Diversity and Distributions, (Diversity Distrib.) (2007) **13**, 237–241

BIODIVERSITY RESEARCH

Computing β-diversity with Rao's quadratic entropy: a change of perspective

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ABSTRACT

Ecologists have traditionally viewed β-diversity as the ratio between γ-diversity and average α-diversity. More recently, an alternative way of partitioning diversity has been proposed for which β-diversity is obtained as the difference between γ-diversity and average α-diversity. Although this additive model of diversity decomposition is generally considered superior to its multiplicative counterpart, in both models β-diversity is a formally derived quantity without any self-contained ecological meaning; it simply quantifies the diversity excess of γ-diversity with respect to average α-diversity. Taking this excess as an index of β-diversity is a questionable operation. In this paper, we show that a particular family of α-diversity measures, the most celebrated of which is Rao's quadratic entropy, can be adequately used for summarizing β-diversity. Our proposal naturally leads to a new additive model of diversity for which, given two or more sets of plots, overall plot-to-plot species variability can be additively partitioned into two non-negative components: average variability in species composition within each set of plots and the species variability between the set of plots. For conservation purposes, the suggested change of perspective in the summarization of β-diversity allows for a flexible analysis of spatial heterogeneity in ecological diversity so that different hierarchical levels of biotic relevance (i.e. from the genetic to the landscape level) can be expressed in a significant and consistent way.

Keywords

Additive diversity models, α- and β-diversity, compositional diversity, dissimilarity, species turnover.

INTRODUCTION

Biological diversity is generally considered a multilevel concept encompassing all scales of natural variation from ecosystems and landscapes down to the molecular level. Nonetheless, whereas a consensus as to the definition and quantification of biological diversity is still lacking, from an operational viewpoint, most ecologists have long recognized three different components of species diversity: α-diversity or local diversity, γ-diversity or regional diversity and β-diversity that measures the variability in species composition and abundances among sampling units for a given area.

For conservation purposes, the central role of variability in species composition has been extensively investigated: from the prioritization of conservation efforts (Justus & Sarkar, 2002; Magurran, 2004) to species–area relationships (Crist & Veech, 2006; O'Dea *et al.*, 2006), there is an increasing call for conservation planning based on measures of spatial conservation options (see Brooks *et al.*, 2006). Su *et al.* (2004) suggest focusing on β-diversity rather than on α-diversity to test the cross-taxon congruency in the context of coarse-filter conservation, whereas Magurran (2004), introducing an operational definition of biodiversity for conservation planning, equates species complementarity with 'beta diversity by another name' (see also Sarkar & Margules, 2002). Accordingly, β-diversity can be defined as a germane expression of ecological diversity in conservation biogeography, with a focus on biodiversity management and conservation planning (Whittaker *et al.*, 2005; Sarkar, 2006).

Whittaker (1960, 1972) proposed to measure the degree to which habitats are partitioned among species by a multiplicative model so that β-diversity can be expressed as the ratio between γ-diversity and average α-diversity ($\bar{\alpha}$) within the set of sample plots:

$$\beta = \gamma/\bar{\alpha} \qquad (1)$$

The major drawback of Whittaker's proposal is that in this multiplicative model β-diversity is dimensionless and hence is quantified in a manner that is not commensurate with the measurement of α- and γ-diversities.

DOI: 10.1111/j.1472-4642.2006.00316.x
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To overcome this drawback, alternative measures of β-diversity have been suggested that are based on additive diversity decomposition such that β-diversity is expressed as (Lande, 1996; Veech *et al.*, 2002; Ricotta, 2003):

$$\beta = \gamma - \bar{\alpha} \tag{2}$$

To obtain meaningful diversity figures, Eqn 2 is based on the decomposition of concave diversity measures δ. This means that the total diversity in a pooled set of plots (γ) should not be lower than the average within-plot diversity ($\bar{\alpha}$).

