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Do commonly used indices of β -diversity measure species turnover?

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Abstract. Indices of β -diversity are of two major types, (1) those that measure among-plot variability in species composition independently of the position of individual plots on spatial or environmental gradients, and (2) those that measure the extent of change in species composition along predefined gradients, i.e. species turnover. Failure to recognize this distinction can lead to the inappropriate use of some β -diversity indices to measure species turnover.

Several commonly-used indices of β -diversity are based on Whittaker's β_w ($\beta_w = \gamma/\alpha$, where γ is the number of species in an entire study area and α is the number of species per plot within the study area). It is demonstrated that these indices do not take into account the distribution of species on spatial or environmental gradients, and should therefore not be used to measure species turnover. The terms ' β -diversity' and 'species turnover' should not be used interchangeably. Species turnover can be measured using matrices of compositional similarity and physical or environmental distances among pairs of study plots. The use of indices of β -diversity and similarity-distance curves is demonstrated using simulated data sets.

Keywords: Alpha diversity; Beta diversity; Dissimilarity index; Gamma diversity; Whittaker.

Introduction

The related concepts of ' β -diversity' and 'species turnover', often used interchangeably in the ecological literature (e.g. Harrison et al. 1992; Harrison 1993; Blackburn & Gaston 1996), require clarification. Both concepts are associated with the description and quantification of differences in species composition among localities, and therefore have potential applications in a wide range of studies concerning species diversity and distribution. Are the two concepts really interchangeable?

β -diversity is defined mathematically by a variety of indices, most of which express the relationship between the total number of species in a set of study plots (γ -diversity) and the average number of species in individual plots (α -diversity). Species turnover is defined as the rate or magnitude of change in species composition

along predefined spatial or environmental gradients. It is important to reiterate that the concept of species turnover implies that there is some sort of structure (e.g. spatial structure) to among-plot variation in species composition. Species turnover through time differs from species turnover in space in being unidirectional, and is not considered here.

I address whether commonly-used indices of β -diversity for presence-absence data accurately reflect the concept of species turnover. In addressing this question, the origin and use of indices of β -diversity for presence-absence data are critically reviewed, focussing on logical interpretations that follow from the index equations. This issue is critical to address before attempts are made to draw comparisons among studies that employ different measures of β -diversity (Gaston & Williams 1996). Following this review, β -diversity and species turnover are evaluated for simple simulated data sets, and recommendations are made for the use of the two terms and for the measurement of species turnover along one or more gradients using presence-absence data.

Measures of β -diversity: a review

The total species richness in a region, often termed γ -diversity, may be partitioned into two components: α -diversity, which is the number of species per locality, and β -diversity, which is the variation in species composition among localities (Whittaker 1972). In theory, β -diversity is measured among different 'communities' (Whittaker 1972) or 'habitats' (Schluter & Ricklefs 1993). In practice, because communities and habitats are most often impossible to delineate, β -diversity is measured among study plots (localities) of some arbitrary size. The area of individual plots may be as small as a few square meters (e.g. Økland et al. 1990) and as large as hundreds of square kilometers (e.g. Blackburn & Gaston 1996).

To describe the calculation of several indices of β -diversity, a data set will be assumed where the presence or absence of species s_1 to s_j is recorded in n study plots, p_1 to p_n . The number of species in plot i is α_i , and the number of plots where species j is present (its fre-

quency) is f_j . The average number of species per plot is α and the average number of plots where a species is found (the average frequency of species) is f .

Whittaker's β_W

A commonly-used measure of β -diversity data was introduced by Whittaker (1960), and is calculated as:

$$\beta_W = \gamma / \alpha \quad (1)$$

To yield a quantity that is interpretable as the number of "full changes in, or turnover of, species composition", an alternative calculation is $\beta_W = \gamma / \alpha - 1$ (Whittaker 1972). While this calculation has been used as the basis for modifications of β_W (Wilson & Shmida 1984; Harrison et al. 1992; see below), I will consider only the original calculation; my criticism applies to both.

By simple algebra, it can be shown that equivalent values of β_W result from dividing the total number of study plots by the average frequency of species: $\beta_W = n/f$. Since the quantity f/n expresses the average proportion of plots where a species is found, β_W reflects only the inverse of the average frequency of species, as has been noted previously (Routledge 1977; Schluter & Ricklefs 1993). Because β_W is independent of any spatial or environmental structure in species distributions, it does not reflect the concept of species turnover. As α and γ are measured at two different spatial scales, β_W is nonetheless scale-dependent (i.e. sampling more smaller plots should increase β_W). However, the important point is that β_W takes no account of plot position along gradients.

