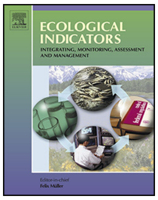
Ecological Indicators 54 (2015) 203–206

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind



Short Communication

A multiple-site dissimilarity measure for species presence/absence data and its relationship with nestedness and turnover

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ARTICLE INFO

Article history:
Received 19 August 2014
Received in revised form 12 February 2015
Accepted 17 February 2015

Keywords:
Beta diversity
Diversity decomposition
Matrix ordering
Species richness
Species turnover

ABSTRACT

Multiple-site dissimilarity may be caused by two opposite processes of meta-community organization, such as species nestedness and turnover. Therefore, discriminating among these contributions is necessary for linking multiple-site dissimilarity to ecosystem functioning. This paper introduces a measure of multiple-site dissimilarity or beta diversity for presence/absence data that is based on information on species absences from the species × sites matrix. It is also shown that the newly proposed dissimilarity index can be additively partitioned into species nestedness and turnover.

1. Introduction

Beta diversity, or the amount of variation in species composition among sampling units (or communities, plots, etc.) has become a fundamental topic for connecting the spatial structure of species assemblages to ecological processes, such as competition and coexistence (Fargione and Tilman, 2002), limited dispersal (Seidler and Plotkin, 2006) or environmental control (Legendre et al., 2005), and for providing a conceptual link between local scale diversity (alpha diversity) and the regional species pool (gamma diversity) (Whittaker, 1972).

Many different measures have been proposed for calculating beta diversity. Among them pairwise (dis)similarity indices are probably the most commonly used (Koleff et al., 2003). Therefore, evaluations of multiple-site dissimilarity are usually based on the average dissimilarity between pairs of sites (e.g. Izsak and Price, 2001). However, a restriction of average dissimilarity across all sites is that it does not tell us to what extent there is a change in shared species between pairs of sites (Diserud and Ødegaard, 2007). To get insight on the identity of species shared across more than two sites a multiple-site dissimilarity measure is required. Examples are the multiple-site indices developed by Diserud and Ødegaard (2007), Baselga et al. (2007), and Chao et al. (2012).

In addition, multiple-site dissimilarity may be caused by two opposite mechanisms, such as species nestedness and turnover (Harrison et al., 1992; Baselga et al., 2007). Nestedness refers to the extent the species composition of small assemblages is a subset of the species composition of larger assemblages (Wright and Reeves, 1992). In nested biotas, common species tend to occur in all sites while rare species tend to occur only in the richest sites. While a number of different deterministic or stochastic processes can lead to nested patterns, all of them reflect selective extinction and colonization processes along environmental gradients (Wright and Reeves, 1992; Gaston and Blackburn, 2000; Ulrich et al., 2009). In contrast, species turnover implies the replacement of some species by others, giving rise to segregated species occurrence matrices in which many species will never co-occur together (Ulrich and Gotelli, 2007a). This pattern is usually attributed to environmental sorting (Baselga, 2010) and interaction mechanisms, such as competition or negative plant–soil feedback (van der Putten et al., 2013). However, species turnover can also be obtained as a consequence of limited dispersal processes (Seidler and Plotkin, 2006) and historical differences among sites (Baselga et al., 2012). Therefore, disentangling these contributions is essential for linking multiple-site dissimilarity to ecosystem functioning. Baselga et al. (2007) developed a multiple-site generalization of the Simpson similarity index, which inherited the ability of the original index to detect changes in species turnover. However, the generalized

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http://dx.doi.org/10.1016/j.ecolind.2015.02.026
1470-160X/

Simpson index proposed by Baselga et al. (2007) is independent of richness gradients thus identifying completely nested biotas as entirely similar (see Baselga et al., 2007).

The aim of this paper is thus to provide an explicit interpretation for a new multiple-site dissimilarity measure for presence and absence data, which is linearly related to classical additive beta diversity. We further show that this dissimilarity measure can be easily partitioned into two additive components: species nestedness and turnover.

2. Materials and methods

2.1. A new look at beta diversity

Whittaker (1960, 1972) first proposed measuring beta diversity as the ratio between regional species richness (gamma diversity) and average species richness within single plots (alpha diversity):

$$\beta_M = \frac{\gamma}{\alpha} \tag{1}$$

More recently an additive formulation of beta diversity first proposed by McArthur et al. (1966) was revitalized by Lande (1996), which put it explicitly in connection with Whittaker's multiplicative measure:

$$\beta_A = \gamma - \alpha \tag{2}$$

An undesirable property of additive beta diversity β_A is its dependence on regional species richness (γ). This dependence can be easily overcome by normalizing beta diversity by gamma (for details see Ricotta, 2008; Tuomisto, 2010):

$$\beta_{AN} = \frac{\gamma - \alpha}{\gamma} = 1 - \frac{\alpha}{\gamma} \tag{3}$$

where the ratio $\psi = \alpha/\gamma$ is the reciprocal of Whittaker's beta (see Lande, 1996), thus emphasizing the relationship between additive and multiplicative beta (Ricotta, 2005). From Eq. (3) it is easily shown that β_{AN} increases with increasing *dissimilarity* among plots, whereas ψ increases with increasing *similarity* among plots.

