



Figure 6.2 Species diversity indices are computed from the community composition data (matrix \mathbf{Y}). Alpha (α) diversity indices are computed for individual sites (rows) i . Gamma diversity (γ) is computed from the vector of column sums of the data matrix using the same indices as for alpha diversity. Beta (β) diversity is of a different nature: it is the variation in community composition among sites. It cannot be computed with the usual entropy of diversity number indices.

3— Species diversity through space

A most interesting property of species diversity is its organization through space. This phenomenon, which is now well known to community ecologists, was first discussed by Whittaker in two seminal papers (1960, 1972) where he described the alpha, beta and gamma diversity levels. The development of multiscale spatial analysis of communities (Chapter 14) is grounded in Whittaker's concept of beta diversity.

Alpha diversity

Alpha (α) diversity is the diversity in species composition at individual sites i (e.g. plots, quadrats; α_i in Fig. 6.2). The indices used to measure alpha diversity estimate, in different ways, the variance in the species identity of individuals observed at a site. A monoculture, for example, has the lowest possible alpha diversity because there is no variance in the species identity of individuals. Alpha diversity is measured by one of Rényi's entropy indices H_0 (eq. 6.33a), H_1 (eq. 6.34a) or H_2 (eq. 6.35a), by Hill's diversity numbers N_0 (richness, eq. 6.33b), N_1 (eq. 6.34b) or N_2 (eq. 6.35b), or by

some other indices such as Fisher's α logarithmic series parameter (Fisher *et al.*, 1943). The most commonly used indices are N_0 , H_1 and N_2 , mentioned in Fig. 6.2.

Gamma diversity

Gamma (γ) diversity is the diversity of the whole region of interest in a study (γ in Fig. 6.2). It is usually measured by pooling the observations from a group of sampling units (which form a *sample* in the statistical sense), i.e. a large number of sites from the area of interest, except in cases where the community composition of an entire area is known, e.g. the CTFS permanent forest plots^{*}. Gamma diversity is measured using the same indices as alpha diversity.

Beta diversity

Beta (β) diversity is of different nature: it is conceptually the variation in species composition among sites in the geographic area of interest (Legendre *et al.*, 2005, Anderson *et al.*, 2006; β in Fig. 6.2). Its value will vary with the extent of the area, the size of the sampling units and the sampling interval in the area under study, which form three aspects of the study scale (Section 13.0).

If the variation in community composition is random and accompanied by biotic processes (e.g. reproduction) that generate spatial autocorrelation in the species data due to limited dispersal (Subsection 1.1.1), a gradient in species composition may appear (called a "false gradient" in Subsection 13.1.2) if the sampling area is small. Beta diversity can then be interpreted in terms of the rate of change, or *turnover*, in species composition along that gradient. Ecologists often refer to this turnover to explain beta diversity. The community spatial structure is often more complex than a single gradient, however: if differentiation among sites is due to environmental factors, which may combine gradient-like and patchy geographic distributions, beta diversity should be analysed with respect to the hypothesized forcing environmental variables. In ecosystems, beta diversity may be caused concurrently by varying proportions of these two processes (i.e. induced spatial dependence and true autocorrelation due to biotic processes, identified in Subsection 1.1.1 as models 1 and 2, respectively). Chapter 14 will show how these two types of hypotheses about the processes that generate beta diversity can be disentangled.

Whittaker (1960, 1972) showed that beta diversity could be estimated using either presence-absence or quantitative species data. Ecologists use both types of measures to study beta diversity, although some researchers only refer to presence-absence data when they talk about the rate of species replacement, or turnover, along an ecological gradient. In the ordination literature, however, ecologists most often use species abundance data to study turnover rates by reference to the appearance and disappearance of species with unimodal distributions along gradients.

A first method, proposed by Whittaker (1960, 1972), for obtaining a global measure of beta diversity from species presence-absence data is to compute the ratio of

^{*} A map of the *Center for Tropical Forest Science (CTFS)* forest plots, and details about each plot, are available on the Web page <http://www.ctfs.si.edu/>.

two diversity indices: $\beta = S/\bar{\alpha}$, where S is the number of species in a composite community composition vector representing the area of interest, and $\bar{\alpha}$ is the mean number of species observed at the original sites. This is a multiplicative approach, where S represents gamma diversity. The ratio $S/\bar{\alpha}$ indicates how many more species are present in the whole region than at an average site, and uses that value as the measure of beta diversity. Other beta diversity indices have been reviewed by Koleff *et al.* (2003), Magurran (2004), Tuomisto (2010) and Anderson *et al.* (2011).