Modifications of β_W

There are several indices of β -diversity that were created to improve on β_W . Wilson & Shmida (1984) reviewed the measurement of β -diversity using presence-absence data, testing six different indices against four criteria: conformity with the notion of turnover, additivity between segments of a gradient, independence from α -diversity, and independence from excessive sample size. Three measures proposed by Routledge (1977), and one proposed by Cody (1975) were rejected, and two measures were recommended: β_W , and a new index named beta-turnover, or β_T (Wilson & Shmida 1984). In the following consideration, Wilson & Shmida's (1984) review is used as a starting point, and only β_T out of the six measures that they evaluated is considered (β_W has already been treated here). Two additional indices of β -diversity were introduced by Harrison et al. (1992), one of which (β_{H1}) was designed to correct for sample size, the other (β_{H2}) to correct for directional trends in α -diversity along gradients. For β_T , β_{H1} , and β_{H2} , many examples can be found in the recent

literature (e.g. Shmida & Wilson 1985; Cowling et al. 1989; Willig & Sandlin 1992; Harrison 1993; Blackburn & Gaston 1996; Oliver et al. 1998; Young et al. 1998; Pharo et al. 1999), and I will focus on these three in my consideration of modifications of β_W .

Beta turnover, β_T

The measure β_T is meant to reflect species turnover by calculating the gain and loss of species along a gradient (Cody 1975), standardized by the average number of species in each plot, α . On the surface, it appears that β_T is calculated in a very different way than β_W :

$$\beta_T = [g(H) + l(H)] / 2\alpha \quad (2)$$

where $g(H)$ and $l(H)$ are the numbers of species gained and lost, respectively, along a (habitat) gradient. If it is assumed that there is one study plot at each of n points along a gradient, then plot p_1 would be at one end of the gradient and plot p_n at the other end, and the number of species gained and lost between plot p_1 and plot p_n would be calculated as follows (Wilson & Shmida 1984; Shmida & Wilson 1985):

$$\begin{aligned} g(H) &= \gamma - \alpha_1 \\ l(H) &= \gamma - \alpha_n \end{aligned}$$

Therefore,

$$\beta_T = [2\gamma - \alpha_1 - \alpha_n] / 2\alpha = \gamma / \alpha - (\alpha_1 + \alpha_n) / 2\alpha \quad (3)$$

On the condition that the number of species in each of the plots at the gradient end points (α_1 and α_n) is about equal to the average number of species per plot (α), or more specifically, if $(\alpha_1 + \alpha_n)/2 \approx \alpha$, then,

$$\beta_T \approx \gamma / \alpha - 1 \quad (4)$$

This is equivalent to the calculation of β_W proposed by Whittaker (1972). So, if the above condition holds, $\beta_T \approx \beta_W$. To the degree that the above condition does not hold, β_T will differ from β_W , though any differences are trivial with respect to measuring species turnover. As expected, the correlation between β_W and β_T is usually close to one (Wilson & Shmida 1984; Blackburn & Gaston 1996). Therefore, β_W and β_T measure the same thing, and there is no reason to use β_T in place of the older β_W .

Corrections for sample size and trends in α -diversity

Harrison et al. (1992) calculated Whittaker's β -diversity as $\beta_W = \gamma / \alpha - 1$; their first modification of β_W , designed to correct for sample size, was calculated as follows:

$$\beta_{H1} = [(\gamma/\alpha - 1)/(n - 1)] \times 100 \quad (5)$$

The basic quantity in β_{H1} is γ/α , just as in β_W , so it therefore suffers from the same drawbacks described above for β_W . However, even as a modification of β_W , there is an error in the logic of dividing by $n - 1$ to allow comparisons of β -diversity calculated using different sample sizes.

The logic behind correcting for sample size stems from the well-known relationship between species and area: as the area sampled (n) increases, more species (γ) will be found. Therefore, variation in γ must be standardized by variation in n to allow measurements made using different sample sizes to be compared. By simply dividing γ by n , the underlying assumptions are that γ varies linearly with n , and that the y-intercept is at zero species. However, a straight line almost never describes the relationship between untransformed values of species number and area (Williamson 1988). Most often, either area, or both area and species number, must be log-transformed prior to fitting a straight line to the data. In some cases, there is no transformation that results in a linear relationship between species number and area. So, a correction for sample size is only possible when the species-area relationship is known, and if so, the correction must involve the appropriate transformation of n , or both n and γ .