From a formal viewpoint, given two species-relative abundance vectors $p = (p_1, p_2, \ldots, p_S)$ and $q = (q_1, q_2, \ldots, q_R)$ along with two weights w_1 and w_2 such that $0 \leq p_j \leq 1$, $0 \leq q_i \leq 1$, $\sum_{j=1}^{S} p_j = \sum_{i=1}^{R} q_i = 1$, and $0 \leq w_1 \leq 1$, $0 \leq w_2 \leq 1$, $w_1 + w_2 = 1$:

$$\delta(w_1 p + w_2 q) \geq w_1 \delta(p) + w_2 \delta(q) \tag{3}$$

In synthesis, Eqn 3 means that diversity increases by mixing (Pavoine *et al.*, 2004, 2005).

In a recent paper, Ricotta (2005a) showed that although additive diversity decomposition is generally considered superior to Whittaker's multiplicative model, both approaches are very similar to each other. Also, as shown by Ricotta (2005a), in both models, β-diversity is a formally derived quantity without any self-contained ecological meaning; it simply summarizes the excess in coarse-scale compositional diversity (γ-diversity) with respect to average fine-scale compositional diversity ($\bar{\alpha}$-diversity). Taking this excess as a measure of plot-to-plot species variability is not necessarily straightforward.

Notice that in this paper, 'compositional diversity' is used to define the diversity within a single species assemblage or plot of variable size (i.e. including α- and γ-diversity), as opposed to the variability in species composition among a given set of plots, or β-diversity.

In this paper, we will show that plot-to-plot species variability or β-diversity can be adequately summarized with a particular family of diversity measures traditionally used for computing compositional diversity, the most celebrated of which is Rao's (1982) quadratic entropy. The proposed change of perspective in the summarization of β-diversity naturally leads to a new additive model of β-diversity for which, given two or more sets of sample plots, overall plot-to-plot species variability can be additively partitioned into two non-negative components: average variability in species composition within each set of plots and the (residual) species variability between the set of plots.

MEASURES OF COMPOSITIONAL DIVERSITY

Given an assembly assemblage composed of S species, traditional measures of α-diversity, such as the Shannon entropy $H = -\sum_{j=1}^{S} p_j \ln p_j$ or the Simpson index $D = 1 - \sum_{j=1}^{S} p_j^2$ are computed solely from the species-relative abundances p_j ($j = 1, 2, \ldots, S$) to the exclusion of other information as the degree of ecological (dis)similarity between the species in the assemblage. From a mathematical viewpoint, these measures summarize the probabilistic uncertainty in predicting the relative abundance of species in a given assemblage (Ricotta & Anand, 2006).

Rao (1982) first proposed a diversity index that incorporates inter-species differences. Quadratic entropy (Q) is defined as the expected dissimilarity between two individuals selected randomly with replacement:

$$Q = \sum_{i=1}^{S} \sum_{j=1}^{S} d_{ij} p_i p_j \tag{4}$$

where d_{ij} is the dissimilarity (i.e. not necessarily a metric distance) between species i and j. There are already several proposals for numerically expressing pairwise inter-species dissimilarities. These dissimilarities can be based on taxonomic or phylogenetic relationships among species (Izsák & Papp, 1995; Warwick & Clarke, 1995; Webb, 2000; Ricotta, 2004), on morphological or functional differences (Izsák & Papp, 1995; Botta-Dukat, 2005; Mason *et al.*, 2005; Ricotta, 2005b) or on more sophisticated molecular methods (Solow *et al.*, 1993; Shimatani, 2001).

