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A novel multiple-site extension to pairwise partitioned taxonomic beta diversity



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ABSTRACT

Our understanding of the causes of variation in taxonomic composition, or beta diversity, is progressing rapidly, thanks in part to recent methodological advances. For example, methods for partitioning beta diversity into its "replacement" and "richness" components have helped reveal patterns that had been undetected by traditional analyses. These partitioning methods are derived from pairwise dissimilarity measures, and are thus well suited to many conventional beta diversity analyses, including "distance decay" relationships. However, pairwise beta diversity measures have limitations, including their lack of information about taxa that are shared among three or more sites. Recently, a new suite of multiple-site counterparts to the pairwise partitioning measures of beta diversity was proposed, but the pairwise analogs upon which these were based were subsequently criticized, and compelling arguments were presented in favor of other partitioning approaches. Here, we introduce multiple-site partitioning measures that address these shortcomings, and illustrate their desirable properties using numerical simulations. We also provide an empirical example of their utility by analyzing the temporal beta diversity of breeding birds within the conterminous USA. We show that temporal beta diversity is predominantly driven by replacement rather than richness differences, and correspondingly, that correlations between temporal beta diversity and productivity and elevation are driven primarily by the replacement component. Furthermore, in contrast to existing multiple-site measures, we show that richness differences do play an important part in driving overall beta diversity patterns. Our new multiple-site measures therefore complement existing methods for analyzing beta diversity, and are especially suitable when compositional heterogeneity is the response of interest.

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1. Introduction

Beta diversity, the change in species composition from one sample to another, has come under increasing scrutiny, particularly since the publication of Hubbell's (2001) neutral theory (Tuomisto and Ruokolainen, 2006). Although originally proposed by Whittaker (1960, 1972) as a multiple-site measure ($\beta = \gamma/\alpha$; where alpha is the average species richness across all samples), it has primarily been calculated in a pairwise manner, using familiar dissimilarity indices such as Sørensen (1948) or Jaccard (1912) dissimilarity for presence/absence data (Tuomisto, 2010a,b;

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Anderson et al., 2011). These pairwise indices are usually evaluated in relation to gradients, often environmental, and correlation tests (e.g. Mantel tests; Anderson et al., 2011; Pellissier et al., 2013) are used to determine if pairwise compositional dissimilarity correlates with pairwise environmental dissimilarity. Another important development is due to Baselga (2010), who demonstrated how to partition Sørensen's dissimilarity (1948; beta diversity) into two components, the turnover component (i.e. richness independent change in composition as measured by the Simpson, 1949 index) and the nestedness-resultant dissimilarity, which is the difference of the Sørensen (1948) and Simpson (1949) indices. Baselga (2012) also derived analogous components for Jaccard's (1912) pairwise dissimilarity. Several studies, including Baselga's own work, have found that the turnover and nestednessresultant components of beta diversity can vield important patterns and insights that would otherwise go unnoticed if only the overall beta diversity measures were analyzed (Baselga, 2010; Azeria et al., 2011; Baeten et al., 2012).

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A vigorous debate has followed Baselga's contributions (Podani and Schmera, 2011; Almeida-Neto et al., 2012; Carvalho et al., 2012, 2013), centering primarily on the nestedness-resultant portion of the partition. Podani and Schmera (2011) and Carvalho et al. (2012) arrived at similar conclusions about Baselga's partition independently and presented identical alternative partitions. The authors of Carvalho et al. (2012) and Podani and Schmera (2011) then collaborated to produce Carvalho et al. (2013: hereafter referred to as 'PSC' to acknowledge the independent development by Podani and Schmera, 2011 and Carvalho et al., 2012), arguing against Baselga's (2010, 2012; hereafter BA) partition of pairwise dissimilarity because, contrary to what should occur, BA's nestedness-resultant dissimilarity decreased as species loss increased. PSC demonstrated that this pattern results from inconsistent scaling factors (denominators) in BA's partition of both Jaccard and Sorensen dissimilarity. They introduced their own partitioning of Jaccard's (1912) dissimilarity (β_{cc}) into richness (β_{rich}) and replacement (β_{-3}) components that is always scaled by the total number of species present (i.e. a + b + c; Table 1). Thus, PSC's additive partition equates with the proportion of species that contribute to richness differences and replacement differences among communities; their sum is the overall beta diversity. As argued by PSC, these measures represent a biologically clear and mathematically sound decomposition of total dissimilarity into its replacement and richness components. It is important to note that the partitioned components proposed by PSC are not distinct measures of compositional dissimilarity and must be considered in relation to overall dissimilarity.

