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On the functional diversity of partially distinct species: some theory and a practical example

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Abstract: Due to its nonlinearity with respect to species addition, some applications of the Rao quadratic diversity are meaningful only if they are first transformed into their equivalent number of species, which is the theoretical species richness of a maximally distinct and perfectly even community with the same diversity as the original community. In this paper, relaxing the requirement of maximal distinction among species, we generalize the notion of the equivalent number of species for the Rao diversity to partially distinct species. The biological meaning of this proposal is illustrated with one dedicated case study in sand dune communities in Italy. According to our results, the proposed approach proved appropriate for comparing the functional diversity of different plant communities with varying levels of environmental constraints.

Introduction

Many diversity indices, like the Shannon entropy or the Gini-Simpson index, are usually nonlinear with respect to species addition, even when all species are equally common (Jost et al. 2010). As already recognized by McArthur (1965, 1972) and Whittaker (1972), all else being equal, each added species leads to a smaller increment in 'diversity' than the species added before it. In the case of the Gini-Simpson index, the effect is so extreme that the diversity measure asymptotically approaches unity, no matter how many species are added.

To solve this problem, McArthur (1965) proposed to convert diversity indices to their 'equivalent number of species', or 'effective number of species', which is the theoretical species richness of a perfectly even community with the same diversity as the original community. That is, the diversity-equivalent number of species S that would result if all species relative abundances $p_i = 1/S$ for all $i = 1, 2, \ldots, S$. Since McArthur's seminal work, a number of formulae were proposed for converting particular diversity measures to their species equivalents (e.g., Hill 1973, Patil and Taillie 1982, Olszewski 2004), while Jost (2006, 2007) derived a general conversion formula for all diversity indices that are monotonic functions of $\sum_{i=1}^{S} p_i^{\alpha}$ with $(0 \le \alpha \le \infty)$ or limits of such functions as α approaches unity. These diversity measures include species richness, the Shannon entropy, all Simpson measures, all Rényi entropies, all Tsallis entropies, and many others (see Jost 2007).

In analogy with Jost (2007), to understand the differences between a traditional diversity index and its species equivalent, imagine a tropical island with 100 equally common species is hit by a tornado that kills half the species. In agreement with our intuition, species richness decreases by 50%, from 100 to 50. To the contrary, using base-10 logarithms, the Shannon entropy decreases from 2 to only 1.699. That is, according to the Shannon index, the magnitude of the diversity drop is roughly 15%. Likewise, the Simpson index decreases from 0.99 to 0.98, meaning that the tornado had virtually no impact on diversity, although the island has half the species it had before. Transforming the Shannon and the Simpson diversities to their species equivalents according to the conversion formulas in Jost (2007, Table 1) makes them behave according to our intuitive biological expectation: if the tornado kills half the island's species, the numbers equivalents of both indices decrease by 50%.

Hill (1973) noted that the 'equivalent numbers of species' possess a general property that ecologists intuitively expect of a diversity measure. Given a community of S species with an arbitrary distribution of abundances $p_i = (p_1, p_2, \ldots, p_S)$ and diversity δ, if the community is replicated N times with different species in each replicated community but with the same abundance distribution of the original community, the diversity of the pooled replicate communities should intuitively be $N\delta$. In ecology, this property is known as the 'doubling property' (Hill 1973) and in econometrics as the 'replication principle' (Chakravarty and Eichhorn 1991). A number of authors (MacArthur 1965, 1972, Whittaker 1972, Hill 1973, Jost 2006, 2007, Jost et al. 2010) have shown that diversity measures that conform to the replication principle provide mathematically, logically and intuitively more correct answers to many ecological questions.

All standard diversity measures discussed so far are based solely on species abundances. However, the value of diversity measures that reflect not only the relative abundances of species, but also the functional differences between them is becoming increasingly recognized (Diaz and Cabido 2001, Hooper et al. 2005). In this framework, Ricotta and Szeidl (2009) extended the notion of equivalent number of species to the Rao's quadratic diversity, while Chao et al. (2010) and Leinster and Cobbold (2012) developed two general families of dissimilarity-based diversities that behave like species equivalents.