The mathematical properties of quadratic entropy have been extensively studied by Shimatani (2001), Champely & Chessel (2002), Pavoine *et al.* (2005) and Ricotta & Szeidl (2006). It is easily shown that for $d_{ij} = 1$ for all $i \neq j$, and $d_{ii} = 0$ for all i, Q is reduced to the Simpson index $1 - \sum_{j=1}^{S} p_j^2$. Also, if the dissimilarities d_{ij} are standardized such that $0 \leq d_{ij} \leq 1$, Rao's Q can be interpreted as the expected conflict among the species of a given assemblage $Q = \sum_{j=1}^{S} p_j \sum_{i \neq j}^{S} (d_{ij} p_i)$. where the term $C(p_j) = \sum_{i \neq j}^{S} d_{ij} p_i$ summarizes the conflict between species j and the remaining species in the assemblage (see Ricotta & Szeidl, 2006).

Regardless of how inter-species dissimilarities are computed, because quadratic entropy incorporates not only species-relative abundances, but also information about the degree of dissimilarity between the species in the assemblage, it comes closer to a modern notion of biological diversity than more traditional measures.

In this view, contrary to the Shannon or the Simpson index, Rao's Q violates the usual diversity axiom that for a given number of species S, the maximal diversity arises for an equiprobable species distribution (i.e. if $p_j = 1/S$ for all j). Although this violation may be disturbing (see Pavoine *et al.*, 2005), it is worth emphasizing that unlike traditional diversity indices that are computed solely from the relative species abundances of a given assemblage, Rao's Q depends on two variables: the pairwise species distances d_{ij} and the species abundances p_j. Therefore, the requirement that the maximum index value is obtained in case of species equiprobability without considering pairwise species distances is by far too restrictive for this kind of diversity measures (Ricotta, 2006).

Under some circumstances, Rao's Q is concave and can be additively decomposed into α-, β- and γ-terms (see Eqn 2). For instance, if the dissimilarities d_{ij} are Euclidean, then quadratic diversity is concave (Champely & Chessel, 2002; Ricotta & Szeidl, 2006). More specifically, a dissimilarity is said to be Euclidean if S points can be embedded in a Euclidean space such that the Euclidean distance between S_i and S_j is d_{ij} (Gower & Legendre, 1986). The reason for discussing the concavity of Rao's Q will be clear in the following sections when dealing with the decomposition of β-diversity within a nested sampling design.

COMPUTING β-DIVERSITY WITH RAO'S QUADRATIC ENTROPY

Imagine a given region is sampled at N sampling plots and the expected species dissimilarity between two plots is computed as the Rao diversity of the N plots. As a result, Q may be seen as a measure of plot-to-plot variability or β-diversity.

In this case, the values of d_{ij} summarize the dissimilarity between plot i and plot j, rather than pairwise species dissimilarities. Obviously, the amount of plot-to-plot variability depends on the multivariate dissimilarity measure used for computing d_{ij} (Legendre & Legendre, 1998; Podani, 2000). In turn, these dissimilarities may be related to various ecological aspects like simple species turnover and functional, morphological, taxonomic or genetic distances among plots, as ecological differences between species assemblages are believed to be reflected in each of these (Desrochers & Anand, 2004).

Also, the values of p_j may embody different plot-specific ecological variables like total biomass within each plot, number of individuals, vegetation cover or any other biological parameter that is thought to influence ecosystem functioning at the plot scale.

The ecological rationale for summarizing β-diversity from variables like biomass values resides in the observation that the extent to which plant communities affect short-term ecosystem functions such as carbon balance or nutrient cycling, is largely determined by the specific and functional diversity of dominant species. This 'mass-ratio' effect (Grime, 1998) is dictated by the fact that for autotrophs such as plant species, a larger body mass involves major participation in syntheses and in inputs to resource fluxes and degradative processes (Aarsen, 1997; Huston, 1997). In this view, there is increasing evidence that complementary resources exploitation as a result of functional differences between co-dominants (e.g. in phenology, rooting depth or reproductive biology) generally confers beneficial effects on ecosystem productivity (Hooper & Vitousek, 1997). By contrast, sub-dominants may control longer-term ecosystem functioning by a 'filter effect', i.e. influencing the recruitment of dominants (Grime, 1998; Polley *et al.*, 2006). Hence, the inclusion of biomass values in the computation of Rao's β-diversity may be beneficial for investigating the effects of spatial variability in species composition on ecosystem processes. For a practical example of the computation of Q for a set of five plots, see Appendix S1 in the Supplementary Material section.