2. The rationale for new multiple-site beta diversity measures

In some instances, however, the focus is not on quantifying variation in pairwise measures of beta diversity, or relating pairwise measures to gradients, but rather (or additionally) on comparing the overall magnitude of beta diversity (including its richness and replacement components) that characterizes a given community type or study unit to that of a different community type or study unit (e.g. Rooney et al., 2004; Royo and Ristau, 2013; Trentanovi et al., 2013). In other words, we often wish to compare magnitudes of "compositional heterogeneity" among categories or groups of assemblages. Likewise, we may wish to determine whether experimental treatments (e.g. disturbance) lead to different magnitudes of beta diversity in a particular community type (e.g. Martin et al., 2005; Smith et al., 2014). Traditionally, such comparisons have been conducted using the pairwise dissimilarity measures (computed within groups) as the observational units (Anderson et al., 2011), analyzed using either non-parametric multivariate analysis of variance [PERMANOVA; (Anderson, 2001); e.g. Martin and Wilsey, 2012; Royo and Ristau, 2013; Smith et al., 2014], or by comparing their averages among groups (e.g. Gaston et al., 2007). However, Diserud and Ødegaard, 2007 and Baselga et al. (2007) noted that averaging pairwise beta diversity values to estimate compositional heterogeneity is less than ideal because (i) it disregards information about species that are shared among three or more sites (or samples), and (ii) it relies on nonindependent sampling units. The PERMANOVA method statistically addresses the non-independence issue for a limited set of sampling/experimental designs (Anderson, 2001; Anderson et al., 2011). The reader is referred to Carvalho et al. (2013) for an example of how PERMANOVA can be used to analyze each of the three components of pairwise beta diversity (β_{cc} , β_{rich} , and β_{-3}). However, because the PERMANOVA approach itself uses pairwise measures, it cannot address the problem that pairwise measures lack information about species that are shared among three or more sites (i.e. higher order (dis)similarity sensu Diserud and Ødegaard, 2007). For this, "multiple-site" measures of beta diversity are required, and ideally these would provide information about the replacement and richness-related components of beta diversity (see Section 1, Baselga et al., 2007).

Diserud and Ødegaard, 2007 proposed such a measure based on the Sørensen index of similarity. However, Baselga et al. (2007) noted that it was therefore prone to the confounding influences of richness differences. Thus, any multiple-site measure based on Sørensen's similarity would be unable to discern whether beta diversity differences were due to richness differences (nestedness) or to species turnover. As a solution, Baselga et al. (2007) proposed a multiple-site similarity measure based on Simpson's index (M_{sim}) that can detect changes in composition while being independent of changing richness values. Baselga (2010, 2012, 2013) then extended M_{sim} to the Jaccard and Sørensen dissimilarity indices of beta diversity by converting M_{sim} to its corresponding dissimilarity measure that captures the turnover component of the Sørensen index of dissimilarity (Baselga, 2010). Following his partition of pairwise beta diversity into turnover and nestednessresultant dissimilarity, BA then developed the corresponding multiple-site indices. However, as explained above, PSC argued that BA's pairwise measures exhibited undesirable properties, and introduced their own solutions (Table 1). To facilitate a full assessment of these two partitioning approaches we require multiple-site measures of beta diversity derived from the reliable pairwise measures of PSC. We introduce such measures below.

3. Derivation of formulae

3.1. Pairwise taxonomic beta diversity

BA published his partition of beta diversity into turnover and nestedness-resultant dissimilarity and PSC countered it with their

Table 1

Partitioned, pairwise Jaccard dissimilarity measures including the partition of Baselga (2010, 2012) and Carvalho et al. (2013). Note that both β_{jac} and β_{cc} refer to Jaccard dissimilarity and are therefore the same. For all formulae, 'a' refers to the number of species shared in a comparison of communities *i* and *j* and 'b' and 'c' refer to the number of species unique to community *i* and *j* respectively. Table modified from Baselga (2012) and Carvalho et al. (2013).

Family	Measure	Notation	Formula	Reference
Jaccard (Baselga)	Jaccard dissimilarity	$eta_{ ext{jac(cc)}}$	$\frac{b+c}{a+b+c}$	Jaccard (1912), Colwell and Coddington (1994), Podani and Schmera (2011), Baselga (2012), Carvalho et al. (2013)
	Turnover of Jaccard	$eta_{ m jtu}$	$2 \times \frac{\min(b,c)}{a+2\min(b,c)}$	Baselga (2010, 2012)
	Nestedness resultant dissimilarity of Jaccard	$eta_{ ext{jne}}$	$\frac{ b-c }{a+b+c} \times \frac{a}{a+2\min(b,c)}$	Baselga (2010, 2012)
Jaccard (Carvalho)	Jaccard dissimilarity	$eta_{ m cc(jac)}$	$\frac{b+c}{a+b+c}$	Jaccard (1912), Colwell and Coddington (1994), Podani and
	Replacement component of Jaccard dissimilarity	eta_{-3}	$2 imes rac{\min(b,c)}{a+b+c}$	Schmera (2011), Baselga (2012), Carvalho et al. (2013) Williams (1996), Cardoso et al. (2009), Carvalho et al. (2012, 2013)
	Richness component of Jaccard dissimilarity	$\beta_{ m rich}$	$\frac{ b-c }{a+b+c}$	Podani and Schmera (2011), Carvalho et al. (2012, 2013)

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