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From alpha to beta functional and phylogenetic redundancy

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Abstract

1. Plot-level redundancy or alpha redundancy is usually defined as the fraction of species diversity not expressed by functional or phylogenetic diversity. Redundancy is zero when all species in one plot are maximally dissimilar from each other. By contrast, redundancy tends to its maximum if the functional or phylogenetic differences between species tend to be minimal.
2. To explore the ecological drivers of community assembly, ecologists also use dissimilarity measures between pairs of plots (a component of beta diversity). Traditional dissimilarity measures summarize compositional differences between pairs of plots based either on species presence and absence data or on species abundances, thus attributing equal distinctiveness between any two species.
3. In the last decades a number of dissimilarity measures which incorporate information on functional or phylogenetic differences among species have been proposed. Based on such improved measures, we can define an index of beta redundancy for a pair of plots as the fraction of species dissimilarity not expressed by functional or phylogenetic dissimilarity.
4. A necessary condition to get a meaningful index of beta redundancy is that for a given pair of plots, the functional or phylogenetic dissimilarity is always lower or equal to the corresponding species dissimilarity. However, many of the existing indices of functional or phylogenetic dissimilarity can lead to values greater than for species dissimilarity.
5. The aim of this paper is thus to introduce a new family of tree-based measures of phylogenetic and functional dissimilarity that conform to this requirement. To show the behavior of the proposed measures, a worked example with data on Alpine vegetation is used.

Keywords: Bray-Curtis index, functional and phylogenetic dissimilarity, functional dendrogram, hierarchical clustering, phylogenetic tree, species-based dissimilarity.

1. Introduction

The maintenance of ecosystem processes under ongoing perturbations causing local species extinctions requires the presence of functionally similar species. This property is usually known as functional redundancy (Walker, 1992; Naeem, 1998). When several species perform similar functions but differ in their responses to disturbances, functional redundancy may enhance community stability, while providing insurance against the loss of ecosystem functions due to a disturbance (Yachi & Loreau, 1999). Therefore, if functional redundancy is high, it is more likely that the loss of a given species will have relatively little effect on ecosystem processes (Petchey, Evans, Fishburn, & Gaston, 2007; Pillar et al., 2013).

Ricotta et al. (2016; see also de Bello et al., 2016) proposed to summarize functional uniqueness within plots (the complement of redundancy) as the ratio of two diversity measures: the Rao quadratic entropy Q , which is calculated using the species abundances and their trait dissimilarities and the Simpson index S , which considers all species maximally dissimilar from each other such that $U_\alpha = Q/S$. Functional uniqueness thus measures the diversity decrease that is obtained by including trait dissimilarities in the calculation of plot-level diversity or alpha diversity. Similarly, since $Q \leq S$, alpha-redundancy can be interpreted as the fraction of species diversity not expressed by functional diversity: $R_\alpha = 1 - U_\alpha = (S - Q)/S$ with R_α ranging between zero and one (Pillar et al., 2013). Redundancy is zero when all species in the assemblage are maximally dissimilar from each other. In this case, Rao's quadratic diversity is equal to the Simpson index. By contrast, if all species in the assemblage are functionally identical, we have $Q = 0$ and hence $R_\alpha = 1$.

In addition, community ecologists increasingly recognize that ecological processes may also be affected by evolutionary differences among species. This is because the branching structure of phylogenetic trees generally mirrors the accumulation of phenotypic differences among species, which may reflect the complexity of ecosystem functioning better than a reduced set of trait

63 differences (Tucker et al., 2017). As for functional redundancy, we can thus define phylogenetic
64 redundancy as the diversity decrease that is obtained by considering the evolutionary
65 relationships among species in the calculation of diversity. Ricotta et al. (2018) thus proposed a
66 normalized measure of plot-level phylogenetic redundancy or alpha redundancy in the range [0,
67 1] that relates the observed phylogenetic diversity of a given species assemblage to the value of a
68 hypothetical assemblage in which all species originate directly from the same ancestor node
69 giving rise to a star phylogeny. For details, see Ricotta et al. (2018).