DISCUSSION

Conservation biogeography, as an interdisciplinary science, is entering a crucial phase in the development of conservation theory and strategy (Whittaker *et al.*, 2005). In this view, the concept of β-diversity plays a key role in detecting the spatial patterns of species distributions and offers a wide spectrum of possible applications ranging from optimizing the task of reserve selection (Margules & Pressey, 2000) to investigating the relationships between species composition and ecosystem processes (Polley *et al.*, 2006).

In addition, the efforts concentrating on priority settings for biodiversity conservation at different scales (Justus & Sarkar, 2002; Su *et al.*, 2004; Brooks *et al.*, 2006; Schwartz *et al.*, 2006) indicate that the classic β-diversity concept needs a change of perspective so that different levels of relevance, i.e. from the genetic to the landscape level, can be expressed in a significant and consistent way.

In this paper, we propose that Rao's Q can be adequately applied for measuring different aspects of plot-to-plot heterogeneity in a very flexible and powerful manner. In principle, given N plots along with an associated relative abundance vector $p = (p_1, p_2, \ldots, p_N)$, one might argue that the same operation can be performed using any measure of α-diversity like Shannon's entropy or the Simpson diversity. However, a major shortcoming related to the application of traditional (probabilistic) α-diversity measures for computing β-diversity is that measures of probabilistic uncertainty treat all events in the probability vector $p = (p_1, p_2, \ldots, p_N)$ as mutually exclusive. That is, in the computation of β-diversity, all plots are equally distinct. For example, a plot containing species A, B and C is equally different from a plot with species A, B and D and from a plot with species D, E and F. However, the species assemblages ABC and ABD possess two common species; by contrast, the assemblages ABC and DEF do not share any species.

Because Rao's quadratic entropy summarizes the expected dissimilarity between two sample plots randomly drawn from the set of N plots, it automatically fixes the previously mentioned shortcoming. Notice that in addition to Rao's Q, virtually any diversity index that incorporates plot-specific relative abundances p_j and a measure of pairwise plot-to-plot dissimilarity d_{ij} can be used for computing β-diversity in a meaningful manner. Examples are the diversity measures proposed by Warwick & Clarke (1995) and Ricotta (2004).

Notice also that the practice of using dissimilarity coefficients for quantifying β-diversity is deeply rooted in ecological theory. For instance, for a given pair of plots, the Whittaker β-diversity (see Eqn 1) computed from species presences and absences can be rewritten as $\beta_W = 2 - d_{Sør}$ where $d_{Sør} = 2a/(2a + b + c)$ is the Sørensen coefficient of similarity and the letters refer to the traditional 2×2 contingency table: a is the number of species present in both plots, b is the number of species present solely in the first plot (and absent from the second plot) and c is the number of species present solely in the second plot (Vellend, 2001; Koleff *et al.*, 2003). More recently, Anderson *et al.* (2006) proposed to measure the β-diversity within a set of plots as the average dissimilarity from individual plots to their group centroid in multivariate space.

Therefore, as a rule of the thumb, we can use any multivariate dissimilarity coefficient for computing plot-to-plot differences in species composition in a meaningful way (Koleff *et al.*, 2003). However, using traditional dissimilarity coefficients, differences in species composition are measured for single pair of plots separately. By contrast, using Rao's Q, we obtain a genuine measure of β-diversity in which species differences are computed simultaneously for the complete set of plots.

