ik}) \quad \text{eqn 1}$$

$$B = \sum_i x_{ij} - \min(x_{ij}, x_{ik}) \quad \text{eqn 2}$$

$$C = \sum_i x_{ik} - \min(x_{ij}, x_{ik}) \quad \text{eqn 3}$$

where x_{ij} is the abundance of species i on site j , and x_{ik} is the abundance of species i on site k . Therefore, A is the number of individuals of each species that exists in both sites j and k , whereas B and C are the number of individuals that are unique to sites j and k respectively. This formulation is very useful because it makes obvious the relationship between the Sørensen (β_{sor}) and Bray-Curtis (d_{BC}) indices, because,

$$\beta_{\text{sor}} = \frac{b + c}{2a + b + c} \quad \text{eqn 4}$$

and,

$$\begin{aligned} d_{\text{BC}} &= \frac{\sum_i |x_{ij} - x_{ik}|}{\sum_i x_{ij} + x_{ik}} \\ &= \frac{\sum_i x_{ij} + x_{ik} - 2 * \min(x_{ij}, x_{ik})}{\sum_i x_{ij} + x_{ik}} \\ &= \frac{B + C}{2A + B + C} \end{aligned} \quad \text{eqn 5}$$

Different patterns of variation in species abundance

The formulation of the Bray-Curtis index of dissimilarity using the abundance-based matching components makes evident that d_{BC} depends on the number of individuals that are unique to any of both sites in relation to the sum of abundances in both sites. Therefore, d_{BC} would attain the same value in all situations in which the relationship between $(B + C)$ and A remains constant, irrespective of the relative contributions of B and C to their sum. In other words, d_{BC} dissimilarity will be

equally affected by (i) balanced changes in species abundances between sites ($B = C$, i.e. the abundance of some species declines from site 1 to site 2 in the same magnitude than the abundance of other species increases from site 1 to site 2); and (ii) abundance gradients ($B > C = 0$, i.e. the abundance of all species equally declines (or increases) from site 1 to site 2). The first situation (Fig. 1a) is analogous to species replacement in incidence-based patterns, as some individuals are substituted by individuals of different species from site to site. To avoid confusion with terms used for incidence-based patterns, I will call this pattern *balanced variation in species abundances*. The second situation (Fig. 1b) is equivalent to species nestedness in incidence-based patterns, as some individuals are lost from one site to the other without any substitution. I will call this pattern *abundance gradient*. These are not reciprocally exclusive patterns, but can simultaneously occur (Fig. 1c), producing intermediate situations in which Bray-Curtis dissimilarity is partially derived from balanced abundance variation and partially derived from abundance gradients.

It should be noted here that other abundance-based dissimilarity indices are also affected by both patterns (i.e. balanced variation and abundance gradients). This is the case of abundance-based dissimilarity indices derived from Hill numbers (e.g. Horn and Morisita-Horn indices), which are monotonic transformations of strict sense beta diversity (i.e. the effective number of distinct communities) for true diversities of any order q (Jost 2007). However, because they are derived from Hill numbers, Horn and Morisita-Horn indices account for changes in relative abundances instead of changes in absolute abundances, as the Bray-Curtis index does. For this reason, Horn (d_{H}) and Morisita-Horn (d_{MH}) indices consider identical the communities in Fig. 1b B1 and B2 ($d_{\text{H}} = d_{\text{MH}} = 0$). This does not imply that they are completely independent of abundance gradients, as both indices would consider that dissimilarity is similar in situation D ($d_{\text{H}} = d_{\text{MH}} = 0.33$) and E ($d_{\text{H}} = 0.31$, $d_{\text{MH}} = 0.33$). The use of relative abundances makes difficult to disentangle the effect of subset patterns (species nestedness and abundance gradients) from substitution patterns (species turnover and balanced variation in abundance). Whether it is possible to separate both components in dissimilarity measures accounting for relative abundances remains open to future research. In this article, a partition of Bray-Curtis dissimilarity into balanced variation and abundance gradient components is provided.