70 Apart from plot-level indicators, ecologists also use dissimilarity measures between pairs of
71 plots to explore the complex mechanisms that drive ecosystem functioning. Classical
72 dissimilarity measures usually summarize compositional differences between pairs of plots based
73 either on species incidence or abundance data, thus attributing equal distinctiveness between any
74 two species (for review, see Podani, 2000 or Legendre & Legendre, 2012). More recently, a
75 number of functional/phylogenetic dissimilarity measures, which incorporate information on
76 functional or phylogenetic differences among species have been proposed (Rao, 1982; Clarke &
77 Warwick, 1998; Izsák & Price, 2001; Pavoine, Dufour, & Chessel, 2004; Chiu, Jost, & Chao,
78 2014; Pavoine & Ricotta, 2014; Pavoine, 2016; Chao et al., 2019). Such new dissimilarity
79 measures are expected to correlate more strongly with ecosystem processes, as species directly
80 or indirectly influence these processes via their traits (Mason & de Bello, 2013).

81 Plot-to-plot dissimilarity is closely related to the concept of beta diversity proposed by
82 Whittaker (1960) to define the amount of species turnover in a given set of plots. Indeed,
83 evaluation of beta diversity is commonly based on the average dissimilarity between pairs of
84 plots (Koleff, Gaston, & Lennon, 2003; Legendre & De Cáceres, 2013, but see Baselga, 2013).
85 Therefore, we can define a measure of beta redundancy R_β for a pair of plots as the fraction of
86 species dissimilarity not expressed by functional or phylogenetic dissimilarity. According to this
87 definition, a necessary condition to obtain a normalized index of beta redundancy in the range [0,

1] is that for a given pair of plots, the functional (or phylogenetic) dissimilarity D_F (or D_P) is always lower or equal to their species dissimilarity D_S , where D_S is the compositional dissimilarity of a hypothetical pair of plots with the same species abundances of the actual pair of plots in which all species are considered equally and maximally dissimilar from each other. In this case, beta redundancy can be summarized as:

$$R_\beta = 1 - U_\beta = (D_S - D_F) / D_S \quad (1)$$

However, under particular circumstances, many of the existing indices of functional or phylogenetic dissimilarity can lead to values greater than for species dissimilarity, thus violating the basic requirement that $D_F, D_P \leq D_T$ (see Appendix S1). The aim of this paper is to introduce a new family of tree-based measures of phylogenetic and functional dissimilarity that conform to the requirement $D_F, D_P \leq D_T$. A worked example with published data on Alpine plant communities along a primary succession on a glacier foreland in northern Italy is used to illustrate our approach.

2. New tree-based measures of phylogenetic beta redundancy

Phylogenetic trees have long been used to represent the evolutionary history and relationships among groups of organisms, such as species (Podani 2017). In ecology, phylogenetic trees have been widely adopted to analyze the phylogenetic component of biodiversity (Tucker et al. 2017). Likewise, most measures of phylogenetic dissimilarity take into account the branching pattern of the species phylogeny (Chiu, Jost, & Chao, 2014; Pavoine, 2016). For a given assemblage, the terminal nodes of the phylogenetic tree usually represent the species in the assemblage, while the interior nodes are ‘hypothetical taxonomic units’ (i.e., the hypothetically most recent common ancestor of all descendent taxa in the phylogenetic tree; Farris, 1970). If the branch lengths are

113 proportional to the time of divergence among species, all species are at the same distance from
 114 the root node and the tree is called ‘ultrametric’. A general method for incorporating the
 115 branching pattern of ultrametric trees like that in Figure 1 in the calculation of a wide range of
 116 phylogenetic diversity metrics has been developed by Pavoine, Love, & Bonsall (2009) and
 117 Chao, Chiu, & Jost (2010).