Because of its close similarity to β_W , it is not recommended that β_{H1} be used to measure species turnover. However, if the average frequency of species (f) is of interest, correcting for sample size may be appropriate because the increase in γ with increasing n is usually a result of more and more rare species being counted, thereby reducing the quantity f/n (i.e. the inverse of β_W). To correct for sample size, empirically-determined transformations based on a species-area curve could be used.

The second measure of β -diversity proposed by Harrison et al. (1992) also included the correction for sample size, with an additional modification to account for possible directional trends in α -diversity:

$$\beta_{H2} = [(\gamma/\alpha_{\max} - 1)/(n - 1)] \times 100 \quad (6)$$

where α_{\max} is the maximum value of species number observed in a single study plot. If directional trends in species number exist (e.g. with latitude), and if α is used in the equation for β -diversity, then no distinction will be made between species loss (e.g. reduction in species number from south to north) and true species turnover (the replacement of one species by another along a gradient) according to the definition of Harrison et al. (1992). The solution to this problem was to use α_{\max} in place of α . Surprisingly, even though β_{H2} was intended

to isolate 'true turnover', the modification included no account of the spatial configuration of study plots, and therefore does not reflect the concept of species turnover. Because the value of α_{\max} is derived from only a single study plot, the sampling variance for β_{H2} will be very large compared to other indices. β_{H2} is unlikely to provide meaningful information.

(Dis)similarities between pairs of plots

There are many coefficients that measure (dis)similarity in species composition between pairs of plots (Legendre & Legendre 1998), and any one of these coefficients may be used as the starting point for measuring β -diversity (Pielou 1975; Magurran 1988). An important distinction of this approach from those already described is that (dis)similarity in species composition is measured for each *pair* of plots separately, rather than for the whole set of plots simultaneously.

For a given pair of plots, the Sørensen coefficient expresses compositional similarity in a straightforward, easily interpretable way, and is calculated as follows:

$$S_s = c / \alpha \quad (7)$$

where c is the number of species shared by both plots and α is average number of species in each plot

Values of S_s range from 0, indicating no species in common, to 1, indicating that every species found in one plot is also found in the other plot. Subtracting S_s from 1 yields a coefficient of dissimilarity (e.g. Colwell & Coddington 1994; Legendre & Legendre 1998). Interestingly, when β_W is calculated for a single pair of plots, it can be shown that $\beta_W = (2 - S_s)$.

Once a matrix of similarities or dissimilarities has been calculated, a common method of quantifying β -diversity is to simply take the mean (dis)similarity between pairs of plots (e.g. Cowling et al. 1989; Rey Benayas 1995; Porembski et al. 1996; Harrison 1997). This is a reasonable measure of unstructured heterogeneity in species composition among plots. However, by using only the mean value, the spatial arrangement of plots, or their ordering along a gradient, is ignored, thereby failing to reflect the concept of species turnover.

Because (dis)similarities are measured between pairs of plots, they can easily be related to physical or environmental distances between the same pairs of plots (Nekola & White 1999), thereby allowing both visualization and quantification of how species composition changes along gradients, the essence of species turnover. To evaluate species turnover on an elevation gradient, Whittaker (1960, 1972) graphed log-transformed Sørensen similarities against the difference in elevation between pairs of plots (see also Cody 1993; Syuzo 1995; Vázquez G. & Givnish 1998; Leach & Givnish 1999;

Nekola & White 1999). Using log-transformed similarities allows interpretation of increments on the y-axis as proportional changes in shared species. By fitting a straight line to the data, Whittaker (1960, 1972) extrapolated values of log-similarity at zero elevation intervals, and at the maximum number of intervals to calculate the magnitude of species turnover as the number of times compositional similarity was reduced by half along the gradient ('half changes'):

$$\beta_{1/2} = [\log(S_{S,d=0}) - \log(S_{S,d=\max})] / \log(2) \quad (8)$$

where d refers to distance, and $S_{S,d=0}$ is the value of S_S between plots at the same elevation, and $S_{S,d=\max}$ is the value of S_S for plots at opposite ends of the gradient (Whittaker 1960). The slope of the line represents the rate of species turnover.

The above-described analysis is a specific example of the more general phenomenon that the similarity between two observations generally decreases as the distance between them increases (reviewed in Nekola & White 1999). If straight lines provide reasonable fits to similarity-distance graphs, then it is possible to test whether turnover rates are significantly different from zero, and also whether turnover rates vary among groups of species observed in the same set of study plots. Randomization procedures can be used for both types of tests. (Because similarity-distance graphs are created with $(n^2 - n)/2$ data points for a set of n study plots, the points are not independent and parametric statistics cannot be used.)