Using an analogous reasoning as for separating the turnover and nestedness components of incidence-based dissimilarity (Baselga 2010, 2012), the balanced variation and abundance gradient components of Bray-Curtis dissimilarity can be separated as follows:

$$\begin{aligned} d_{\text{BC}} &= d_{\text{BC-bal}} + d_{\text{BC-gra}} \equiv \frac{B + C}{2A + B + C} \\ &= \frac{\min(B, C)}{A + \min(B, C)} + \frac{|B - C|}{2A + B + C} * \frac{A}{A + \min(B, C)} \end{aligned} \quad \text{eqn 6}$$

where $d_{\text{BC-bal}}$ and $d_{\text{BC-gra}}$ are the *balanced variation component* and the *abundance gradient component* of BC dissimilarity,

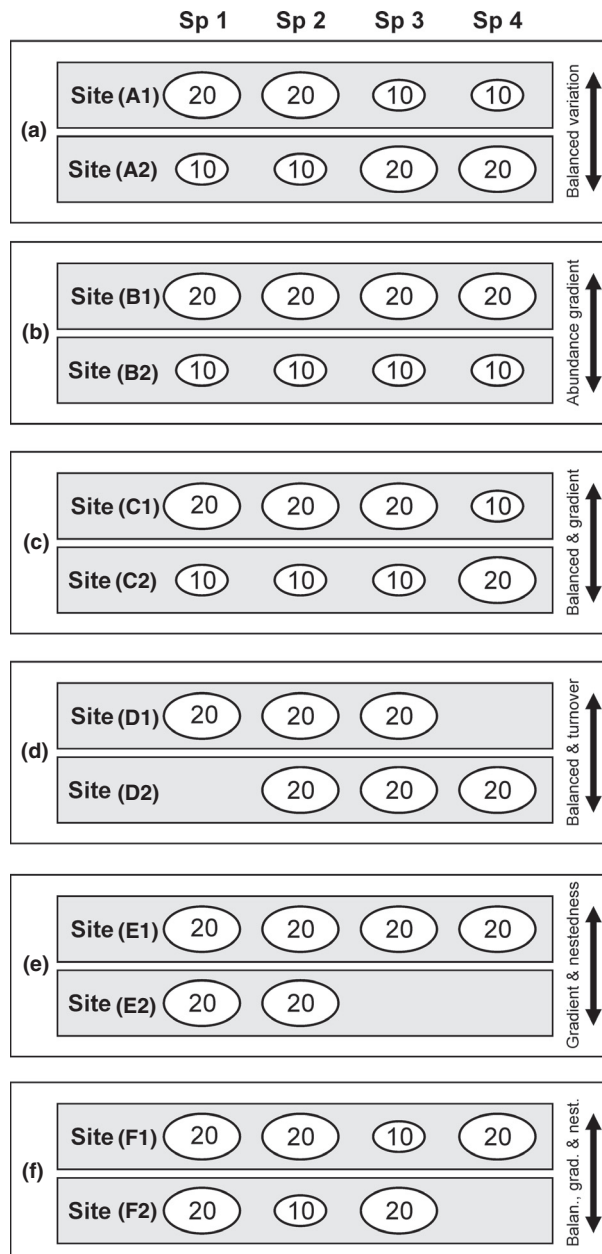


Fig. 1. Idealized examples involving four species and two sites in each situation (a–f), showing that biotic dissimilarity in terms of variation in species abundances may be linked to two antithetic phenomena. In all situations, the total number of individuals (120) and the sum of absolute differences in species abundances (40 individuals) are exactly the same and, in consequence, Bray-Curtis dissimilarity is identical in all situations ($d_{BC}=0.33$). However, in situation (a) the decrease of abundance in species 1 and 2 from site A1 to A2 is perfectly balanced by the increase of the abundance of species 3 and 4, whereas in situation (b) all species decrease its abundance from B1 to B2. In situation (c) both patterns are mixed, as the decrease in abundance of species 1–3 from C1 to C2 is only partially balanced by the increase of abundance of species 4. In situation (d), the balanced variation in abundance is associated with species turnover, while in situation (e) the abundance gradient is associated with species nestedness. Note that any combination of all these patterns that keep constant the relationship between the total number of individuals and the sum of absolute differences in abundances would yield the same Bray-Curtis dissimilarity. For example, situation (f) combines balanced variation, abundance gradient and nestedness.

respectively, and A , B and C are extended abundance-based matching components as formulated above. In the same way that Bray-Curtis dissimilarity (d_{BC}) reduces to the Sørensen index (β_{sor}) when incidence data are used, d_{BC-bal} and d_{BC-gra} reduce to the Simpson index of dissimilarity (β_{sim}) and the nestedness-resultant component (β_{sne}) respectively.