Finally, if quadratic diversity is concave (i.e. if pairwise species distances d_{ij} are Euclidean), the use of quadratic entropy for

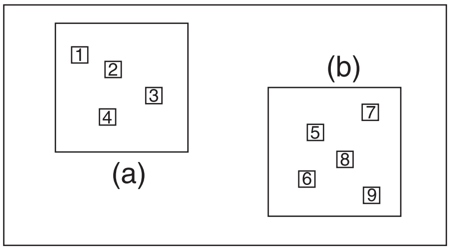

Figure 1 Schematic example of a nested sampling design in which two blocks, a and b, are located at random across a given landscape. Within blocks a and b, four and five plots are established, respectively. According to Eqn. (5), if Rao's Q is concave, the total β-diversity (Q_{Tot}) of the pooled sets of plots (i.e. the expected dissimilarity among plots 1–9 in blocks a and b) can be additively partitioned into two non-negative components: average within-block β-diversity (Q_{Within}) that reflects the average heterogeneity in species composition that is obtained by computing quadratic diversity separately within blocks a and b, and between-block β-diversity, $Q_{\mathrm{Between}} = Q_{\mathrm{Tot}} - \bar{Q}_{\mathrm{Within}}$ that embodies the increase in β-diversity that is obtained by pooling together all plots within the blocks a and b.

computing β-diversity automatically leads to a new additive model of diversity that is based on the decomposition of species spatial variability at different scales.

Imagine the vegetation of a given region is sampled according to the following nested sampling design (Fig. 1): first, M blocks of a given size are located at random (or according to any other approved sampling scheme) across the study area. Within each block, a given number of plots that can vary from block to block is established, and all vascular plants are recorded within each plot.

We define p_{jm} as the relative abundance of plot j in block m and w_m as the weight associated to block m such that $\sum_{m=1}^{M} w_m = 1$ and $\sum_{j=1}^{N_m} p_{jm} = 1$, where N_m is the number of plots in block m.

The weights w_m associated to the different blocks may be equal (i.e. $w_m = 1/M$), or may reflect properties as diverse as their conservation value (e.g. the number of red-listed species), the proportions of selected land cover types within each block, etc. Furthermore, let Q_{Tot} be the total quadratic diversity of the pooled sets of plots computed using the weighted plot relative abundances within the blocks $p_{j\mathrm{Tot}} = w_m p_{jm}$.

According to Eqn 2, if Rao's Q is concave, the total β-diversity (Q_{Tot}) of the pooled sets of plots (i.e. the expected dissimilarity among all plots in the M blocks) can be additively partitioned into two non-negative components: the average within-block β-diversity ($\bar{Q}_{\mathrm{Within}}$), which reflects the average heterogeneity in species composition that is obtained by computing quadratic diversity separately within each block, and the between-block β-diversity, $Q_{\mathrm{Between}} = Q_{\mathrm{Tot}} - \bar{Q}_{\mathrm{Within}}$, which embodies the increase in β-diversity that is obtained by pooling together all plots within the M blocks. It follows:

$$Q_{\mathrm{Tot}} = \bar{Q}_{\mathrm{Within}} - Q_{\mathrm{Between}} \tag{5}$$

Unlike Eqn 2 in which the variability in species composition of a given region is expressed as the difference between two compositional diversities measured at different scales, all terms in Eqn 5 represent β-diversities. Accordingly, Eqn 5 summarizes the increase in β-diversity within a given region that is obtained measuring the variability in species composition at different hierarchical levels within a nested sampling design.

As a result, the proposed additive decomposition of β-diversity is flexible in that heterogeneity in species composition within a given region can be partitioned along a nested sampling hierarchy on the basis of any categorical factor such as habitat, land use, land management or soil type. Therefore, conformity to the proposed additive partitioning model can be considered a very desirable feature of β-diversity measures that may eventually lead ecologists to use it as a conceptual framework for understanding the relations between species variability and ecosystem functioning at various spatial scales, and help conservation biologist for doing spatial reserve planning in a manner that effects of landscape structure to species distributions are accounted for.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 Worked example showing how Rao's quadratic entropy is used for computing β-diversity.

This material is available as part of the online article from:

htpp://www.blackwell-synergy.com/doi/abs/10.1111/j.1472-4642.2006.00316.x
(This link will take you to the article abstract).