To maintain the connection to the original definition of an equivalent number of species for standard diversity measures, Ricotta and Szeidl (2009) defined the species equivalent of Rao's quadratic diversity Q as the number of equally likely and '*maximally distinct'* species needed to produce the given value of Q. Here, the notion of maximum distinction implies that there should not be any functional overlap between the equivalent species in the 'null' assemblage, such that two randomly selected individuals either belong to the same species or always differ by the same, maximal amount (see Gregorius and Gillet 2008, Leinster and Cobbold 2012). Therefore, all pairwise species dissimilarities d_{ij} ($0 \leq d_{ij} \leq 1$) between species i and j in the equivalent community are equal to 1 for all $i \neq j$, while $d_{ii} = 0$. However, actual biological communities show at least some degree of functional redundancy, and species often provide similar functions. It follows that, from a biological viewpoint, it is more relevant to allow a certain extent of functional overlap among equivalent species. In this paper we generalize the notion of the equivalent number of species of the Rao diversity to partially distinct species for which $d_{ij} \leq 1$. The biological meaning of this proposal is illustrated with one dedicated case study in sand dune communities in Italy.

Relaxing the notion of 'maximally distinct species'

Quadratic diversity is defined as the expected dissimilarity between two individuals i and j of a given species assemblage selected at random with replacement:

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

where S is species richness, d_{ij} is the pairwise (functional) dissimilarity between species i and j, and p_i and p_j are the species relative abundances.

Some relevant mathematical properties of Q have been studied by a number of authors (Shimatani 2001, Champely and Chessel 2002, Pavoine et al. 2005, Ricotta and Szeidl 2006, 2009, Pavoine and Bonsall 2009, Rao 2010, Pavoine 2012) and the reader is directed to their papers for details. Here, it is simply worth mentioning that for $d_{ij} = 1$ for all $i \neq j$, and $d_{ii} = 0$, Q reduces to the well-known Gini-Simpson index $1 - \sum_{i=1}^{S} p_i^2$. Accordingly, being part of the Gini-Simpson index family, the Rao quadratic diversity is characterized by strong nonlinearity with respect to species addition, even if all species are equally abundant.

Ricotta and Szeidl (2009) proposed a way for calculating the species equivalents E of the Rao quadratic diversity if the interspecies distances d_{ij} are in the range [0, 1]. To maintain the connection to the original definition of McArthur (1965) for standard abundance-based diversity indices, Ricotta and Szeidl (2009) founded their work on the idea that all equivalent species need to be equally abundant (each species with abundance $1/E$) and maximally distinct (all pairwise species dissimilarities $d_{ij} = 1$ for all $i \neq j$). Given these assumptions, the formula for calculating the species equivalent of Rao's quadratic diversity is the same that is used for calculating the species equivalent of the Simpson diversity (Ricotta and Szeidl 2009):

$$E = 1/(1-Q) \tag{2}$$

Note that since $d_{ij} \leq 1$, it follows that in Eq. (2) $Q \leq 1$. Of course, for any dissimilarity measure with an upper bound $D > 1$, division by D gives a standardized measure in the range [0, 1]. Likewise, for dissimilarities that do not have an upper bound (like e.g., the Euclidean distance) it is still possible to locally normalize all d_{ij} values in the range [0, 1] by dividing each term by the highest value (d_{max}) found in the data set, such that the species equivalent of the Rao index after normalization becomes:

$$E' = \frac{1}{\left(1 - Q/d_{\max}\right)} = \frac{1}{\left(1 - Q'\right)}$$

$$\text{with} \quad Q' = \sum_{i,j}^{S} \frac{d_{ij}}{d_{\max}} p_i p_j \tag{3}$$

Another way of thinking about Eq. (3), which is inspired by the work of Chao et al. (2010), consists in asking the following question: given a species assemblage together with a symmetric matrix of pairwise species dissimilarities in the range [0, ∞], what is the equivalent number of species E' of the Rao index calculated for this assemblage if we want all these equivalent species be equally dissimilar from each other with dissimilarity d'?