With this additive partition it is possible to quantify the total dissimilarity between two assemblages in terms of variation in species abundances (d_{BC}), and to separate the fractions of this total dissimilarity that are linked to balanced variation in abundances (d_{BC-bal}) or linked to abundance gradients (d_{BC-gra}). In the six idealized examples in Fig. 1, the total abundance-based dissimilarity as measured by the Bray-Curtis index is exactly the same ($d_{BC} = 0.33$), but the partition correctly identifies that (i) dissimilarity in case A is completely due to balanced variation in abundances ($d_{BC-bal} = 0.33$, $d_{BC-gra} = 0$); (ii) dissimilarity in case B is completely due to balanced variation in abundances ($d_{BC-bal} = 0$, $d_{BC-gra} = 0.33$); and (iii) dissimilarity is partially due to both phenomena in case C ($d_{BC-bal} = 0.20$, $d_{BC-gra} = 0.13$). In general terms, in the absence of any difference in total abundance between two sites (i.e. no abundance gradient), $d_{BC-gra} = 0$ and $d_{BC} = d_{BC-bal}$, ranging from 0 (i.e. equal species abundances in both sites) to 1 (i.e. both sites have completely different species and the abundance of species in one site is perfectly balanced by the abundance of species in the other site). In the absence of any balanced variation in species abundances (i.e. all species abundances that change from one site to the other do it with the same sign), $d_{BC-bal} = 0$ and $d_{BC} = d_{BC-gra}$, ranging from ≈ 0 (i.e. almost equal species abundances in both sites) to ≈ 1 (i.e. the difference in species abundance is very large and in the same direction in all species). Of course, multiple combinations including partially balanced changes in species abundances and abundances gradients (Fig. 1c) are possible. Moreover, balanced variation in abundances can be associated with species turnover (Fig. 1d) and abundance gradients can be associated with species nestedness (Fig. 1e), and all these patterns can be mixed in multiple ways (i.e. Fig. 1f). The usefulness of the partition presented above is that different patterns behind dissimilarity can now be separated, allowing to explore their respective relationships with different potential determinants. Note that the framework presented here is analogous to the partition of beta diversity into turnover and nestedness components (Baselga 2010, 2012), as it extends the concepts of substitution (Fig. 1a) and subset (Fig. 1b) to abundance-based measures of dissimilarity.

An example: assemblage dissimilarity in tropical forests

Distance decay of assemblage similarity or, equivalently, the increase of assemblage dissimilarity with geographical distance is one of the best known and most analysed ecological patterns (Nekola & White 1999; Condit *et al.*

2002; Tuomisto, Ruokolainen & Yli-Halla 2003). When abundance data are available, the Bray-Curtis index is one of the most widely used measures of dissimilarity but, as explained above, d_{BC} results from the summation of two antithetic sources of dissimilarity: balanced changes in species abundances and unidirectional abundance gradients. Because these two components of variation in species abundances can have different patterns in different regions, if they are not separated we can fail to discover important differences between ecological systems. I exemplify this by comparing the patterns of increase in assemblage dissimilarity with spatial distance in the tropical lowland forests of Panama (Condit *et al.* 2002) and the tropical montane forests of Chiapas (Cayuela, de la Cruz & Ruokolainen 2011). Both data sets are available from the mentioned papers and include the abundance of tree species in plots or forest fragments, as well as the spatial coordinates of each sampling unit. Using the equations presented above, I computed d_{BC} , d_{BC-bal} and d_{BC-gra} between all pairs of sites in each data set, and assessed the relationship between assemblage dissimilarity (d) and spatial distance (s) using the model $d = 1 - a * e^{b*s}$. Note that this model is equivalent to the exponential decay models used for similarity, and therefore perfectly matches the theoretical requirement of asymptotic increase towards maximum dissimilarity ($d = 1$). This requirement is not accomplished by simpler linear or logarithmic models. All calculations were performed in R (R Development Core Team 2011), using the function `bray.part` (available as R script in Suppl. Mat. and to be implemented in package `betapart`; Baselga & Orme 2012) to compute the dissimilarities, the `vegan` package (Oksanen *et al.* 2011) to assess the significance of relationships using Mantel tests, and the `boot` package (Canty & Ripley 2008) to estimate frequency distributions of slopes, which were used to assess the significance of differences in slopes between regions by empirically comparing the estimated distributions of parameters.