For plots defined by spatial positions in two dimensions, one potential limitation of using similarity-distance curves is the implicit assumption of isotropy (Philip Dixon pers. comm.). However, this can be overcome by creating separate matrices of Euclidean distance for each of two dimensions (e.g. north-south vs. east-west). This would allow a test of differences in turnover rate along two spatial dimensions (see next section). This technique could be extended to multiple environmental gradients, though I know of no applications of such a technique.

A test with simulated data

I created artificial data sets on a 5×5 grid of plots to simulate three scenarios: (1) Strong isotropic species turnover through space; (2) Strong anisotropic species turnover (greater along one dimension than the other); (3) No species turnover in space, but with the same α and γ as in (1). Fig. 1 illustrates the design of these simulations. For the first two data sets, 50 species with contiguous ranges of 5×3 plots were placed in random positions in or around the 5×5 grid with the one

requirement that each species be present in at least two plots in the grid. In data set 1, half of the species' ranges were oriented vertically, the other half horizontally. In data set 2, all species' ranges were oriented vertically, with the resulting expectation that species turnover would be greater along the horizontal axis than the vertical. For data set 3, the spatial position of the species' presences from data set 1 within the 5×5 grid were completely randomized.

For each data set, β_W was calculated. β_T applies only to linear gradients (and in such cases does not differ appreciably from β_W), and because the same number of plots was used in all cases, corrections for sample size (β_{H1} , β_{H2}) were unnecessary. A matrix of Euclidean distances between each pair of plots, matrices of Euclidean distance along the horizontal (x) and vertical (y) dimensions separately, and a matrix of Sørensen's similarity coefficient were also calculated for each data set. The mean value of S_S was calculated for each data set. Individual values of log-transformed S_S were plotted against the Euclidean distance between each pair of plots, and against Euclidean distances in the x and y dimensions separately; straight lines were fit to the data using linear regression. Zero values of S_S were assigned a value of 0.05 to allow the log transformation. The number of half changes ($\beta_{1/2}$) were calculated using the fitted values of S_S at $d = 4$ (the maximum distance in each dimension) as $S_{S,d=\max}$, and the fitted values for adjacent plots as $S_{S,d=0}$.

Significant differences of individual slopes from zero were tested using Mantel tests (Mantel 1967). For structured data sets, differences in slope between the x and y dimensions were tested using a randomization procedure whereby random sets of 50 species were simulated as for artificial data set (1) above. For each of 1000 iterations, the difference in regression slopes in the x and y dimensions were calculated. Comparison of the observed difference in slope to the distribution of differences in slope in the randomized data sets allowed a test of significance.

The results for the simulated data showed that β_W and mean Sørensen's similarity were essentially invariant among the three data sets, while $\beta_{1/2}$ and the similarity-distance slopes varied greatly (Table 1). For overall Euclidean distance, both of the structured data sets showed strong negative relationships with pairwise Sørensen similarities ($p < 0.001$); the random data set showed no pattern ($p > 0.7$; Fig. 1, Table 1). There was no significant difference between slopes of the similarity-distance curves in the x and y dimensions for the isotropic structured or random data sets ($p > 0.67$), but a clear and significant difference for the anisotropic structured data set ($p < 0.001$).

