Individual-based multiple-unit dissimilarity: novel indices for assessing temporal variability in community composition

Running title: Individual-based multiple-unit dissimilarity

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Abstract

1. Beta-diversity was originally defined spatially, i.e., as variation in community composition among sites in a region. However, the concept of beta-diversity has since been expanded to temporal contexts. This is referred to as “temporal beta-diversity”, and most approaches are simply an extension of spatial beta-diversity.

2. The persistence and turnover of individuals over time is a unique feature of temporal beta-diversity. Nakadai (2020) introduced the “individual-based beta-diversity” concept, and provided novel indices to evaluate individual turnover and compositional shift by comparing individual turnover between two periods at a given site. However, the proposed individual-based indices are applicable only to pairwise dissimilarity, not to multiple-temporal (or more generally, multiple-unit) dissimilarity.

3. Here, individual-based beta-diversity indices are extended to multiple-unit cases.

4. To demonstrate the usage the properties of these indices compared to average pairwise measures, I applied them to a dataset for a permanent 50-ha forest dynamics plot on Barro Colorado Island in Panama.

5. Information regarding “individuals” is generally missing from community ecology and biodiversity studies of temporal dynamics. In this context, the method proposed here is expected to be useful for addressing a wide range of research questions regarding temporal changes in biodiversity, especially studies using individual-tracked forest monitoring data.

Introduction

The concept of beta-diversity was introduced by Whittaker (1960, 1972) to define the variation in community composition among sites in a region. Several other beta-diversity indices have subsequently been proposed (reviewed by Koleff et al., 2003, Anderson et al., 2011, Jost et al., 2011, Legendre & De Cáceres, 2013). Recent studies have focused on temporal changes in community composition at both single sites and multiple sites surveyed repeatedly over time (Magurran 2011, Legendre & Condit, 2019). Temporal changes in community composition are referred to as "temporal beta-diversity" (Hatosy et al., 2013, Legendre & Gauthier, 2014, Shimadzu et al., 2015), which is simply an extension of spatial beta-diversity. Only a few studies have focused on methodological developments of temporal beta-diversity (Shimadzu et al., 2015, Legendre, 2019, Nakadai, 2020). The persistence and turnover of individuals over time is a key feature of temporal beta-diversity (Magurran et al., 2019, Nakadai, 2020). The speed and frequency of compositional change over time is associated with the speed of individual turnover, and must be considered in community comparisons because even randomly high individual turnover can result in high temporal beta-diversity (Nakadai, 2020). To address this, Nakadai (2020) proposed the "individual-based beta-diversity" concept, and provided novel indices to evaluate individual turnover and compositional shift by comparing individual turnover between two periods at a given site.

Diserud and Ødegaard (2007) first proposed a multiple-site (or more generally, a multiple-unit) similarity measure, which has conceptual and methodological advantages over conventional approaches, which calculate average pairwise similarities (Koleff & Gaston, 2002; Gaston et al., 2007, Baselga et al., 2007). Average pairwise dissimilarity indices generally cannot take into account components shared among more than three units (i.e., sites or temporal units) (Baselga et al., 2007). Many dissimilarity indices have been extended to multiple-unit indices (Baselga, 2013, 2017).

The pairwise indices proposed by Nakadai (2020) are limited by the typical problems associated with the application of multiple-unit datasets; in particular, the presence of long-lived individuals resulted in underestimates of individual turnover when the average values of the pairwise indices were used. Extending individual-based indices to multiple-temporal datasets may allow accurate assessment of the temporal variability of community composition based on individual turnover. Therefore, the purpose of this paper was to develop new multiple-unit indices that can quantify compositional variability across time according to the speed of individual turnover. I extended individual-based beta-diversity indices to multiple units after briefly reviewing the history of pairwise and multiple-unit indices. Then, I applied these indices to data from a 50-h forest dynamics plot on Barro Colorado Island (BCI) in Panama (Condit et al., 2019), as a case study to demonstrate the usage and properties of indices compared to average pairwise measures.

Materials and methods

Conventional incidence-based and abundance-based indices and novel individual-based indices

Two types of dissimilarity indices have been proposed in previous studies: incidence-based and abundance-based dissimilarity indices (Baselga et al., 2013, Nakadai, 2020). Specifically, the widely used Bray–Curtis dissimilarity index (Bray & Curtis, 1957, which was originally proposed as a proportional difference index by Odum (1950), is an abundance-based extension of the Sørensen index (Legendre & Legendre, 1998, Baselga et al., 2013). Conventional beta-diversity indices are based on intersection (*A*, *a*) and relative complement (*B*, *b* and *C*, *c*) components. For example, the Sørensen dissimilarity index (d_{sor}; Sørensen, 1948) is formulated as follows:

$$d_{sor} = \frac{b+c}{2a+b+c} \qquad \text{equation 1}$$

where a is the number of species common to both sites, b is the number of species that occur at the first but not the second site, and c is the number of species that occur at the second but not the first site. Similarity, the Bray–Curtis dissimilarity index (Bray & Curtis, 1957) is formulated as follows:

$$d_{bc} = \frac{B+C}{2A+B+C}. \qquad \text{equation 2}$$

The abundance-based components are as follows:

$$A = \sum_i \min\,(x_{ij}, x_{ik}) \qquad \text{equation 3a}$$

$$B = \sum_i x_{ij} - \min\,(x_{ij}, x_{ik}) \qquad \text{equation 3b}$$

$$C = \sum_i x_{ik} - \min\,(x_{ij}, x_{ik}) \qquad \text{equation 3c}$$

where x_{ij} is the abundance of species i at site j, and x_{ik} is the abundance of species i at site k. Therefore, A is the number of individuals of each species at both sites j and k, whereas B and C are the numbers of individuals unique to sites j and k, respectively.