118 For an ultrametric phylogeny composed of N species, let A and B be two plots and x_{Ai} be the
 119 abundance of species i ($i = 1, 2, \dots, N$) in plot A . The phylogenetic tree is first divided into K
 120 evolutionary periods as follows: the tree is sliced at each node and the node ages are labeled in
 121 temporal order as t_k with $t_0 = T$ (the age of the root node) and $t_K = 0$ (the present-day time). The
 122 root node can either be the common ancestor of the species in A and B or the common ancestor
 123 of a larger group of species defined e.g. at regional scale, depending on the question at hand (see
 124 Ricotta et al., 2018).

125 Two adjacent slices delimit an evolutionary period $\Delta_k = t_{k-1} - t_k$ with $\sum_{k=1}^K \Delta_k = T$. Any
 126 given evolutionary period k ($k = 0, 1, \dots, K$) contains M_k lineages ($M_k \leq N$) with abundances χ_{km}
 127 ($m = 1, 2, \dots, M_k$). The abundance of each lineage is obtained as the sum of the abundances of all
 128 its descendent species in the phylogenetic tree.

129 Given two plots A and B , the corresponding lineage abundances χ_{Akm} and χ_{Bkm} can be then
 130 used for calculating a lineage dissimilarity D_k between A and B for each node age t_k of the tree.
 131 The lineage dissimilarity at time t_K is the usual present-day dissimilarity calculated from the
 132 species abundances x_{Ai} and x_{Bi} . The overall phylogenetic dissimilarity D_p is then obtained by
 133 averaging the measures D_k over the time intervals of the corresponding evolutionary periods
 134 (Ricotta et al., 2018):

$$135 \quad D_p = \sum_{k=1}^K D_k \times \tau_k \quad (2)$$

137

138 where $\tau_k = \Delta_k/T$ is the duration of the k -th evolutionary period after rescaling the tip-to-root
 139 length to unit, and Δ_0 (and hence τ_0) = 0 by definition. D_p thus measures the phylogenetic
 140 dissimilarity between plots A and B incorporating information about the branching pattern of the
 141 species phylogeny and its lineage abundances.

142 If phylogenetic dissimilarity at time t_k is calculated with the Bray-Curtis index (Bray &
 143 Curtis, 1957), the present-day species dissimilarity $D_S = D_K = \sum_{i=1}^N |x_{Ai} - x_{Bi}| / \sum_{i=1}^N (x_{Ai} + x_{Bi})$ is
 144 always greater than or equal to any other lineage dissimilarity D_k (proof in Appendix S2).
 145 Therefore, $D_p \leq D_S$ and we can get a normalized index of phylogenetic beta redundancy (R_p) or
 146 beta uniqueness (U_p) as $R_p = 1 - U_p = (D_S - D_p) / D_S$.

147 This measure represents the fraction of species dissimilarity between a pair of plots not
 148 expressed by phylogenetic dissimilarity. Note that for a pair of plots A and B with given species
 149 abundances x_{Ai} and x_{Bi} , the uniqueness component $U_p = D_p / D_K$ can be interpreted as a measure
 150 of phylogenetic dissimilarity between both plots normalized by its maximum value. This
 151 maximum is the phylogenetic dissimilarity of a pair of plots with identical abundance vectors but
 152 in which all species had independent evolution. In phylogenetic terms, this means that all
 153 terminal branches originate from a single polytomy at the root node, thus forming a star
 154 phylogeny (Ricotta et al., 2018). Likewise, the complement of uniqueness, beta redundancy
 155 $R_p = 1 - U_p$, can be interpreted as a normalized measure of phylogenetic *similarity* in the range
 156 $[0, 1]$.