To get the right answer we can apply the general recipe proposed by Jost (2006) for deriving the species equivalent of any diversity index: "Calculate the diversity index for E' equally-common species (each species therefore with a frequency of $1/E'$), set the resulting expression equal to the actual value of the diversity index, and solve that equation for E'. Accordingly, we have $Q = \sum_{E'} \frac{1}{E'} \frac{1}{E'} \times d'$, and solving the equation for E' we obtain:

$$E' = 1/(1-Q/d') \tag{4}$$

which is identical to Eq. (4.10) of Chao et al. (2010) and to Eq. (3) in this paper, only with d' at the place of d_{max}. Note that for a fixed value of Q, the species equivalent E' decreases with increasing values of d'. Note also that in Eq. (4) we need to impose the restriction $d' > Q$, otherwise a negative number of equivalent species is obtained. The species equivalent E' conforms to the replication principle for any value of d'. The demonstration is reported in Appendix 1.

This way of calculating the species equivalent of Rao's Q differs from the original definition of Ricotta and Szeidl (2009) as in this case we do not need to invoke '*maximal species dissimilarity*' (with $d_{ij} = 1$ for all $i \neq j$), but rather an a-priori defined '*mean species dissimilarity*' d' for all $i \neq j$. Setting $d' = d_{max}$, we rescale all distances in Q within the range [0, 1],

Table 1. Description of the functional traits used in this study (see also Ricotta et al. 2012). All quantitative traits were measured in the field. Seed shape is calculated according to Thompson et al. (1993) as the variance of the three main dimensions after dividing all values by length. The sources for the binary, ordinal and nominal traits are: Pignatti (1982), Tutin et al. (1964-1993).

Trait description	Data type	Attribute
Plant height at maturity	Quantitative	[cm]
Seed mass	Quantitative	[mg]
Specific leaf area (leaf area/dry weight)	Quantitative	[mm^2/mg]
Leaf dry matter content (dry weight/fresh weight)	Quantitative	[mg/g]
Leaf area	Quantitative	[cm^2]
Leaf thickness	Quantitative	[mm]
Seed shape	Quantitative	variance
Flowering phenology	Ordinal	1. April and before; 2. May; 3. June; 4. July and after
Clonality	Binary	0. Clonal; 1. Non-clonal
Leaf persistence	Binary	0. Deciduous; 1. Evergreen
Plant life span	Binary	0. Annual; 1. Biennal-Perennial
Pollination system	Binary	0. By wind or non-specialized; 1. By insects or birds
Raunkiaer life form	Nominal	1. Phanerophyte; 2. Chamaephyte; 3. Hemicryptophyte; 4. Geophyte; 5. Therophyte
Growth form	Nominal	1. Short basal; 2. Long-semibasal; 3. Erect leafy; 4. Cushions, tussocks and dwarf shrubs; 5. Shrubs, trees and climbers
Dispersal mode	Nominal	1. Anemochorous; 2. Barochorous; 3. Zoochorous
Leaf texture	Nominal	1. Succulents; 2. Malacophyllous; 3. Semi-sclerophyllous; 4. Sclerophyllous

thus recovering Ricotta and Szeidl (2009). Here, for low values of d', we may have $E' > S$ (where S is the actual number of species in the assemblage). This means that, if the reference null assemblage is composed of highly overlapping species, a very high number of such species is needed to get the same diversity value of the actual assemblage. The following example in which we examine how coastal dune communities occupy their alpha functional space may help in clarifying the ecological meaning of mean species dissimilarity.

