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Influence of rare species on beta diversity estimates in marine benthic assemblages

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ABSTRACT

Beta diversity measures the variability in species composition, and Whittaker's index has become the most widely used measure of β-diversity. However, on soft bottom benthic assemblages Whittaker's index is heavily influenced by the number of species recorded in a single sample (defined as rare species). This over-weighting of rare species induces biased estimates of the heterogeneity, so it becomes difficult to compare assemblages containing an high proportion of rare species. In benthic communities the unusual large number of rare species is frequently attributed to a combination of sampling errors and insufficient sampling effort. In order to reduce the influence of rare species on the measure of beta diversity, we developed an alternative index based on simple probabilistic considerations. It turns out that our probability index is an ordinary Michaelis-Menten transformation of Whittaker's index but behaves more favourably when species heterogeneity increases. Our suggested index therefore seems appropriate when comparing patterns of complexity in marine benthic assemblages.

1. Introduction

In order to quantify different spatial aspects of biodiversity, Whittaker (1960) partitioned species diversity into alpha, beta and gamma components. Alpha diversity (α) describes the number of species occurring on a local scale (local assemblage), and gamma diversity (γ) describes the total number of species occurring in a larger defined geographical area (regional assemblage). Beta diversity, or species turnover, is a measure of the difference in species composition either between two or more local assemblages (Whittaker, 1960; Clarke and Lidgard, 2000; Gray, 2000), or between local and regional assemblages (Koleff et al., 2003). At a smaller spatial scale, a measure of point diversity for a single sampling unit has been defined (Whittaker 1972; Gray, 2000, 2001). Such measure is not necessarily confined to a particular habitat or assemblage and thus seems appropriate where sampling may regarded as 'blind' (e.g. grabs or trawls in marine habitat; see Gray 2000, 2001).

Different expressions for measuring beta diversity have been proposed (for a review see Magurran, 2004; Gaston et al., 2007). These techniques involve comparison of two or more samples and are frequently based on similarity/dissimilarity coefficients (Legendre and Legendre, 1998). Different aspects of beta diversity have been addressed in the suggested measures: (1) patterns of species distribution across geographical or environmental gradients (Mourelle and Ezcurra, 1997; Harrison et al., 1992; Wilson and Shmida, 1984; Routledge 1977), (2) biogeographic boundaries (Ruggiero et al., 1998; Williams et al., 1999) or (3) transition zones (Poynton and Boycott, 1996; Gaston et al., 2001). Beta diversity can also assist in achieving effective conservation planning by identifying spatial distribution of habitats that influence the species diversity at a larger spatial scale (Harborne et al., 2006).

In several reviews of the various proposed measures of beta diversity (Wilson and Shmida, 1984; Gaston et al., 2007), the advantages of Whittaker's index has been pointed out, but it has also been underlined that this index is highly influenced by the sampled area. A general feature of marine soft bottoms is a complex spatial pattern of patchy distributions (Morrisey et al., 1994; Barry and Dayton, 1991). Most studies on the distribution of soft sediment fauna are implemented by sampling different sites (sampling units), collecting a low number of widely spaced samples (grabs) per site (e.g. 5 or 10 replicates spaced up to hundred meters from each other; see Neff et al., 1989; Olsgard and Gray, 1995). These designs do not allow an effective determination of scales of spatial heterogeneity in species distribution (Morrisey et al., 1992). This is particularly true for species that occur at low densities (Schlacher et al., 1998). Moreover, low sampling intensity may artificially increase the proportion of species that occur in only a few samples (Gray et al., 2005). Since the spatial distributions of these species are not properly estimated, it is very difficult to compare patterns among assemblages with different spatial heterogeneity.

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According to Hannon et al. (2004) species with low densities and restricted spatial distribution may be classified as “rare species”. In this study we therefore define a "rare species" as a species that is found in only one sample per site. Although this classification will be affected by the number of replicates, our approach must be regarded as pragmatic since in many investigations there will be little variability in sampling effort over the studied area.

It has been known for a long time that the proportion of rare species strongly influences the value of Whittaker's beta diversity (Routledge, 1977). It is therefore difficult to compare homogeneous (i.e. a high proportion of widely distributed species) and heterogeneous (i.e. a high proportion of rare species) assemblages with Whittaker's index. The aim of the present study is to develop a new measurement of beta diversity (a Probabilistic beta diversity index, β_p) that is less influenced by variation in the number of rare species. It will be shown that this index is related to the Whittaker beta diversity index (β_W) by the ordinary Michaelis-Menten transformation. The performance of the new expression is investigated by using a large data set on biodiversity of soft bottom benthic assemblages of the North-western Adriatic Sea (BIODIVADR; Abbiati et al., 2007). The sampled area covered by this project includes a variety of assemblages with different compositional heterogeneity. We therefore used the BIODIVADR data base to compare the Probabilistic (β_p) index with Whittaker's (β_W) index.