157

158 **3. New tree-based measures of functional beta redundancy**

159 In principle, the same tree-based approach can be used to assess functional dissimilarity. This
 160 requires to organize functional differences between species to obtain a hierarchical structure as

161 first suggested by Petchey & Gaston (2002). Functional dendrograms can be constructed by first
162 calculating functional dissimilarities between species and then using any hierarchical clustering
163 approach to obtain a rooted tree from these dissimilarities with species as tips (Pavoine &
164 Ricotta, 2019). There are several clustering methods for constructing a tree-like classification in
165 which species are aggregated into hierarchical clusters (Podani, 2000; Legendre & Legendre,
166 2012). The structure of the resulting functional dendrogram is thus sensitive to the methods used
167 to define a tree hierarchy from functional dissimilarities between species.

168 Much of the discussion on tree-based functional measures has been focused around the
169 selection of appropriate clustering methods (Podani & Schmera, 2006; Petchey & Gaston, 2007;
170 Mouchet et al., 2008). Nonetheless, there is a lack of agreement over which method produces the
171 best representation of species distribution in hierarchical trait space. For example, Weitzman
172 (1992) developed an algorithmic measure of (functional) diversity, which can be geometrically
173 represented as the length of a rooted dendrogram, while Blackburn, Petchey, Cassey, & Gaston
174 (2005) and Petchey & Gaston (2007) suggested to adopt case by case the clustering algorithm
175 that maximizes the cophenetic correlation between pairwise species dissimilarities in trait space
176 and the corresponding pairwise dissimilarities across the functional dendrogram.

177 Podani & Schmera (2006, 2007) argued that the ideal requirement of maximizing the
178 cophenetic correlation is hardly feasible in practice as the virtually infinite number of available
179 clustering procedures (see Lance & Williams, 1966) would unnecessarily overcomplicate the
180 calculations. They suggested instead to use group average (i.e., unweighted pair group method
181 with arithmetic mean, UPGMA) as a standard clustering procedure. Mouchet et al. (2008)
182 proposed to use consensus trees, which incorporate features common to a number of different
183 clustering methods. Additional hierarchical clustering methods may rely on the maximization of
184 within-cluster homogeneity based on some a-priori defined criteria, such as variance, sum of
185 squares or within-cluster average similarity of objects (see Podani, 1989).

186 In this paper, we used the UPGMA clustering method because it represents a good
 187 compromise between the methodological extremes of a continuous series of space-contracting
 188 and space-dilating algorithms (Gordon, 1999). Space-contracting algorithms, such as the single
 189 linkage method, tend to contract the input dissimilarity structure significantly. Therefore, they
 190 may leave some clusters undetected even if the input data space shows a clear group structure.
 191 Space-dilating algorithms, such as the complete linkage method, tend to produce a clustered
 192 structure even if it is not apparent in the input data space. Within this continuous series of
 193 clustering procedures, UPGMA generally preserves a large proportion of the input dissimilarity
 194 structure, thus tending to minimize the distortion induced by transforming the input dissimilarity
 195 matrix into a functional dendrogram (Podani & Schmera, 2006).

196 As for the phylogenetic case, the functional dendrogram obtained from the UPGMA
 197 algorithm can then be used for calculating a measure of pairwise functional dissimilarity among
 198 plots D_F together with the corresponding measures of functional redundancy and uniqueness
 199 $R_F = 1 - U_F = (D_S - D_F) / D_S$.

200 Note that, irrespective of the clustering method, the functional dendrogram needs to be rooted
 201 and scaled to unit height from the tips to the root, so that two species sharing no branch in the
 202 tree would have maximum possible functional differences between them (for details, see
 203 Appendix S3).