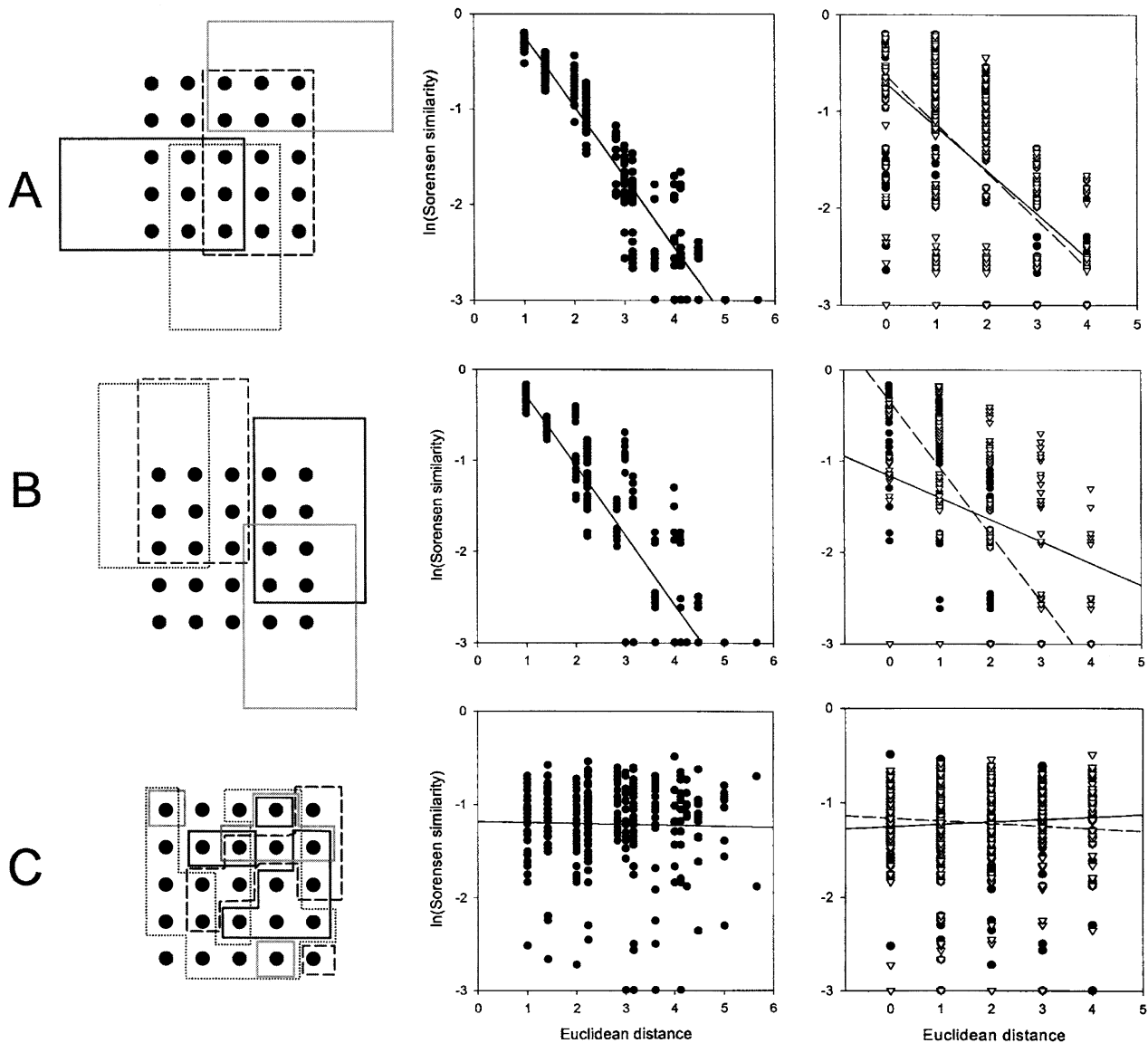


Fig. 1. Simulated data sets and resulting similarity-distance graphs. Diagrams in the left column illustrate the distribution of 4 of 50 species in each data set across an array of 5×5 study plots. **A.** Rectangular species ranges placed in random positions with the restriction that each species be present in at least two of the grid plots; half of the ranges were oriented vertically, the other half horizontally. **B.** Set up as in **A**, except that all ranges were oriented vertically. **C.** Presences of each species from **A** completely randomized. Graphs in the middle column are for Euclidean distance in two dimensions, and graphs in the right column are for Euclidean distance in the horizontal (x) dimension (filled circles, dashed line) and vertical (y) dimension (open triangles, solid line) separately.

Table 1. Measures of β -diversity and species turnover for the three simulated data sets shown in Fig. 1.

Data set	Whittaker's β -diversity (β_W)	Mean Sørensen similarity (S_S)	Total half changes ($\beta_{1/2}$)	Overall regression slope	Half changes ($\beta_{1/2}$) in the x dimension	x dimension regression slope	Half changes ($\beta_{1/2}$) in the y dimension	y dimension regression slope
Structured isotropic	3.85	0.32	3.19	-0.74	2.15	-0.50	1.95	-0.45
Structured anisotropic	3.88	0.30	3.31	-0.76	3.18	-0.73	1.04	-0.24
Random	3.85	0.32	0.04	-0.009	0.12	-0.03	-0.11	0.03

Discussion

I have demonstrated that the calculation of β_W , and therefore all of its descendants (β_T , β_{H1} , β_{H2}), is independent of the distributions of species on spatial or environmental gradients. A simple examination of the equation for β_W showed that variation in this quantity is caused only by variation in the proportion of study plots where each species is found. Simulated data sets, either with a high degree of spatial structure or with random species distributions, yielded virtually identical values of β_W (Table 1). Mean Sørensen similarity also failed to distinguish structured from unstructured heterogeneity in species composition. In contrast, similarity-distance plots showed strong negative relationships for structured data sets, and no relationship for the random data set (Fig. 1), and were also able to detect differences in species turnover along the horizontal vs. vertical dimensions (Fig. 1).