In Nakadai (2020), I developed an individual-based temporal beta-diversity approach for the Bray–Curtis dissimilarity index (i.e., an abundance-based temporal beta-diversity index). Over time, some individuals replace others, so ecological communities are always dynamic and vary by at least some degree in space and time (Mori et al., 2018). In addition, some individuals of long-lived species (e.g., trees and vertebrates) persist over the long term, whereas individuals of short-lived species are replaced by conspecifics or different species (Nakadai, 2020). Therefore, it should be possible to distinguish the community dynamics component of persistence (P) from those that change over time, i.e., mortality and recruitment (M and R, respectively). M refers to individuals occurring at time 1 (abbreviated T1) that die before time 2 (abbreviated T2), thereby representing the death of individuals during the time

between T1 and T2. *R* identifies individuals that were not alive at T1 but were subsequently found at T2, thereby representing *R* during the period between T1 and T2. Component *P* refers to the persistence of individuals from T1 to T2. Although *P*, *M*, and *R* relate to components *A*, *B*, and *C*, respectively, here I have used different characters to emphasize the processes represented by each component. The respective abundances were calculated as follows:

$$P = \sum_o \min\,(z_{o1}, z_{o2}) \qquad \text{equation 4a}$$

$$M = \sum_o z_{o1} - \min\,(z_{o1}, z_{o2}) \qquad \text{equation 4b}$$

$$R = \sum_o z_{o2} - \min\,(z_{o1}, z_{o2}) \qquad \text{equation 4c}$$

where z_{l1} is individual *o* at time T1, and z_{o2} is individual *o* at time T2. Both z_{o1} and z_{o2} take a value only of 1 or 0 (presence and absence, respectively). Therefore, *P* is the number of individuals present at both T1 and T2, whereas *M* and *R* are the numbers of individuals unique to T1 and T2, respectively (Nakadai 2020). This formulation of the individual-based temporal beta-diversity index for Bray–Curtis (d_{MR}) dissimilarity can be expressed as follows:

$$d_{MR} = \frac{M+R}{2P+M+R} \qquad \text{equation 5}$$

In some cases, there is turnover of different individuals belonging to the same species even when the community composition is stable over time, which contributes to a dynamic compositional equilibrium across time periods. Therefore, the components that change over time (*M* and *R*) are separated into two further components: compositional equilibrium (*E*) and shift (*B* and *C*), respectively (Nakadai 2020). Component *M* can be partitioned into lost individuals that contribute to compositional change in a community (*B*) and lost individuals replaced by

conspecifics, contributing substantially to equilibrium in community composition (E_{loss}). Similarly, component R can be partitioned into gained individuals that contribute to compositional change in a community (C) and gained individuals replacing conspecifics, thereby contributing substantially to equilibrium in community composition (E_{gain}). By definition, the numbers of E_{loss} and E_{gain} individuals are identical; hence, I replaced both E_{loss} and E_{gain} with the coefficient E, i.e., the component that contributes to dynamic compositional equilibrium (Nakadai 2020). Furthermore, components M and R can also be analyzed in the same manner as community data (Nakadai, 2020). Therefore, the Bray–Curtis dissimilarity between communities can be calculated based on M and R as follows:

$$v_s = \frac{B+C}{2E+B+C} = \frac{B+C}{M+R}. \qquad \text{equation 6}$$

where v_s indicates the speed of compositional shifts in a community relative to the total speed of individual turnover associated with M and R. If v_s is 0, then individual turnover would not contribute to compositional shifts in a community; i.e., M and R are identical, and an equilibrium state exists. If v_s is 1, all individual turnovers contribute to compositional shifts, and M and R are completely different. It is also possible to calculate v_s as d_{BC}/d_{MR}, as follows:

$$\frac{d_{BC}}{d_{MR}} = \frac{B+C}{2A+B+C} \div \frac{M+R}{2P+M+R} = \frac{B+C}{2(P+E)+B+C} \div \frac{M+R}{2P+M+R} = \frac{B+C}{2P+M+R} \div \frac{M+R}{2P+M+R} = \frac{B+C}{2E+B+C} = v_s \qquad \text{equation 7}$$