204

205 **4. Worked example**

206 **4.1. Data**

207 We analyzed the functional and phylogenetic beta redundancy of plant communities collected
 208 by Caccianiga et al. (2006) along a primary succession on glacial deposits. The data set is
 209 composed of 59 plots, each of about 25 m² in size sampled above the tree line at the foreland of
 210 the Rutor Glacier (Italy). See Caccianiga et al. (2006) for additional information on the study
 211 site. Based on the age of the moraine ridges, the plots were assigned to three successional stages:

early-succession (17 plots), mid-succession (32 plots) and late-succession (10 plots). For each plot, species abundances were measured with a five-point ordinal scale transformed to ranks.

The 45 species sampled were classified in terms of Grime's (1974) plant strategy theory, as competitors (C), stress tolerators (S) and ruderals (R) with fuzzy-coded values in the range 0–100, such that the sum of C+S+R was equal to 100 (all data are available in Ricotta et al., 2016, Appendix S2). A functional dissimilarity matrix between species was then obtained by applying the Bray-Curtis coefficient to the CSR species classification. Finally, we used the phylogeny of the 45 species available in Appendix A of Ricotta et al. (2015) after rescaling its tip-to-root length to unit.

4.2. Methods

We calculated functional and phylogenetic beta uniqueness U_F and U_P for all pairs of plots in each successional stage. All calculations were done with a new R function “DP” available in Appendix S3. We next tested for differences in the dispersion of U_F and U_P among the three successional stages. Since the beta uniqueness of a pair of plots A and B is basically a normalized measure of dissimilarity between A and B , we used the PERMDISP test (Permutational Analysis of Multivariate Dispersions) of Anderson (2006) to test for differences in the average dissimilarity of individual plots from their group centroid among successional stages. This test has been extensively used in ecology for comparing the beta diversity among groups of plots.

First, starting from the functional and phylogenetic beta uniqueness between pairs of plots, we calculated for each successional stage the normalized dissimilarity (uniqueness) of each individual plot from its group centroid. Next, a permutational t-test for pairwise differences in average dissimilarity from the group centroids is performed. P-values were obtained using 9999 pairwise permutations of the dissimilarities of individual plots from the corresponding group centroids.

4.3. Results

The phylogenetic and functional dendrograms of the 45 species used in this study are shown in Appendix S4 and the behavior of functional and phylogenetic beta uniqueness along the successional stages is summarized in Table 1. As shown by Caccianiga (2006) and Ricotta et al. (2016, 2018) the colonization of the glacial deposits by the first pioneer species in the early-successional stage is mainly driven by random dispersal mechanisms, while in the mid- and late-successional stages, a general tendency towards an increased structural homogeneity is observed. At the plot level, the increased uniformity of vegetation structure over time is associated with a functional and phylogenetic shift from early-successional ruderal forbs to late-successional stress-tolerator graminoids that goes together with an increase in functional and phylogenetic alpha redundancy.

Looking at the beta component of uniqueness, Table 1 shows that, due to the low structural homogeneity of the pioneer vegetation, the species, functional and phylogenetic turnover among the early-successional plots is generally higher than that of the mid- and late successional plots. More specifically, while traditional species turnover does not differ significantly among the three successional stages, the functional turnover and uniqueness of the 17 plots in the early successional stage are both significantly higher than those in the mid- and late successional stages. This means that in the mid- and late-successional stages the species in one plot tend to be replaced by functionally related species in the other plot. As a result, functional uniqueness U_F tends to be low. By contrast, due to the more random nature of the dispersal mechanisms, in the early-successional stage, the species in one plot tend to be replaced by functionally unrelated (or, at least, less related) species. Therefore, functional uniqueness tends to be higher. The same pattern is shown by the phylogenetic uniqueness, although in this case the statistical differences among the three successional stages are not always significant at $p < 0.05$.

5. Discussion

In this paper, we introduced the notion of beta redundancy. In analogy to plot-level redundancy or alpha redundancy, beta redundancy can be defined as the fraction of species dissimilarity between pairs of plots not expressed by functional or phylogenetic dissimilarity. In its very essence, beta redundancy tells us to what degree the species-based similarity between two plots is associated to the functional or phylogenetic similarities among the species in both plots.