An alternative, additive approach had been present in the literature since MacArthur *et al.* (1966), Levins (1968) and Allan (1975). It was revived by Lande (1996) and has been widely used since then (Veech *et al.* 2002). In that approach, $D_T = D_{\text{among}} - \bar{D}_{\text{within}}$ where D_T is the total (gamma) diversity. This approach can be applied to species richness N_0 (eq. 6.33b) as well as Shannon information H_1 (eqs. 6.1 and 6.34a) and Simpson diversity $D = (1 - \lambda)$ (eq. 6.41); see Lande (1996) for details. Because diversities are variances, one recognizes an analysis of variance approach in that equation.

Whittaker (1960, 1972) suggested that beta diversity could also be estimated from distance matrices computed among sites. This approach is based on the fact that a distance between two sites, computed from community composition data, provides a measure of the variation, or beta diversity between these sites. Distance matrices computed using appropriate indices (Chapter 7) thus assess the pairwise beta diversity among all pairs of sites. To obtain an overall index of beta diversity over a group of sites, Whittaker (1972) suggested to use *the mean* (not the variance) of the dissimilarities among sites: “the mean CC [Jaccard’s coefficient of community, eq. 7.10 in this book] for samples of a set compared with one another [...] is one expression [of] their relative dissimilarity, or beta differentiation” (Whittaker 1972: 233). Whittaker derived his concept from the *index of biotal dispersity* suggested fifteen years before by Koch (1957). Whittaker thus acknowledged the fact that dissimilarities (i.e. distances, Chapter 7) are themselves measures of the differentiation between sites.

Box 6.1 shows that the total variation of a data matrix \mathbf{Y} , e.g. the one shown in Fig. 6.2, can be computed either from \mathbf{Y} itself or from a distance matrix \mathbf{D} derived from \mathbf{Y} . This equality is pertinent here since it shows the equivalence of Whittaker’s overall measure of beta diversity computed from a distance matrix \mathbf{D} with the definition of beta diversity given above, which states that the variation in species composition among sites can be measured by the total variation in data matrix \mathbf{Y} , $SS(\mathbf{Y})$. Indeed, $SS(\mathbf{Y})$, can also be computed from matrix \mathbf{D} using eq. 6.56. For distance matrices that are not Euclidean but whose square root is Euclidean, one may use eq. 6.58. The distance functions that Whittaker (1972) was citing (i.e. Jaccard, Sørensen, Whittaker, and percentage difference) pertain to that group. Box 6.1 shows that eq. 6.58 is a logical choice for the computation of $SS(\mathbf{Y})$ for such distance functions.

SS(Y), Var(Y)**Box 6.1**

The total variation in a data matrix \mathbf{Y} with n rows and p columns can be computed in two ways, which produce the same result.

- First method — Centre each column of \mathbf{Y} on its mean using eq. 1.9 to obtain matrix $\mathbf{Y}_{\text{cent}} = [y_{\text{cent}.ij}]$, then compute the sum of these centred values squared:

$$\text{SS}(\mathbf{Y}) = \sum_{j=1}^p \sum_{i=1}^n (y_{ij} - \bar{y}_j)^2 = \sum_{j=1}^p \sum_{i=1}^n y_{\text{cent}.ij}^2 \quad (6.55)$$

This is the total variation, or total sum of squares, of matrix \mathbf{Y} . It is noted $\text{SS}(\mathbf{Y})$, or e_k^2 in eq. 8.5.

- Second method — Compute a Euclidean distance matrix $\mathbf{D} = [D_{ih}]$ among the n rows of \mathbf{Y} using distance function D_1 (eq. 7.32, Chapter 7). Then, calculate

$$\text{SS}(\mathbf{Y}) = \left(\sum_{i \neq h} D_{ih}^2 \right) / n \quad (6.56)$$

using the $n(n-1)/2$ distances from the upper [or lower] triangular portion of \mathbf{D} . $\text{SS}(\mathbf{Y})$ computed in this way is called e_k^2 in eq. 8.6. The equivalence of these two ways of computing $\text{SS}(\mathbf{Y})$ (Fig. 8.18) is demonstrated in Appendix 1 of Legendre & Fortin (2010).

The total variance in \mathbf{Y} can be calculated from $\text{SS}(\mathbf{Y})$ computed either way:

$$\text{Var}(\mathbf{Y}) = \text{SS}(\mathbf{Y}) / (n - 1) \quad (6.57)$$

Besides eq. 6.56, there are three other ways of computing $\text{SS}(\mathbf{Y})$ from \mathbf{D} :

- $\text{SS}(\mathbf{Y})$ is the trace of the Gower-centred distance matrix Δ_1 derived from \mathbf{D} (eqs. 9.20 and 9.21, Chapter 9).
- $\text{SS}(\mathbf{Y})$ is the sum of the eigenvalues of Δ_1 , i.e. the eigenvalues of the principal coordinate analysis (PCoA) of \mathbf{D} .
- $\text{SS}(\mathbf{Y})$ is the total sum of squares of the principal coordinates of \mathbf{D} (e.g. Table 9.7).