Conventional multiple-unit beta-diversity indices

Multiple-site dissimilarity indices were first proposed by Diserud and Ødegaard

(2007), and make it possible to consider species information shared among more than three units using the inclusion–exclusion principle (Erickson, 1996). Since then, various multiple-unit beta-diversity indices have been proposed (Baselga et al., 2007, Baselga, 2013), including several new multiple-unit indices based on pairwise dissimilarity indices (Baselga et al., 2007, Baselga, 2010, 2012, 2017). Specifically, these multiple-unit dissimilarity indices share the *A* (*a*), *B* (*b*), and *C* (*c*) components of indices based on abundance (incidence). a_{mu}, b_{mu}, and c_{mu} correspond to *a*, *b*, and *c*, respectively, of incidence-based pairwise dissimilarity indices. These components are as follows:

$$a_{mu} = \sum_j S_j - S_{\mathrm{T}} \qquad \text{equation 8a}$$

$$b_{mu} = \sum_{j<k} \min\left(p_{jk}, p_{kj}\right) \qquad \text{equation 8b}$$

$$c_{mu} = \sum_{j<k} \max\left(p_{jk}, p_{kj}\right) \qquad \text{equation 8c}$$

where S_j is the total number of species at site *j*, S_T is the total number of species at all sites considered together, and p_{jk} and p_{kj} are the numbers of species exclusive to units *j* and *k*, respectively, when compared pairwise (Baselga, 2010). Specifically, p_{jk} is the number of individuals included in unit *j* but not in unit k, and *vice versa*.

A_{mu}, B_{mu}, and C_{mu} correspond to *A*, *B*, and *C*, respectively, from abundance-based pairwise dissimilarity indices:

$$A_{mu} = T_{A\mathrm{B}} - \sum_i^S \max\left(x_{ij}, x_{ik}, x_{il}, x_{im}, x_{in} \ldots\right) \qquad \text{equation 9a}$$

$$B_{mu} = \sum_{j<k} \min\left(\sum_i^S\left[x_{ij} - \min\left(x_{ij}, x_{ik}\right)\right], \sum_i^S\left[x_{ik} - \min\left(x_{ij}, x_{ik}\right)\right]\right)$$

equation 9b

$$C_{mu} = \sum_{j<k} \max\left(\sum_i^S\left[x_{ij} - \min\left(x_{ij}, x_{ik}\right)\right], \sum_i^S\left[x_{ik} - \min\left(x_{ij}, x_{ik}\right)\right]\right)$$

equation 9c.

where T_{AB} is the total abundance in the data set (details see Baselga, 2017).

Multiple-unit indices for Sørensen and Bray–Curtis are formulated as follows (Baselga, 2010, 2013),

$$d_{sor.mu} = \frac{b_{mu}+c_{mu}}{2a_{mu}+b_{mu}+c_{mu}} \qquad \text{equation 10}$$

$$d_{BC.mu} = \frac{B_{mu}+C_{mu}}{2A_{mu}+B_{mu}+C_{mu}}. \qquad \text{equation 11}$$

Novel individual-based multiple-unit beta-diversity indices

In this study, I developed individual-based components and novel indices for multiple-unit data sets, as follows:

$$P_{mu} = \sum_j I_j - I_{\mathrm{T}} \qquad \text{equation 12a}$$

$$M_{mu} = \sum_{j<k} \min\left(q_{jk}, q_{kj}\right) \qquad \text{equation 12b}$$

$$R_{mu} = \sum_{j<k} \max\left(q_{jk}, q_{kj}\right). \qquad \text{equation 12c}$$

where I_j is the total number of individuals in a unit j, I_T is the total number of individuals in all units considered together, and q_{jk} and q_{kj} are the numbers of individuals exclusive to units j and k, respectively, when compared pairwise.

The multiple-unit individual-based index is formulated as follows:

$$d_{MR.mu} = \frac{M_{mu}+R_{mu}}{2P_{mu}+M_{mu}+R_{mu}}. \qquad \text{equation 13}$$

Furthermore, as an extension of equation 9, I also introduced $v_{\mathrm{s.mu}}$, which indicates the compositional variability in a community relative to the individual turnover, as follows:

$$v_{s.mu} = d_{BC.mu}/d_{MR.mu}. \qquad \text{equation 14}$$

Case study: the permanent 50-ha forest dynamics plot on BCI in Panama

To demonstrate the use of the new individual-based multiple-unit indices, I analyzed the data from Condit et al. (2019). The permanent 50-ha forest dynamics project plot on BCI in Panama was established in 1981 by Robin Foster and Stephen Hubbell (Hubbell & Foster, 1983). Data from this plot have been used in many scientific papers, and descriptions of the area and survey methods are widely available (e.g., Legendre & Condit, 2019). Some statistics about the plot are provided in Table 1. This 50-ha plot has been subjected to eight detailed surveys since its inception: in 1982, 1985, 1990, 1995, 2000, 2005, 2010, and 2015. The BCI data were divided into 1,250 quadrats (20 m × 20 m). Harms et al. (2001) classified quadrats into six habitat zones and one mixed zone (Table S1).