In both data sets, Panama and Chiapas, d_{BC} dissimilarity was positively related with spatial distance (Fig. 2). In the case of Panama, the model fitted much better the data, and the estimated slopes (Table 1) were significantly steeper than those in Chiapas ($P = 0.012$). However, when both components of variation in species abundances were separated, the slope for the balanced variation component (d_{BC-bal}) showed no significant differences between Chiapas and Panama ($P = 0.306$), whereas the slope for the abundance gradient component (d_{BC-gra}) was significantly different between Chiapas and Panama ($P < 0.001$). In fact, the abundance gradient component was not significantly related with spatial distance in Panama, but negatively correlated with spatial distance in Chiapas (Fig. 2). In other words, the widely used Bray-Curtis dissimilarity index would suggest that tree assemblages change faster with spatial distance in Panama than in Chiapas. However, as the partitioned dissimilarities show, this difference does not stem from a faster rate of substitution in

Panama, but from the existence of more pronounced abundance gradients in Chiapas. In Panama, no marked abundance gradients exist at any spatial distance ($SD/\text{mean abundance} = 0.25$), while in Chiapas close forest pairs in some cases present unidirectional gradients in species abundances ($SD/\text{mean abundance} = 0.65$) in which one forest is just a subset of the other, but with lower abundances of the same species. In consequence, Bray-Curtis dissimilarities are inflated at shortest distances by abundance gradients in Chiapas but not in Panama, making the slope of the relationship for d_{BC} in Chiapas flatter than that in Panama. Therefore, separating both components allows assigning the patterns in dissimilarity to the specific phenomena behind these patterns. In the example above, it is the strength of abundance gradients and not the rate of substitution what changes between regions. Because substitution is the intuition we usually have in mind as representing dissimilarity, the proposed partition is useful as it allows explicitly separating the amount of dissimilarity derived from both sources of variation.

General implications

In general terms, the method introduced here may be useful in a wide range of research questions. Pairwise dissimilarity matrices underlie numerous multivariate analyses dealing with assemblage variation and, therefore, the distinction between patterns of substitution and abundance gradients could be crucial. For example, biogeographic regionalizations are performed using clustering algorithms that make use of dissimilarity matrices. As already argued in the context of incidence-based dissimilarities, biogeographic regionalizations have to be performed based on substitution patterns only, removing the effect of subset patterns (Kreft & Jetz 2010; Svenning, Flojgaard & Baselga 2011). Thus, if species abundance variation is to be accounted for, regionalization has to be based in the balanced component of dissimilarity. Other types of analyses include the assessment of the correlates of patterns of variation of assemblage composition or patterns of variation of dissimilarity (Legendre, Borcard & Peres-Neto 2005; Tuomisto & Ruokolainen 2006). The variation in assemblage composition in terms of species abundances can be caused, as explained above (Fig. 1), by balanced variation or abundance gradients. Those antithetic phenomena can be linked to different underlying determinants, so inference based on unpartitioned abundance-based dissimilarity may be misleading. The same occurs for the assessment of patterns of variation of dissimilarity with spatial or environmental distances, as shown above in the example on tropical forests. In sum, the proposed partition may be useful in a wide range of biodiversity analyses.

As a final consideration, it should be stressed that the methods proposed here rely on the assumption that species abundance can be measured without bias. This could be realistic for some taxa with stable and well visible populations, like trees or some sessile animals, but less so for many other organisms. The need for unbiased measures of abundance is not specific of