An example from coastal dune plant communities

Data

For this study, we used a vegetation database containing georeferenced plots of 2 m × 2 m in size. The plots were randomly sampled from 2005 to 2010 on the holocenic dunes of the Tyrrhenian coast of the region Lazio (ca. 250 km in central Italy), including most of the best conserved remnant dune systems of the region. For further details see Carboni et al. (2011) and Santoro et al. (2012).

The study area is characterized by a Mediterranean climate and the holocenic dunes generally occupy a narrow strip along the seashore. The vegetation follows a compressed zonation along the sea-inland environmental gradient: from the pioneer communities of the upper beach to the woody communities (Mediterranean macchia and evergreen forests) of the inland fixed dunes (Acosta et al. 2003). The main gradient is the sea-inland environmental gradient due to varying wind intensity, sand burial, salt spray, drought and soil development in relation to distance from the sea (Carboni et al. 2011).

Here, we selected 272 plots covering three of the most typical coastal dune habitats: (i) embryo dunes (70 plots), (ii) mobile dunes (131 plots) and (iii) transition dunes (71 plots). In each plot all vascular plant species were recorded and the cover of all species was visually estimated using a 10%-interval rank scale. A subset of 46 dominant species, which collectively made up at least 80% of the standing live biomass of each dune habitat (Santoro et al. 2012) were described by a set of 16 functional traits that are related to plant responses to the environment (Table 1). Previous studies support that a reliable description of the community functional diversity is obtained if the species sampled account for ~ 80% of the standing live biomass (Pakeman and Quested 2007, Ricotta et al. 2012, Jucker et al. 2013). For each species we measured seven continuous traits, related to the leaf-height-seed (LHS) plant strategy scheme (Westoby 1998): plant height, leaf size, leaf thickness, seed mass, seed shape, leaf dry mass content and specific leaf area). We also collected from regional and national floras information for nine additional categorical, binary and ordinal traits, which relate to species growth form, phenology, dispersal ability and pollination (see Table 1 and Ricotta et al. 2012 for a full description and sources).

Methods

From the functional traits of Table 1, we first calculated a pairwise species distance matrix using the Gower mixed-variables coefficient proposed by Pavoine et al. (2009). Based on the pairwise species distance matrix, together with the species abundances in each plot, we then calculated a number of diversity measures for each plot, including species richness S, The Rao quadratic diversity Q, and the species equivalent E computed with $d' = 1$ according to Eq. (2).

All these measures summarize different aspects of community diversity without taking into account the limiting effects of environmental constraints along the sea-inland gradient. For instance, Ricotta et al. (2012, Figure 1) calculated the functional rarefaction curves of the three coastal vegetation types showing an increase in expected functional diversity at the plateau of the rarefaction curves from the embryo dunes to the transition dunes. That is, the *available* functional space of the three vegetation types is not the same; rather, it varies along the coastal zonation as a function of the main environmental constraints related to the sea-inland environmental gradient (Carboni et al. 2011). This available functional space influences how species are packed into the community: the more limited the space available, the more difficult the functional segregation among species. Therefore, to investigate how coastal dune communities occupy their available functional space once the limiting effects of the environmental gradients are removed, we also calculated the species equivalent E' using different values of d' for the three vegetation types (see Eq. 4). The different values of d' should reflect the available functional space of each community, such that increasingly lower values of d' mirror increasingly limiting effects on the functional space that can be occupied by the species of a given community.

In principle, one intuitive method for selecting adequate values for d' may consist in taking the asymptotic values of the functional rarefaction curves of each community shown in Ricotta et al. (2012). However, as rarefaction methods are basically smoothing operations, this choice does not ensure the condition $d' > Q$. That is, it may happen that the Rao diversity of single plots is higher than the expected diversity of the average community composition.