First, I calculated both the average values of individual-based beta-diversity indices (d_{MR}, v_s) and newly developed multiple-unit indices ($d_{MR.mu}$, $v_{s.mu}$), and tested the relationships using simple linear regression. Second, because high turnover can result in high compositional variability within a community, I tested the relationship between newly developed multiple-unit indices ($d_{MR.mu}$) and two previous ones ($d_{BC.mu}$, $d_{sor.mu}$). Finally, I analyzed the difference in composition variability ($v_{s.mu}$) using the Wilcoxon rank sum test, which allows for pairwise comparisons between groups with correction for multiple testing. The p-values were adjusted by the Holm method. All analyses were conducted in R software (ver. 4.0.3; R Development Core Team, 2020). The *betapart* R package (Baselga & Orme, 2012) was used to calculate multiple-unit versions of the Bray–Curtis and Sørensen dissimilarity indices, and the function *pairwise.wilcox.test* was used to compare the differences among habitats.

Results

Simple linear regression showed a significant correlation between d_{MR} and $d_{MR.mu}$

(*adjusted-*R^2 = 0.971, $p < 0.0001$; Fig. 1a). A significant correlation between v_s and $v_{s.mu}$ (*adjusted-*R^2 = 0.899, $p < 0.0001$; Fig. 1b) was also found. Both multiple-unit indices were lower than the average values of the pairwise indices at all times. $d_{BC.mu}$ and $d_{sor.mu}$ increased significantly with increasing $d_{MR.mu}$ (*adjusted-*R^2 = 0.756, $p <$ 0.0001 and *adjusted-*R^2 = 0.444, $p < 0.0001$, respectively; Fig. 2). The $v_{s.mu}$ differed considerably among habitat zones, especially group 4 (swamp), which was significantly different from all other habitats (Fig. 3, Table S2).

Discussion

Individual turnover is a major driver of compositional change and variability within a community, although it has rarely been discussed. Higher individual turnover clearly facilitates higher variability in community composition; thus, compositional variability over time can occur even when considering only ecological drift. Hubbell's unified neutral theory of biodiversity (Hubbell, 2001) postulates ecological neutrality among species within communities and emphasized the role of ecological drift in biodiversity patterns. To elucidate compositional variability, the impact of individual turnover (i.e., ecological drift) should be excluded. However, almost no methods exist to quantify the impact of individual turnover on compositional variability.

The individual-based indices introduced herein can assess compositional variability considering the contribution of individual turnover. The case study clearly demonstrated that the novel individual-based index significantly correlated with conventional incidence- and abundance-based indices (Fig. 2); however, variations among communities still exist. The $v_{s.mu}$ (= $d_{BC.mu}/d_{MR.mu}$) differed among habitat zones, especially for group 4 (swamp), which was significantly different from all other habitats (Fig. 3, Table S1). Compositional change over time in this swamp habitat has also been reported in terms of responses to a drought event at the BCI plot (Legendre and Condit 2019). The present results indicated significant compositional variability in

the swamp even after controlling for individual turnover.

Although temporal beta-diversity has attracted attention (Magurran, 2011, Magurran et al., 2019), it is simply an extension of spatial beta-diversity. Both methodological and conceptual frameworks rooted in community dynamics should be used. Above all, information from "individuals" has been absent from studies of temporal dynamics in community ecology and biodiversity. In this context, the method proposed here is expected to be useful for addressing a wide range of research questions related to temporal changes in biodiversity, especially studies using individual-tracked forest monitoring data. For example, tree censuses using identity tags for individuals (Condit, 1998) have been conducted globally, and data are now available for many forest plots across the world, for example from the Forest Global Earth Observatory database (https://forestgeo.si.edu/explore-data) (Legendre & Condit et al., 2019). It is expected that new methods for analyzing temporal variation in biodiversity will continue to be developed, including null models that assume the replacement of individuals.

Author contribution

R.N. conceived the study, designed the methods described herein, analyzed the empirical data, and wrote the manuscript.

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Data Availability

Data are available from the Dryad Digital Repository (https://doi.org/10.15146/5xcp-0d46; accessed on 10th of April in 2020) (Condit et al.,

2019).

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Legends

Figure 1 Correlations between novel multiple-unit indices and the average values of conventional pairwise indices (d_{MR}-$d_{MR.mu}$; *adjusted*-R^2 = 0.971, $p < 0.0001$, v_s-$v_{s.mu}$; *adjusted*-R^2 = 0.899, $p < 0.0001$)

Figure 2 Correlations between a novel individual-based multiple-unit index ($d_{MR.mu}$) and conventional multiple-unit indices ($d_{BC.mu}$-$d_{MR.mu}$; *adjusted*-R^2 = 0.756, $p < 0.0001$, $d_{sor.mu}$-$d_{MR.mu}$; *adjusted*-R^2 = 0.444, $p < 0.0001$).

Figure 3 Comparison of the composition variability ($v_{s.mu}$) among habitat zones using the Wilcoxon rank sum test, which allows for pairwise comparisons between groups with correction for multiple testing. The same letters indicate the same group based on the p-values, which were adjusted by the Holm method. Detailed information on the habitat zones is shown in Table S1.