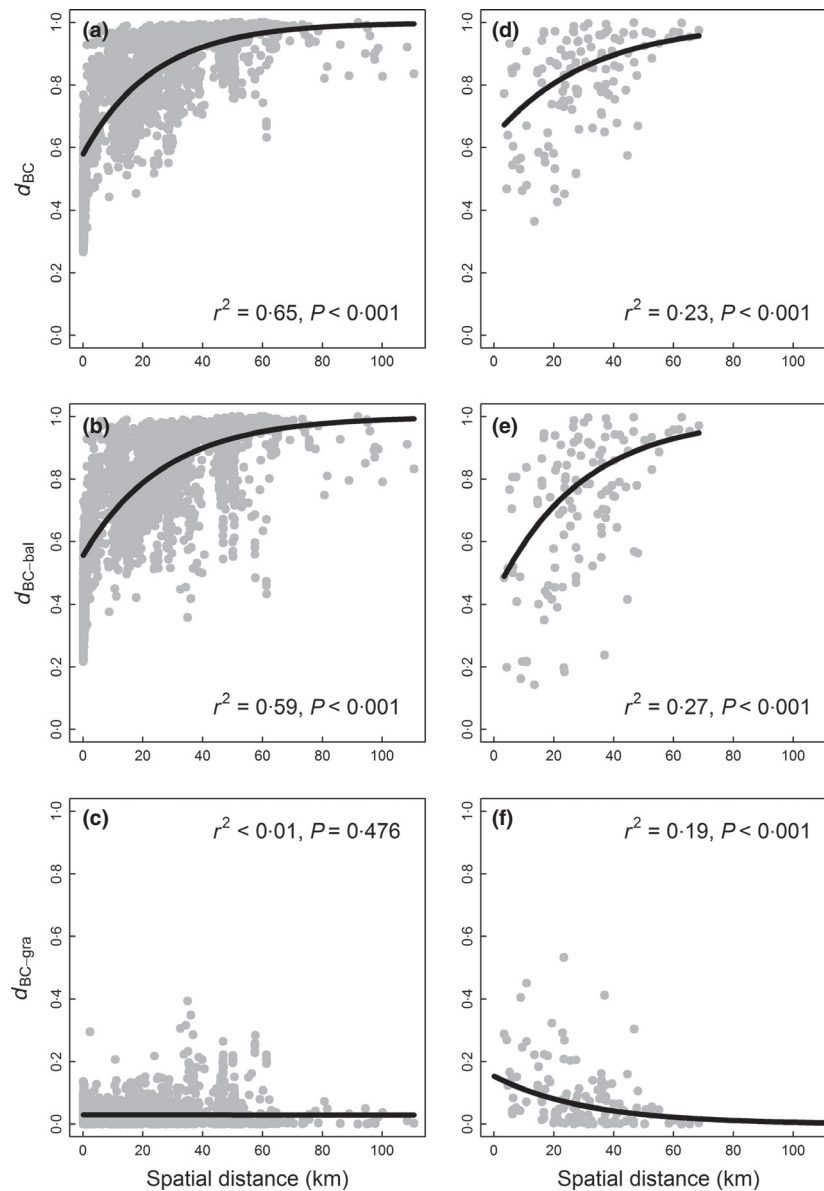


Fig. 2. Relationship between biotic dissimilarity and spatial distance in the tropical forests of Panama (a–c) and Chiapas (d–f), as measured with the Bray-Curtis index (d_{BC}) and its balanced variation (d_{BC-bal}) and abundance gradient (d_{BC-gra}) components. Black curves are the fitted functions. The coefficient of determination (r^2) and significance (p , computed using Mantel tests) of each relationship are shown.

the partitioning framework developed here, but to the very concept of abundance-based patterns, including abundance-based dissimilarity measures as the widely used Bray-Curtis

Table 1. Estimated parameters (a = intercept, and b = slope) of the relationship between abundance-based dissimilarity and spatial distance for the different dissimilarity indices and both data sets from Panama (Condit *et al.* 2002) and Chiapas (Cayuela, de la Cruz & Ruokolainen 2011)

Dissimilarity	Panama		Chiapas	
	a	b	a	b
d_{BC}	0.58	0.042	0.64	0.031
d_{BC-bal}	0.55	0.037	0.42	0.036
d_{BC-gra}	0.03	~0.000	0.15	−0.032

index. When this assumption cannot be met, incidence-based methods would represent a more robust methodological alternative.

Conclusions

Abundance-based dissimilarity can be derived from two anti-thetic patterns: (i) balanced variation in abundance, whereby the individuals of some species in one site are substituted by the same number of individuals of different species in another site or, in other words, species abundances change from site to site with different signs for different species and changes balance each other; and (ii) abundance gradients, whereby some individuals are lost from one site to the other or, in other words, all the species that change their abundance from one

site to the other make it with the same sign. The widely used Bray-Curtis index of dissimilarity is the result of summing these two sources of dissimilarity, and therefore might consider equivalent patterns that are markedly different. The partition of d_{BC} dissimilarity into two components of balanced abundance variation and abundance gradient, respectively, may thus be useful to assess biodiversity patterns and to explore their causes, as substitution and loss of individuals are patterns that can derive from completely different processes.