Appendix S1 Worked example showing how Rao’s quadratic entropy is used for computing β-diversity.

To show how Rao’s quadratic entropy works in practice for computing β-diversity, we used the data gathered from the five control plots studied by Chiarucci et al. (1998). The plots of 1 m^2 in size were randomly sampled in a serpentine garigue located near the village of Casciano di Murlo on an ultramafic outcrop in the Ombrone hydrographic basin (central Italy). In spring 1996, when most of the species had reached peak biomass and were flowering or fruiting, all plants growing in each plot were harvested at ground level and sorted per species. The material was dried at 80°C for 48 h and then weighed. In Table 1, all species presences and absences in each plot are reported along with the total above-ground biomass of all plots. According to Eq. (4), the frequencies p_j were computed normalizing the biomass values in Table 1 to a probability space. The pairwise plot-to-plot dissimilarities d_{ij} were computed from the species presences and absences in each plot using the Jaccard index of dissimilarity 1-[a/(a+b+c)] (see Table 2). Finally, Rao’s quadratic entropy was computed as follows:

$$
\begin{aligned}
Q = \quad & p_1 \times (p_2 d_{12} + p_3 d_{13} + p_4 d_{14} + p_5 d_{15}) + \\
& p_2 \times (p_1 d_{12} + p_3 d_{23} + p_4 d_{24} + p_5 d_{25}) + \\
& p_3 \times (p_1 d_{13} + p_2 d_{23} + p_4 d_{34} + p_5 d_{35}) + \\
& p_4 \times (p_1 d_{14} + p_2 d_{24} + p_3 d_{34} + p_5 d_{45}) + \\
& p_5 \times (p_1 d_{15} + p_2 d_{25} + p_3 d_{35} + p_4 d_{45}) = \quad 0.394
\end{aligned}
$$

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Species	Plot Code				
	1	2	3	4	5
Aira elegans	1	0	1	1	1
Allium sphaerocephalon	0	1	1	1	1
Alyssum bertolonii	1	1	1	1	1
Asperula cynanchica	0	0	1	1	0
Brachypodium distachyon	1	0	0	0	0
Bromus erectus	0	1	0	1	0
Cerastium ligusticum	1	0	0	1	1
Danthonia alpina	0	0	0	1	0
Dianthus sylvestris	0	0	1	0	0
Echium vulgare	0	0	0	0	1
Festuca inops	1	0	1	1	1
Galium corrudifolium	1	0	1	1	0
Genista januensis	1	0	1	0	1
Helichrysum italicum	0	1	1	1	1
Herniaria glabra	1	1	1	0	0
Hypochoeris achyrophorus	1	0	0	0	0
Iberis umbellata	1	1	1	1	1
Jasione montana	0	1	1	0	1
Linum trigynum	1	1	1	1	1
Onosma echioides	0	0	1	1	0
Plantago holosteum	1	0	1	0	0
Psilurus incurvus	0	0	0	0	1
Sedum rupestre	1	0	0	0	1
Teucrium montanum	0	0	0	0	1
Thymus acicularis	1	1	1	1	1
Trinia glauca	0	1	1	1	0
Total biomass [gm^{-2}]	69.15	11.98	50.21	97.53	25.31
Normalized biomass values	0.272	0.047	0.197	0.384	0.100

Table 1

Species presences and absences for the five plots of the serpentine garigue of central Italy along with their biomass values [gm^{-2}].

Plot Code						
1	2	3	4	5		
0	0.737	0.524	0.619	0.550	1	Plot Code
	0	0.500	0.529	0.611	2	
		0	0.400	0.545	3	
			0	0.571	4	
				0	5	

Table 2

Plot-to-plot quadratic dissimilarity semimatrix for the five plots of the serpentine garigue of central Italy obtained from the Jaccard dissimilarity coefficient computed from species presences and absences.