Accordingly, we followed another way: first, we calculated the maximum pairwise functional dissimilarity d_{max} between the species of each plot. These values represent the maximum functional difference that is actually observed between two species that co-occur in the same portion of biotic space under the same environmental constraints. Next, for each vegetation type, we averaged these maximum dissimilarities over all plots obtaining three different values of d'. We believe that averaging the local maxima over all plots reduces the influence of functionally-uncommon occasional species on the values of d', thus obtaining meaningful measures of the available functional space in each vegetation type. The mean values of S, Q, E, E', and d_{max} for the three vegetation types used in this study were finally compared with ANOVA.

Results

Figure 1 displays the box plots of S, Q, E, E', and d_{max} for the three coastal dune vegetation types. As shown in Figure 1,

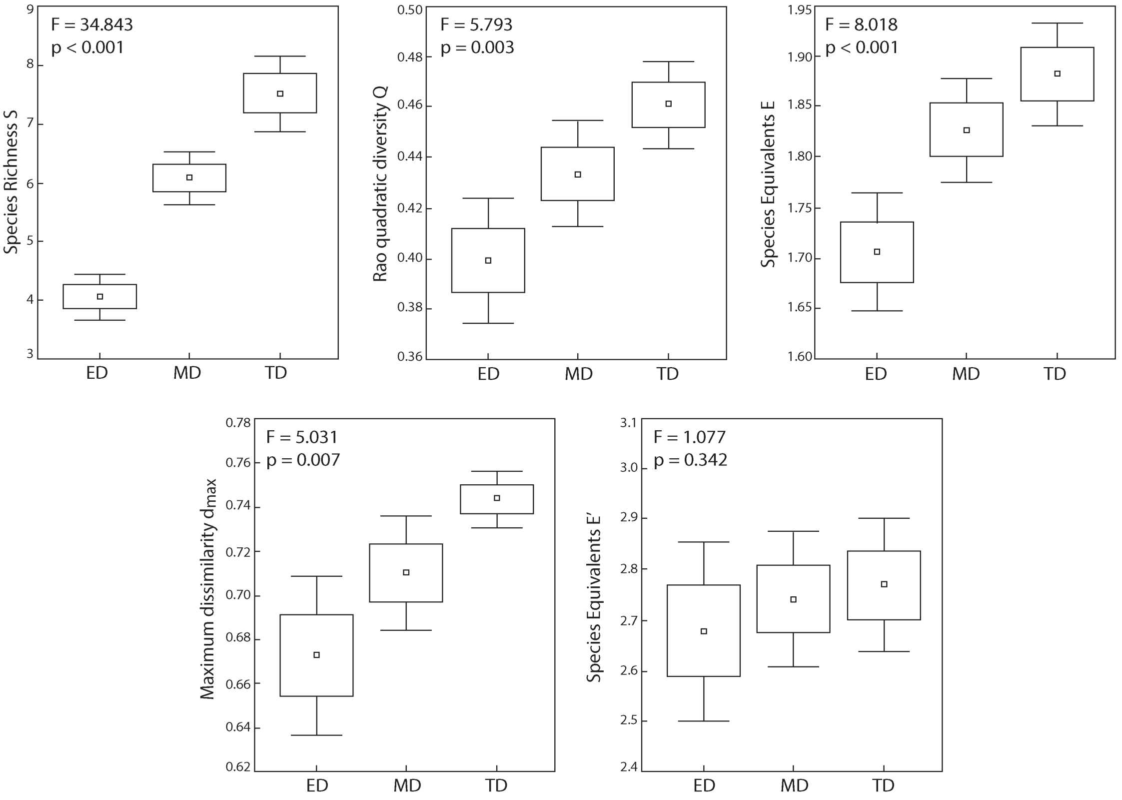

Figure 1. Box plots of the diversity measures S, Q, E, E', and d_{max} for the three coastal dune vegetation types used in this study (ED = embryo dunes, MD = mobile dunes, TD = transition dunes). The F tests are from a one-way ANOVA. S = species richness, Q = Rao quadratic diversity, E = species equivalents of Q (calculated according to Eq. 2), d_{max} = maximum dissimilarity between two species in the same plot averaged over all plots of each vegetation type, E' = species equivalents of Q/d' (calculated according to Eq. 4).