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References

- Baselga, A. (2010) Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, **19**, 134–143.
- Baselga, A. (2012) The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. *Global Ecology and Biogeography*, **21**, 1223–1232.
- Baselga, A., Gómez-Rodríguez, C. & Lobo, J.M. (2012) Historical legacies in world amphibian diversity revealed by the turnover and nestedness components of beta diversity. *PLoS ONE*, **7**, e32341.
- Baselga, A. & Orme, C.D.L. (2012) betapart: an R package for the study of beta diversity. *Methods in Ecology and Evolution*, **3**, 808–812.
- Canty, A. & Ripley, B. (2008) *boot: Bootstrap R (S-Plus) Functions*. R package version 1.2-32. <http://CRAN.R-project.org/package=boot> (accessed on 2 August 2011).
- Cayuela, L., de la Cruz, M. & Ruokolainen, K. (2011) A method to incorporate the effect of taxonomic uncertainty on multivariate analyses of ecological data. *Ecography*, **34**, 94–102.
- Condit, R., Pitman, N., Leigh, E.G., Chave, J., Terborgh, J., Foster, R.B., Nunez, P., Aguilar, S., Valencia, R., Villa, G., Muller-Landau, H.C., Losos, E. & Hubbell, S.P. (2002) Beta-diversity in tropical forest trees. *Science*, **295**, 666–669.
- Hortal, J., Diniz-Filho, J.A.F., Bini, L.M., Rodríguez, M.A., Baselga, A., Nogués-Bravo, D., Rangel, T.F., Hawkins, B.A. & Lobo, J.M. (2011) Ice age climate, evolutionary constraints and diversity patterns of European dung beetles. *Ecology Letters*, **14**, 741–748.
- Jost, L. (2007) Partitioning diversity into independent alpha and beta components. *Ecology*, **88**, 2427–2439.
- Koleff, P., Gaston, K.J. & Lennon, J.K. (2003) Measuring beta diversity for presence-absence data. *Journal of Animal Ecology*, **72**, 367–382.
- Kreft, H. & Jetz, W. (2010) A framework for delineating biogeographical regions based on species distributions. *Journal of Biogeography*, **37**, 2029–2053.
- Legendre, P., Borcard, D. & Peres-Neto, P.R. (2005) Analyzing beta diversity: partitioning the spatial variation of community composition data. *Ecological Monographs*, **75**, 435–450.
- Legendre, P. & Legendre, L. (1998) *Numerical Ecology*, 2nd edn. Elsevier, Amsterdam.
- Leprieux, F., Tedesco, P.A., Hugueny, B., Beauchard, O., Dürr, H.H., Brosse, S. & Oberdorff, T. (2011) Partitioning global patterns of freshwater fish beta diversity reveals contrasting signatures of past climate changes. *Ecology Letters*, **14**, 325–334.
- Leprieux, F., Albouy, C., De Bortoli, J., Cowman, P.F., Belwood, D.R. & Mouillot, D. (2012) Quantifying phylogenetic beta diversity: distinguishing between 'true' turnover of lineages and phylogenetic diversity gradients. *PLoS ONE*, **7**, e42760.
- Nekola, J.C. & White, P.S. (1999) The distance decay of similarity in biogeography and ecology. *Journal of Biogeography*, **26**, 867–878.
- Oksanen, J., Blanchet, G., Kindt, R., Minchin, P.R., Legendre, P., O'Hara, B., Simpson, G.L., Solymos, P., Stevens, M.H.H. & Wagner, H. (2011) *vegan: Community Ecology Package*. R package version 2.0-2, available at <http://cran.r-project.org/> (accessed on 23 November 2012).
- R Development Core Team (2011) *R: A Language and Environment for Statistical Computing*. Version 2.13.1. Available at <http://www.r-project.org> (accessed on 2 August 2011).
- Svenning, J.C., Fløjgaard, C. & Baselga, A. (2011) Climate, history and neutrality as drivers of mammal beta diversity in Europe: insights from multiscale deconstruction. *Journal of Animal Ecology*, **80**, 393–402.
- Tamas, J., Podani, J. & Csontos, P. (2001) An extension of presence/absence coefficients to abundance data: a new look at absence. *Journal of Vegetation Science*, **12**, 401–410.
- Tuomisto, H. & Ruokolainen, K. (2006) Analyzing or explaining beta diversity? Understanding the targets of different methods of analysis. *Ecology*, **87**, 2697–2708.
- Tuomisto, H., Ruokolainen, K. & Yli-Halla, M. (2003) Dispersal, environment, and floristic variation of western Amazonian forests. *Science*, **299**, 241–244.
- Villegier, S., Grenouillet, G. & Brosse, S. (2013) Decomposing functional β -diversity reveals that low functional β -diversity is driven by low functional turnover in European fish assemblages. *Global Ecology and Biogeography*, doi: 10.1111/geb.12021.

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Supporting Information

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

Data S1. R Script