While functional and phylogenetic dissimilarity D_F and D_P are absolute measures that take into account the abundances and the functional or phylogenetic differences among the species in both plots, beta redundancy R_β and its complement beta uniqueness $U_\beta = 1 - R_\beta$ are standardized coefficients that relate D_F and D_P to plot-to-plot species dissimilarity D_S . A fundamental requirement to get a meaningful index of beta redundancy is thus that $D_F, D_P \leq D_S$. However, contrary to common belief, many of the existing indices of functional or phylogenetic dissimilarity do not conform to this requirement. Therefore, they cannot be used to calculate an appropriate measure of beta redundancy. To solve this problem, we introduced a family of tree-based indices of functional and phylogenetic dissimilarity that conform to this requirement. Regardless of whether beta redundancy is calculated from functional or phylogenetic data, D_F and D_P have a great potential for future research on community organization, as both measures are variations on the theme of the classical index of Bray & Curtis (1957), the properties of which have been studied by ecologists for decades (e.g. Legendre & De Cáceres, 2013; Ricotta & Podani, 2017).

Being based on a hierarchical structure of species differences, the proposed phylogenetic measures take into account the branching pattern of the phylogenetic tree, which is the more natural way for describing the evolutionary relationships among the species. By contrast, a tree-based representation of the species functional relationships may not be the most appropriate

289 solution. However, if we accept the idea of Petchey and Gaston (2007, p. 1422) that from a
290 statistical viewpoint “the functional dendrogram can be thought of as a description of the
291 functional relationships shared by the species it includes, in the same way as a phylogenetic tree
292 describes phylogenetic relationships (although without any associated inference about
293 evolutionary relationships)”, we obtain a powerful and flexible framework for the calculation of
294 different facets of functional diversity, richness and redundancy.

295 From a more technical viewpoint, our approach requires that the tip-to-root length T of the
296 phylogenetic or functional tree be normalized to the unit interval. This can be done either by a-
297 priori normalizing the (functional) dissimilarities among species in the range [0-1], or by a-
298 posteriori normalizing the length of the resulting dendrogram. Since there is no univocal way to
299 normalize tree length, flexibility is important to adapt the way the data are transformed to the
300 specific objectives of our work. A short guide on how to normalize the length of a hierarchical
301 dendrogram according to the specific question at hand can be found in Pavoine, Marcon, &
302 Ricotta (2016, Appendix S3).

303 In conclusion, we see this work more as a starting point for the summarization of beta
304 redundancy rather than as an ultimate solution, and many questions remain still open. For
305 example, how do the proposed beta redundancy metrics respond to large differences in species
306 richness and evenness? (Here, it will also be important to explore which among rare and
307 common species contribute most to redundancy, as this is related to the metrics sensitivity to
308 sampling effort). How does species splitting affect the index values or, more generally, how
309 sensitive is phylogenetic redundancy to taxonomic changes (see Robuchon et al., 2019)?

310 Also, functional and phylogenetic dissimilarity measures need not necessarily be based on a
311 tree. For example, we could also consider evolutionary distances calculated from molecular data
312 before any tree is derived from these distances. Therefore, apart from tree-based indices, are
313 there other classes of measures of functional or phylogenetic dissimilarity which conform to the
314 requirement $D_F, D_P \leq D_S$? Which additional properties should these measures possess? In

Appendix S1 we show that eight existing indices of plot-to-plot dissimilarity fulfill the requirement $D_F, D_P \leq D_S$. However, for the same indices, we also show some unexpected and counter-intuitive behaviors: part of these measures attribute positive dissimilarity values to two identical plots, whereas, by definition, the dissimilarity between a plot and itself should be zero. Other indices retain only nearest-neighbor distances between species for the calculation of functional or phylogenetic dissimilarity (see Appendix S1 and Ricotta, Bacaro & Pavoine, 2015). Further studies should thus consider a range of properties fulfilled by any potential index of plot-to-plot functional or phylogenetic dissimilarity, rather than focusing exclusively on the requirement $D_F, D_P \leq D_S$.