Figure 1

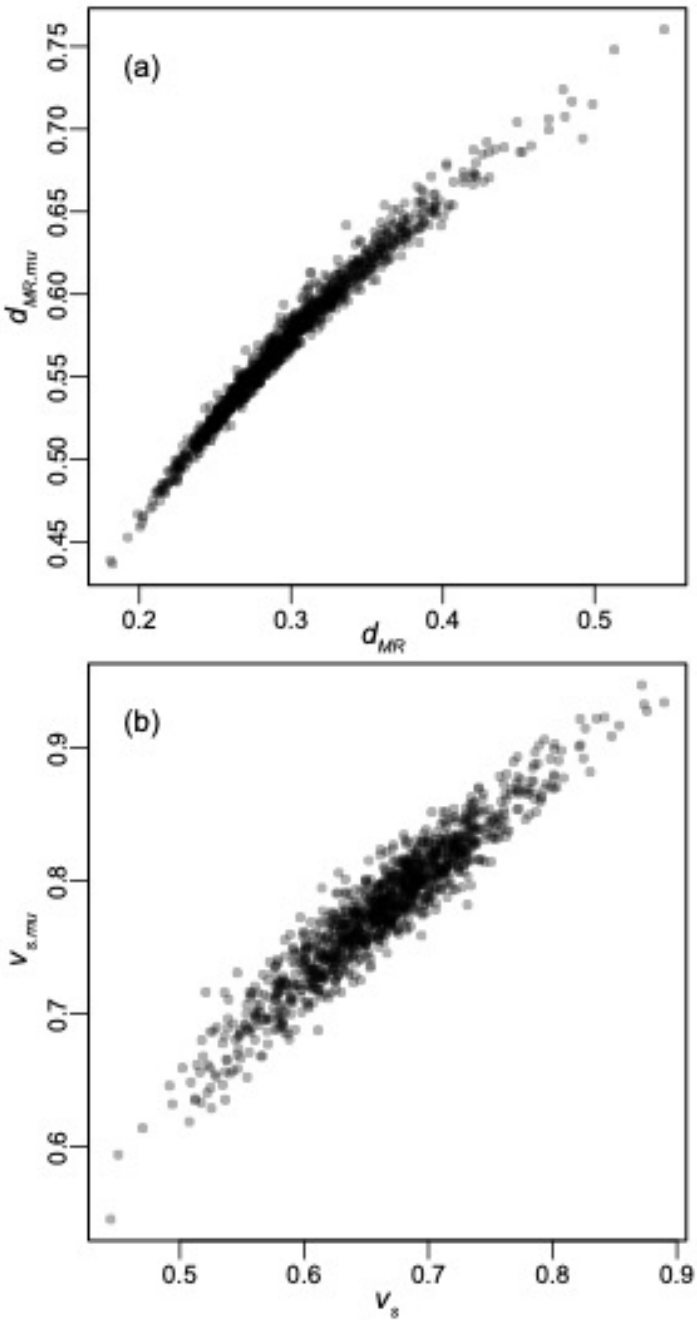

(a)
0.45
0.50
0.55
0.60
0.65
0.70
0.75
$d_{MR,mu}$
0.2
0.3
0.4
0.5
d_{MR}
(b)
0.6
0.7
0.8
0.9
$v_{s,mu}$
0.5
0.6
0.7
0.8
0.9
v_s