To get deeper insight into the properties of beta diversity, Eq. (3) can be reformulated as (Ricotta, 2008):

$$\beta_{AN} = \frac{\gamma - \alpha}{\gamma} = \frac{1}{S}\sum_i \left(1 - \frac{N_i}{N}\right) = \sum_i \frac{N - N_i}{S \times N}$$

where $\alpha = \sum_i N_i/N$, N is the total number of plots, N_i is the number of plots that contain species i, and $S = \gamma$ is the total number of species in the N plots.

β_{AN} measures the turnover in species composition among plots in the range $[0, (N-1)/N]$. Therefore, in order to compare beta diversity between communities of different species richness, β_{AN} must be transformed onto the unit interval. The simplest way to rescale a given quantity X between zero and one is to use the linear transformation $(X - X_{\min})/(X_{\max} - X_{\min})$. This gives the relative measure of additive beta diversity:

$$\beta^{+} = \sum_i \frac{N - N_i}{S \times N} \times \frac{N}{N-1} = \sum_i \frac{N_{i0}}{S \times (N-1)} \tag{4}$$

where the term $N_{i0} = N - N_i$ is the number of absences of species i. For presence and absence data, the rescaled expression for additive beta diversity β^{+} thus measures multiple-site dissimilarity as the total number of absences in the matrix of S species × N plots divided by the maximum possible number of absences $S \times (N-1)$, which is obtained if all species occur only once in the N plots. For simplicity, in this paper we did not consider 'degenerate' plots without any species recorded.

Due to the complementarity of β_{AN} and ψ, it is also easily shown that the rescaled version of ψ onto the unit range can be formulated as:

$$\bar{\beta}^{\times} = \sum_i \frac{N_i - 1}{S \times (N-1)} \tag{5}$$

where the numerator $N_i - 1$ is the number of species presences exceeding the first and the bar on multiplicative beta diversity $\bar{\beta}^{\times}$ indicates that $\bar{\beta}^{\times}$ reflects how similar sites are, such that $\beta^{+} + \bar{\beta}^{\times} = 1$. Proof in the electronic supplementary material (Appendix S1). $\bar{\beta}^{\times}$ thus measures multiple-site similarity as the number of presences exceeding the first in the $S \times N$ matrix divided by its maximum possible number. Hence, according to Eq. (5), only species occurrences from the second onwards contribute to multiple-site similarity. When calculated for two plots only, $\bar{\beta}^{\times}$ is equal to the Jaccard similarity coefficient, thus reflecting a multiple-site Jaccard similarity (Gotelli and Chao, 2013), while β^{+} reflects its dissimilarity counterpart. Proof in the electronic supplementary material (Appendix S2). In Appendix S2 we also show that, starting with β_{M} instead of β_A, a similar framework can be developed where the complement of beta diversity associated with two plots is the Sørensen similarity coefficient, instead of the Jaccard coefficient.

2.2. Disentangling species turnover from nestedness

Multiple site dissimilarity may be produced by two different patterns of meta-community organization: species nestedness and turnover, which result from two opposite processes, such as species loss and species replacement, respectively (Baselga, 2010). Therefore, disentangling the contribution of nestedness from species turnover is crucial for understanding the ecological drivers of beta-diversity patterns.

Both patterns may be measured in a variety of ways from presence–absence matrices (see Ulrich et al., 2009 and references therein). In the framework of this paper, the contribution of species turnover to multiple-site dissimilarity β_T may be adequately measured by the unexpected species absences that deviate from a perfectly nested pattern *sensu* Patterson and Atmar (1986) divided by the maximum number of absences:

$$\beta_T = \sum_i \frac{N_{iT}}{S \times (N-1)} \tag{6}$$

where N_{iT} is the count of how often species i is absent from a site with equal or greater richness than the species poorest site in which the species occurs (see Ulrich et al., 2009). This definition implies that nestedness relationships are restricted to species 'poorer' and 'richer' sites, such that in nested incidence matrices the species composition of small assemblages is a nested subset of the species composition of larger assemblages (Podani and Schmera, 2012).

According to Eq. (6) the contribution of species nestedness to multiple-site dissimilarity β_N is simply:

$$\beta_N = \beta^{+} - \beta_T = \sum_i \frac{N_{iN}}{S \times (N-1)} \tag{7}$$

where $N_{iN} = N_{i0} - N_{iT}$ is the number of absences of species i that conform to a perfectly nested pattern, such that $\beta_N + \beta_T + \bar{\beta}^{\times} = 1$. For a worked example see Fig. 1; an *R* function (R Development Core Team, 2014) for calculating β_N, β_T, β^{+} and $\bar{\beta}^{\times}$ from presence/absence data is available in the electronic supplementary material (Appendix S3).

Note that, given a species incidence matrix most nestedness measures require some kind of matrix ordering. Usually the matrix is ordered with the most common species placed by convention in the top row, and the most species-rich site placed in the leftmost column. The remaining species and sites are packed towards the