Box 6.1 (continued)

Equation 6.56 can be applied to any distance matrix, Euclidean or not:

- Euclidean distances — For distances that have the Euclidean property (Table 7.2), the rectangular matrix \mathbf{Y}' obtained by principal coordinate analysis of \mathbf{D} contains real numbers only. The distances among the rows of \mathbf{Y}' computed using the Euclidean distance function D_1 (eq. 7.32) are equal to the distances in \mathbf{D} (Subsection 9.2.3). Thus the total sum of squares in \mathbf{Y}' computed through eq. 6.55 is equal to $SS(\mathbf{Y})$ computed by applying eq. 6.56 to \mathbf{D} . Among the Euclidean distance functions recommended for community composition data in Table 7.3, the chord distance D_3 (eq. 7.35), the distance between species profiles D_{18} (eq. 7.54), the chi-square distance D_{16} , (eq. 7.56) and the Hellinger distance D_{17} (eq. 7.57) have an additional property: eq. 6.55 computed from community composition data transformed using the chord (eq. 7.67), profile (eq. 7.68), chi-square (eq. 7.70) or Hellinger transformation (eq. 7.69) produces values of $SS(\mathbf{Y})$ identical to those computed using eq. 6.56 from the chord, species profiles, chi-square and Hellinger distance matrices.

- Non-Euclidean distances — Examples of distance functions described in Chapter 7 that do not have the Euclidean property in their basic form are the Jaccard distance ($1 - S_7$), the Sørensen distance ($1 - S_8$), the percentage difference distance ($D_{14} = 1 - S_{17}$; D_{14} is also called the Bray-Curtis distance), and the Whittaker distance (D_9); they may produce negative eigenvalues in principal coordinate analysis (PCoA, Section 9.2). For these distances, one can still compute eq. 6.56, but the corresponding matrix \mathbf{Y}' of principal coordinates contains both real and complex (imaginary) axes (Subsection 9.2.4). Eq. 6.55 can still be computed for \mathbf{Y}' (McArdle & Anderson 2001) with the result that $SS(\mathbf{Y}')$ is equal to the total sum of squares computed from \mathbf{D} using eq. 6.56. Ecologists may not be comfortable, however, in considering a matrix \mathbf{Y}' that contains complex axes as a fair representation of community composition data. Luckily, there is another way: matrix $\mathbf{D}' = [D_{ih}^{0.5}]$, which contains the square roots of the distances, is Euclidean for these (and some other) distance functions, as shown in Table 7.2. Hence, $SS(\mathbf{Y})$ computed by applying eq. 6.56 to \mathbf{D}' is equal to the total variation (eq. 6.55) of the rectangular data matrix \mathbf{Y}'' obtained by principal coordinate analysis (PCoA) of \mathbf{D}' , and this time \mathbf{Y}'' only contains real axes. So, for these non-Euclidean distance functions, because D_{ih} is equal to $\sqrt{D_{ih}^2}$, an appropriate formula for computing $SS(\mathbf{Y})$ for the original matrix $\mathbf{D} = [D_{ih}]$ is:

$$SS(\mathbf{Y}) = \left(\sum_{i \neq h} D_{ih} \right) / n \quad (6.58)$$

To sum up, beta diversity can be estimated as the total variation in \mathbf{Y} using two different equations: computing eq. 6.55 from the raw data table \mathbf{Y} , or computing eq. 6.56 on distances that have the Euclidean property, e.g. the Euclidean, chord, chi-square and Hellinger distances. Equation 6.58 is a reasonable alternative choice for distances whose square root is Euclidean, e.g. the Jaccard, Sørensen, Whittaker and percentage difference distances.

An interesting observation is that for the chord and Hellinger distances, the maximum possible value of total variance $\text{Var}(\mathbf{Y})$, computed by applying eq. 6.56 followed by eq. 6.57, is 1. The maximum values are obtained when all sites in table \mathbf{Y} have entirely different species compositions. Similarly for community composition data transformed using the chord or Hellinger transformations (Section 7.7), the maximum possible value of $\text{Var}(\mathbf{Y})$, computed using eq. 6.55 followed by eq. 6.57, is 1. Hence, using these transformations or distances, the values of $\text{Var}(\mathbf{Y})$, which are estimates of beta diversity, are easily comparable since they fall in the range 0 to 1.

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