Figure 2

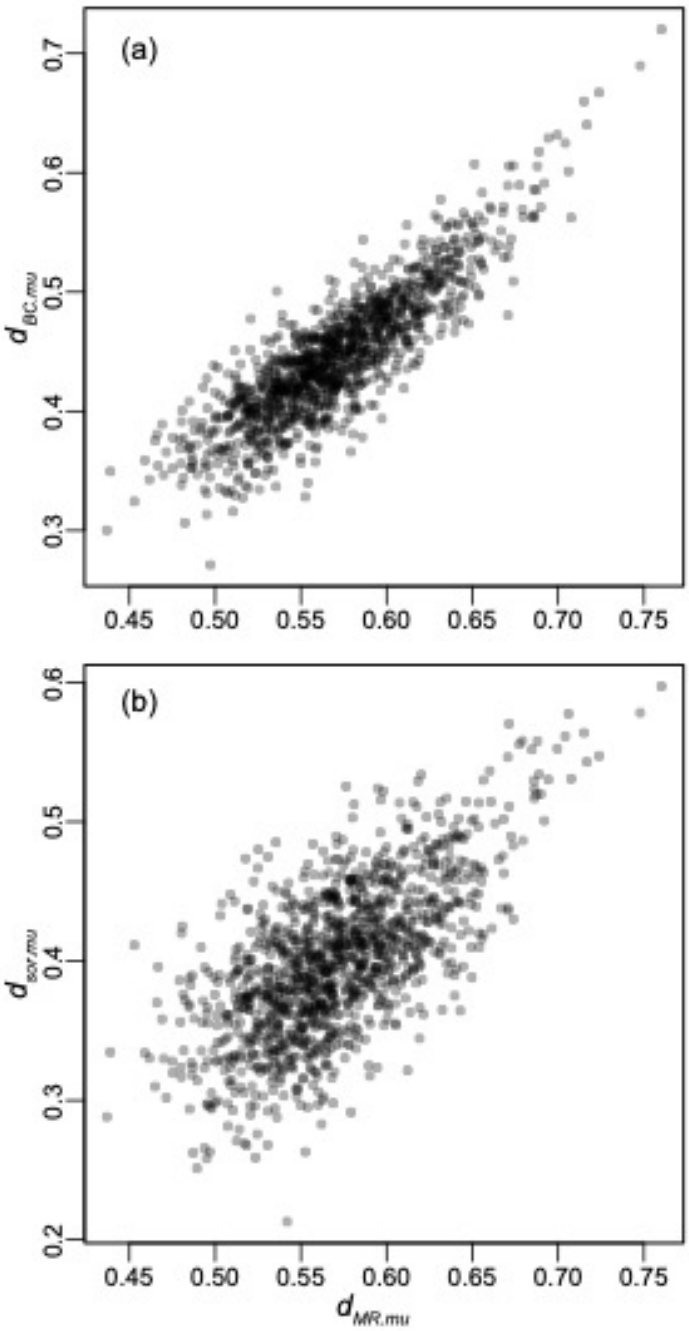
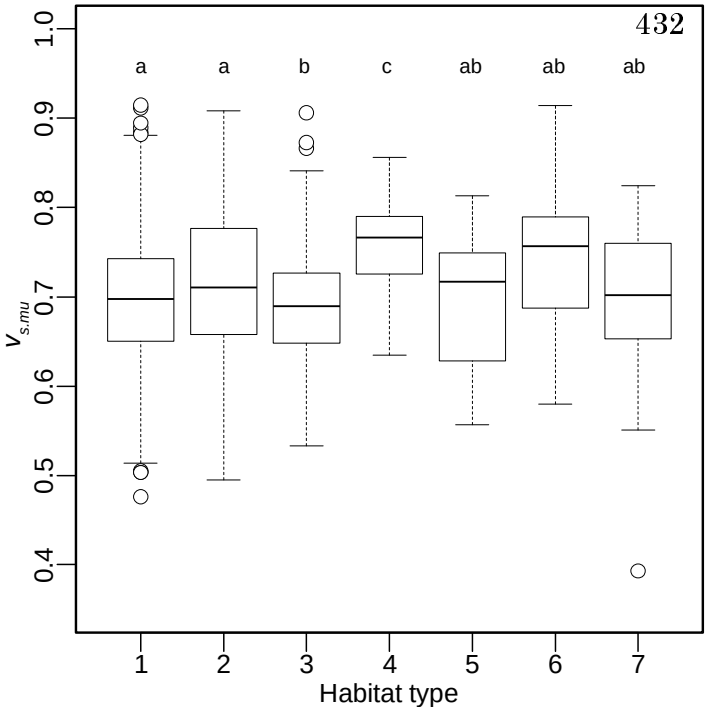

(a)
$d_{BC.mu}$
0.3
0.4
0.5
0.6
0.7
0.45
0.50
0.55
0.60
0.65
0.70
0.75
(b)
$d_{SOY.mu}$
0.2
0.3
0.4
0.5
0.6
0.45
0.50
0.55
0.60
0.65
0.70
0.75
$d_{MR.mu}$