the results of the ANOVA illustrate a statistically significant increase of species richness S ($F = 34.843$; $p < 0.001$), the Rao diversity Q ($F = 5.793$; $p = 0.003$) and the species equivalents E ($F = 8.018$; $p < 0.001$) from the embryo dunes to the transition dunes. The increasing diversity along the coastal zonation could be related to the well-known sea-inland environmental gradient described for many coastal dune ecosystems worldwide (Wilson and Sykes 1999, Hesp 2004, Fenu et al. 2013). In fact, the embryo dune vegetation is closer to the sea, and hence more exposed to salt spray, winds and sand burial, while the vegetation of the mobile dunes and the transition dunes is progressively less exposed. Accordingly, the embryo dune vegetation is characterized by plant species with similar functional traits that are well adapted to this extreme environment, while the vegetation of the mobile dunes and the transition dunes is less affected by limiting factors, thus showing an increasingly higher functional dissimilarity (Ricotta et al. 2012). This pattern is clearly visible looking at the values of d_{max}, which show a significant increase along the sea-inland gradient, ranging from 0.67 for the embryo dunes to 0.74 for the transition dunes ($F = 5.031$; $p = 0.007$). This means that the maximal functional diversity observed between two species in the same plot is significantly lower for the plant assemblages of the embryo dunes compared to the assemblages of the mobile dunes and the transition dunes. On the other hand, the species equivalents E' do not show any significant difference among the three plant assemblages ($F = 1.077$; $p = 0.342$). That is, in the specific case of our study, if we standardize (absolute) diversity with respect to available functional space, then differences in (relative) diversity E' among the different assemblages vanish.

Discussion

It is generally understood that, as ecological data are generally multivariate of high dimension, no single diversity index is able to adequately summarize all aspects of this multifaceted concept. A more complete picture is obtained if, instead of a single index, one uses a parametric family of diversity indices whose members have varying sensitivities to the rare and abundant species. Several such families have been developed (e.g., Hill 1973, Smith and Grassle 1977, Patil and Taillie 1982, Tóthmérész 1995, Ricotta 2003, Ricotta and Szeidl 2006, Liu et al. 2007, Jost 2007, Chao et al. 2010, Jost 2010, Leinster and Cobbold 2012). Given such a parametric measure, the diversity can be plotted against the parameter to compare the resulting diversity profiles of the various communities under study. However, in spite of their theoretical interest, the application of parametric index families did not prove productive in ecology. This is because diversity profiles work reasonably well only if a limited number of communities are to be compared; with larger numbers of communities it becomes increasingly difficult to identify groups of communities having similar diversity patterns (Taillie 1979). Dealing with a large number of species assemblages, a more convenient approach may consist in selecting a restricted number of diversity measures that are directly related to the ecological process under scrutiny (Mason et al. 2005, Villéger et al. 2008, Ricotta and Moretti 2011). Due to the well-known relationship of Rao's index with variance (Champely and Chessel 2002, Rao 2010, Ricotta and Moretti 2011, Pavoine 2012), in this paper we used a generalized version of the species equivalents of quadratic diversity to shed insight onto the functional organization of coastal dune communities. According to our results, the proposed index seems appropriate for comparing the functional diversity of different plant communities with varying levels of environmental constraints (and hence varying levels of available functional space), like the plant assemblages along a coastal zonation.