Last but not least, in diversity theory alpha and beta diversity have been usually related to gamma or regional diversity either by an additive model $\alpha + \beta = \gamma$ (McArthur, Recher, & Cody, 1966) or by a multiplicative model $\alpha \times \beta = \gamma$ (Whittaker, 1960). Will it be possible to develop a similar model for alpha and beta redundancy? These are critical questions, and their answers may provide new tools for analyzing the complex processes that drive community assembly and species co-occurrence.

330

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334

335 **Authors' Contributions**

336 C.R. and S.P conceived the ideas and formulated the research problem. F.L. and L.S. provided
337 important feedback which helped shape the research. C.R. and S.P. analyzed the data. C.R. took
338 the lead in writing the main text of the manuscript and S.P. in writing the appendixes. All authors
339 revised the manuscript critically and approved the final version.

340

341 **Data accessibility**

342 The data and the R code used in this paper are deposited in the Dryad repository:
343 <https://doi.org/10.5061/dryad.ttdz08ktg>

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456 **Supporting Information**

457 Additional supporting information may be found online in the Supporting Information section at
458 the end of the article.

459 **Table 1.** Mean (SD) dissimilarity values of each individual plot from its group centroid for the
 460 three successional stages on the moraine deposits of the Rutor Glacier. Pairwise comparisons of
 461 index differences between the successional stages were performed with permutational t-tests for
 462 pairwise differences in average dissimilarity from the group centroids (9999 permutations). For
 463 each dissimilarity coefficient, numbers followed by the same letter do not differ significantly at P
 464 < 0.05 . D_s = species dissimilarity (Bray-Curtis dissimilarity); D_f = functional dissimilarity; D_p =
 465 phylogenetic dissimilarity; U_f/U_p = functional/phylogenetic uniqueness.

	Functional data		
	Early-succ. stage	Mid-succ. stage	Late-succ. stage
D_s	0.399 (0.071) ^a	0.357 (0.084) ^a	0.354 (0.101) ^a
D_f	0.118 (0.034) ^a	0.085 (0.024) ^b	0.073 (0.033) ^b
$U_f = D_f/D_s$	0.203 (0.045) ^a	0.168 (0.035) ^b	0.144 (0.069) ^b
	Phylogenetic data		
	Early-succ. stage	Mid-succ. stage	Late-succ. stage
D_s	0.399 (0.071) ^a	0.357 (0.084) ^a	0.354 (0.101) ^a
D_p	0.291 (0.070) ^a	0.214 (0.053) ^b	0.222 (0.063) ^{ab}
$U_p = D_p/D_s$	0.498 (0.076) ^a	0.422 (0.072) ^b	0.427 (0.101) ^{ab}

469

470 **Figure 1.** Ultrametric phylogenetic tree showing the evolutionary relationships among the species
 471 of an artificial assemblage. The abundances of the five species are denoted as $x_1, \dots, x_5$. By
 472 slicing the phylogeny at each node we can define four non-overlapping evolutionary periods Δ_k .
 473 The age of each node is labeled as t_k ($k = 0, 1, \dots, K$) such that $t_0 = T$ (the age of the root node),
 474 $t_K = 0$ (the present-day time), and $\Delta_k = t_{k-1} - t_k$. Any evolutionary period k contains M_k lineages
 475 with abundances χ_{km} ($m = 1, 2, \dots, M_k$). The abundances of each lineage along the phylogeny
 476 are calculated by summing the abundances of all descendent species in the phylogeny. For
 477 example, $\chi_{11} = \chi_{31} = x_1 + x_2$, $\chi_{12} = x_3 + x_4 + x_5$, and $\chi_{K1} = x_1$.
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