Figure 3

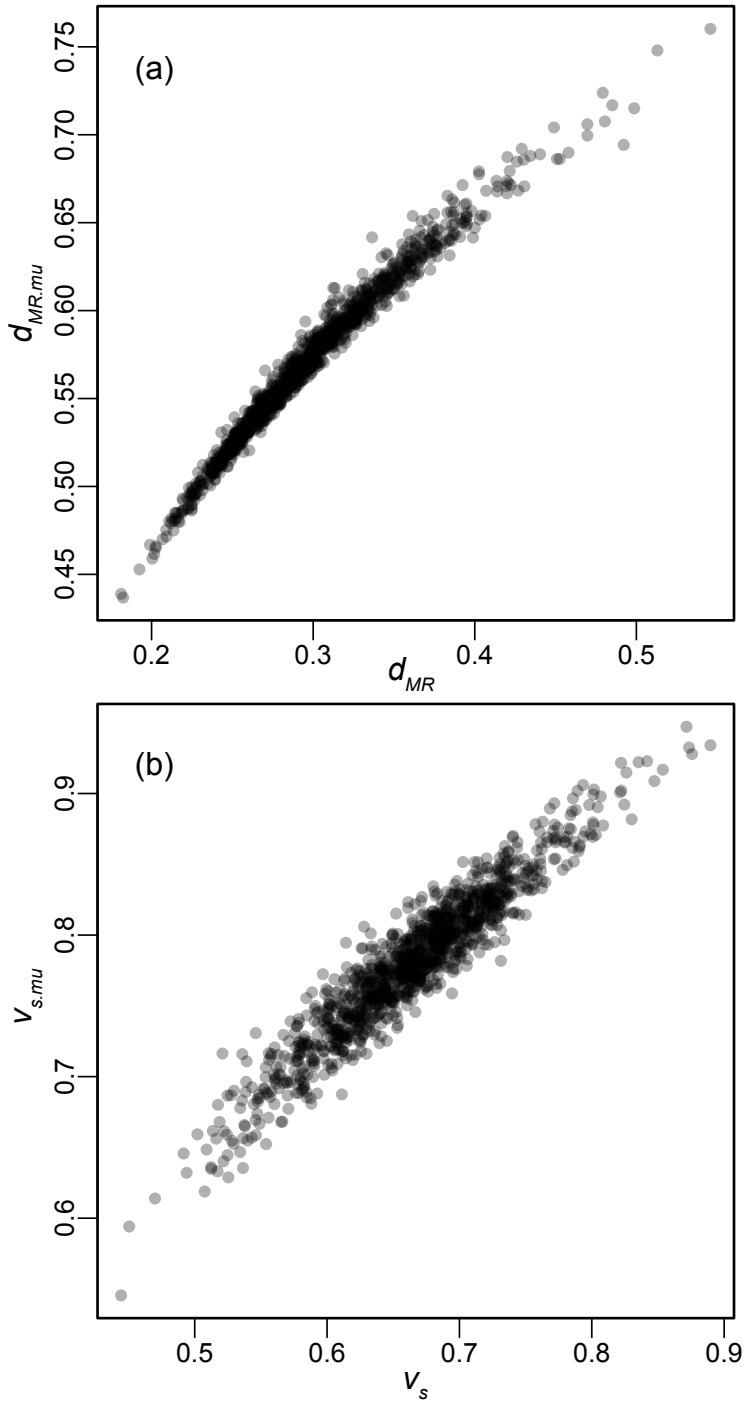


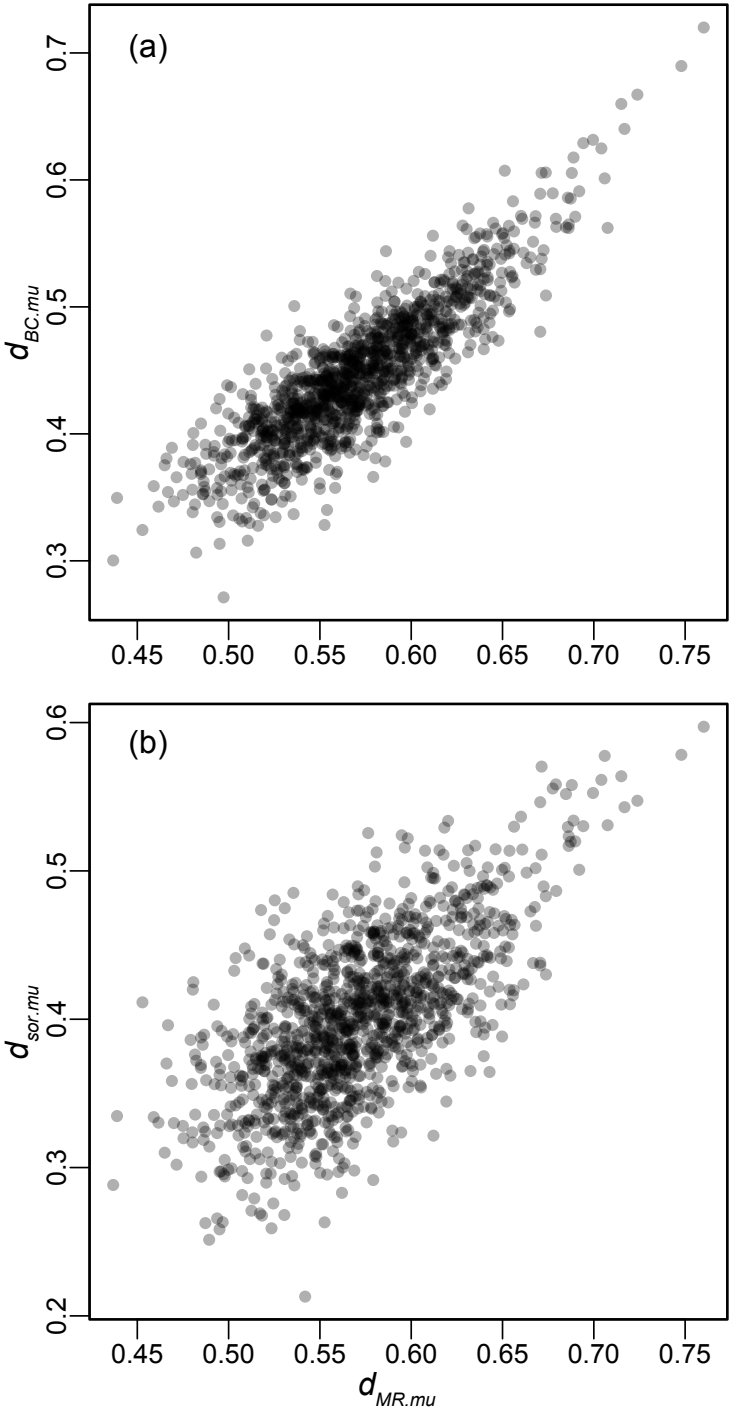
Appendices

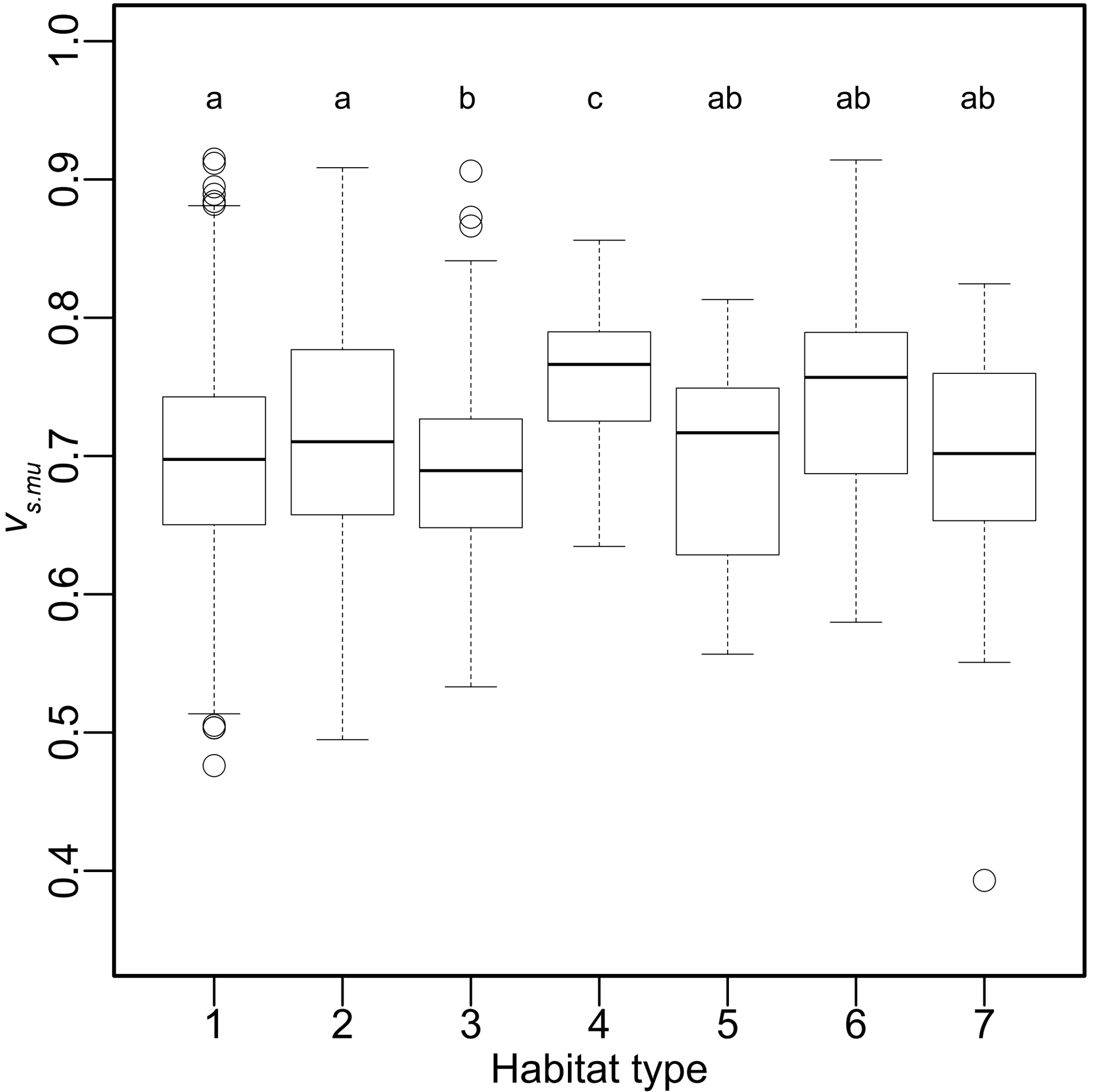
Table S1 Habitat clarification in Harms et al. (2001). Group 1: old forest, low plateau; group 2: old forest, high plateau; group 3: old forest, slope; group 4: old forest, swamp; group 5: old forest, streamside; group 6: young forest; and group 7: mixed habitats.

Table S2 Results of the pairwise Wilcoxon rank sum test. The p-values were adjusted by the Holm method.

Supplementary File 1 R script for the individual-based multiple-unit beta-diversity calculations performed using sample data.


(a)
0.75
0.70
0.65
0.60
0.55
0.50
0.45
$d_{MR.mu}$
0.2
0.3
0.4
0.5
d_{MR}
(b)
0.9
0.8
0.7
0.6
$v_{s.mu}$
0.5
0.6
0.7
0.8
0.9
v_s


(a)
$d_{BC.mu}$
0.3
0.4
0.5
0.6
0.7
0.45
0.50
0.55
0.60
0.65
0.70
0.75
(b)
$d_{sor.mu}$
0.2
0.3
0.4
0.5
0.6
0.45
0.50
0.55
0.60
0.65
0.70
0.75
$d_{MR.mu}$


a
a
b
c
ab
ab
ab
1.0
0.9
0.8
0.7
0.6
0.5
0.4
$V_{s.mu}$
1
2
3
4
5
6
7
Habitat type