The presence of environmental gradients provides a methodological challenge in quantifying community diversity in large-scale environmental studies. Relaxing the notion of maximal species dissimilarity enabled us to eliminate the impact of natural environmental gradients when calculating functional diversity. In this view, substituting the notion of mean species dissimilarity for maximal dissimilarity raises the question of how to select ecologically reasonable values of d'. Dealing with phylogenetic distances, Chao et al. (2010, p. 3604) suggest to select d' such that a basic property of the community phylogenetic tree, like Faith's (1992) phylogenetic diversity (PD) is retained. Likewise, dealing with functional distances, Chao (pers. comm.) suggests to calculate d' keeping the community functional attribute diversity, FAD, of Walker et al. (1999) unchanged. However, both indices, PD and FAD, are calculated only on the basis of pairwise distances between species, without considering the species relative abundances. Therefore, we fear that this line of attack will not be fully adequate to represent the degree of species packing (in terms of interspecies distances *and* species abundances) into different plant communities with varying levels of environmental constraints. More generally, we think that there is no universal recipe for the calculation of d'. Rather, the values of d' should be selected case by case based on the specific ecological question asked.

One might argue that, when species richness is low, as it is the case of our coastal dune communities, the Rao quadratic diversity is positively correlated to species richness, such that the increase of Q and E along the coastal zonation simply mirrors the increase in species richness S. However, the parallel and significant increase in maximum diversity d_{max} is too great to ignore its role in driving the increase in functional diversity along the sea-inland gradient. One might also argue that the lack of significance of E' in discriminating the functional diversity of the coastal dune vegetation types is not really surprising, since the new measure is a function of Q/d_{max} and these two quantities were highly correlated. However, this result reflects the biology of our system, rather than any statistical bias: after normalizing Q taking into account the maximum functional space available for each vegetation type, the apparent increase in (relative) functional diversity along the sea-inland gradient vanishes.

The increased flexibility of the proposed method has not only a theoretical value; rather, several studies report difficulties in detecting the impact of human disturbance on biological diversity due to the masking effects of natural environmental gradients (Heino et al. 2007, Schmera et al.

2012). Therefore, to test the response of community diversity to human disturbance correctly, first the species variability along natural environmental gradients needs to be removed (for a thorough discussion of this topic, see Schmera et al. 2012). This is particularly important in the wake of increasing human pressure on natural resources caused by population growth (Laliberté et al. 2010) and our proposal offers a potential line of attack to this problem.

Finally, one relevant question remains. While we discussed how to calculate the species equivalent of partially distinct species within the context of alpha diversity only, we did not address the question of diversity partitioning into alpha, beta and gamma components. While this problem was extensively studied by Jost (2007) and Chao et al. (2010) within the context of traditional abundance-based diversities and phylogenetic diversities, respectively, the problem of how to extend their findings to partially distinct species remains very much open.

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Appendix 1. Proof that the generalized species equivalent E′=1/(1–Q/d′) conforms to the replication principle

Given N equally diverse and equally large assemblages in which each assemblage has quadratic diversity Q and the dissimilarity between each pair of species in two different assemblages is d' (with $Q < d' \leq 1$), if these assemblages are pooled, the species equivalent of the pooled assemblage must be N times the species equivalent of the individual assemblages E'. That is: $E'_{Tot} = NE'$, where Q_{Tot} is the Rao diversity of the pooled assemblages and $E'_{Tot} = 1/(1-Q_{Tot}/d')$ is the corresponding species equivalent.

Since the quadratic entropy Q_{Tot} is the expected dissimilarity between two individuals drawn at random with replacement from the pooled set of plots, it can be expressed as the following sum of two conditional expected values:

Term 1. Probability that both individuals are drawn from the same plot, times the expected dissimilarity of the individuals in this plot, $N(1/N^2)\times Q$.

Term 2. Probability that both individuals are drawn from different plots, times the expected dissimilarity between two individuals in different plots, which is d' by definition $N(N-1)/N^2 \times d'$.

The sum of these two terms gives the quadratic entropy of the pooled plots: $Q_{Tot} = N(1/N^2)\times Q + N(N-1)/N^2 \times d'$ Substituting this expression in the formula for E'_{Tot}, we obtain $E'_{Tot} = N/(1-Q/d')$, proving that the generalized species equivalent of quadratic diversity satisfies the replication principle.