2. Materials and methods

2.1. A probabilistic definition of beta diversity (β_P)

Suppose we take n samples containing S_{tot} number of species. Let the i-th species be represented in n_i of the n possible samples. Thus the i-th species is represented in the fraction n_i/n of the samples. The average fraction over all the species is the probability that a randomly chosen species is represented in a randomly chosen sample (P_R):

$$P_R = (n_1/n + \ldots + n_{Stot}/n)/S_{tot} \quad (1)$$

A possible measure of the beta diversity (β_P) is the probability that a randomly chosen species is *not* represented in a randomly chosen sample:

$$\beta_P = 1 - P_R = 1 - [(n_1/n + \ldots + n_{Stot}/n)/S_{tot}] \quad (2)$$

For n samples the maximum probability occurs when each species is represented in only one sample:

$$\beta_{P\max} = 1 - 1/n \quad (3)$$

This maximum value will be approximately 1 for large sample sizes.

Whittaker's beta diversity was first formulated as:

$$\beta_W = (S_{tot} - S_\alpha)/S_\alpha \quad (4)$$

where $S_\alpha = (S_1 + \ldots + S_n)/n$ is the average number of species in the n samples. However, this expression can be written in the alternative form (Routledge, 1977):

$$\beta_w = (n/\overline{m}) - 1 \quad (5)$$

which may be rewritten as:

$$\beta_w = (n - \overline{m})/\overline{m} \quad (6)$$

where $\overline{m}$ is the average number of samples in which a species is found, i.e. $\overline{m} = (\Sigma_i\, m_i)/S_{tot}$, with m_i = the number of samples in which species i is found.

The probabilistic measure of the beta diversity (2) may therefore be expressed as:

$$\beta_P = 1 - (n_1/n + \ldots + n_{Stot}/n)/S_{tot} = 1 - [(n_1 + \ldots + n_{Stot})/S_{tot}]/n$$

Since $(n_1 + \ldots + n_{Stot})/S_{tot} = (\Sigma_i\, m_i)/S_{tot} = \overline{m}$ we obtain

$$\beta_P = 1 - (\overline{m}/n) \quad (7)$$

which may be transformed to

$$\beta_P = (n - \overline{m})/n \quad (8)$$

We thus see that the analytical relationship between the Whittaker (6) and Probability (8) beta diversity indices is:

$$\beta_P = \beta_w/(1 + \beta_w) \quad (9)$$

which is recognized as an ordinary Michaelis-Menten relationship.

From the expressions (5) and (7) it is seen that the two indices behave quite differently when the number of rare species increases (i.e. when $\overline{m}$ decreases): Whittaker's index will increase hyperbolically to its upper limit of infinity, while the Probabilistic index will increase along a straight line to its upper limit of 1 (Fig. 1). Our suggested index is thus seen to be far less sensitive to the fraction of rare species.

2.2. The BIODIVADR data base

The BIODIVADR data base on the soft bottom benthic assemblages of the North-western Adriatic Sea is described in Abbiati et al. (2007). An area of about 2400 square kilometers off the east coast of Italy

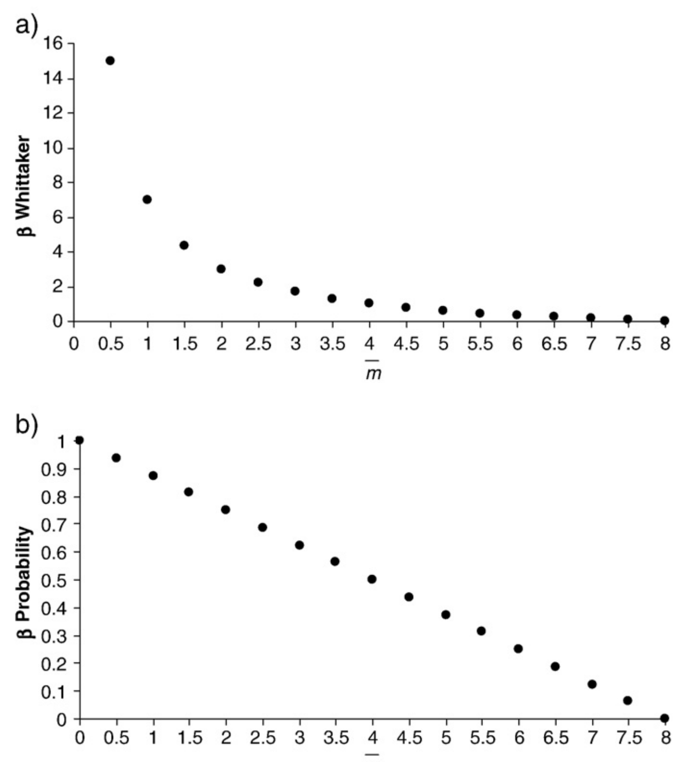

Fig. 1. Theoretical trend of a) Whittaker beta diversity index and b) Probability beta diversity index as a function of the average number of samples in which a species is found ($\overline{m}$).