Despite that β_W and its descendants do not measure species turnover, indices of unstructured heterogeneity in species composition, such as β_W , are useful for addressing certain ecological questions. When underlying gradients are unknown, β_W can be used to test the degree to which heterogeneity in species composition varies among functional groups (e.g. herbs vs. trees), or among different regions for which gradients are difficult to compare. If measures of environmental characteristics cannot be explicitly matched with vegetation plots, β_W could also be used to test for relationships between environmental heterogeneity and compositional heterogeneity among different regions. Simple indices of β -diversity will remain useful for asking how total species diversity is partitioned within and among plots when specific gradients are not of interest (e.g. Loreau 2000).

When changes in species composition along spatial or environmental gradients are of primary interest, the use of β_W and its descendants is inappropriate. For example, Harrison (1993) was interested in “broad *spatial* patterns of diversity that might be generated by dispersal limitation” (*italics mine*), but proceeded to use indices of unstructured variation in species composition (β_{H1} and β_{H2}) as the primary means of addressing the issue. To address hypotheses regarding compositional change along gradients, measuring the rate and magnitude of species turnover using similarity-distance curves is appropriate and useful. Along altitudinal gradients, does the composition of the herb community change more rapidly than the composition of the tree community? Does the rate of species turnover differ along different gradients? Do ant-dispersed species have more compact distributions than bird-dispersed species and therefore higher turnover through

space? Such questions require explicit consideration of study-plot position in physical or environmental space.

Measures of species turnover and β -diversity are almost invariably used in a comparative context. Comparisons have been made among taxonomic groups (Harrison 1993; Pharo et al. 1999), vegetation strata (Whittaker 1960; McCune & Antos 1981), scales of observation (Økland et al. 1990; Nekola & White 1999), and biogeographic regions (Blackburn & Gaston 1996). Similarity-distance curves are attractive because they can be compared both visually and quantitatively.

An important consideration in constructing similarity-distance curves is the choice of similarity coefficient. For presence-absence data, Sørensen's coefficient of similarity is simple to calculate, and carries a straightforward interpretation. The use of Sørensen's similarity also allows calculation of $\beta_{1/2}$, which is interpretable as the number of times the proportion of shared species is reduced by half, relative to adjacent study plots. Another commonly used coefficient of similarity for presence-absence data is Jaccard's (J), which is similar to Sørensen's:

$$J = S_S / (2 - S_S) \quad (8)$$

However, J does not allow calculation of a turnover magnitude with an interpretation as straightforward as that for $\beta_{1/2}$. β_W has also been used to measure pairwise dissimilarities in species composition, though when measured for only two plots it is simply a transformation of S_S to yield a dissimilarity rather than a similarity coefficient: $\beta_W = 2 - S_S$. Given the above arguments, the use of Sørensen's similarity coefficient for presence-absence data is recommended. Consistent use of the same coefficient in different studies will maximize their comparability, and therefore our understanding of patterns of species turnover.

Conclusions

1. Different measures of β -diversity reflect quite different properties of a given data set. β_W and its descendants measure the inverse average frequency of species. Mean dissimilarity represents the expected difference in species composition between a randomly chosen pair of plots. Whittaker's half-changes represents the magnitude of species turnover, and the slope of a similarity-distance graph gives the rate of species turnover per unit distance. Using the same term (β -diversity) for all of these measures is not advised, because it invites comparisons among studies that are in fact not comparable.

2. Because α and β are meant to represent components of total (γ) diversity, I feel that the term β -diversity should be reserved for a value that can be related mathematically to α - and γ -diversity. However, neither γ/α (Whittaker 1960) nor $(\gamma - \alpha)$ (Lande 1996) reflect the notion of species turnover, and the terms ' β -diversity' and 'species turnover' should not be used interchangeably. The term 'species turnover' has a straightforward and intuitive meaning. ' β -diversity' is an abstract concept whose utility needs to be limited if it is to retain meaning.

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