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1 ABSTRACT

2 Rarity reflects the low abundance of a species while distinctiveness reflects its quality of
3 being easy to recognize because it has unique functional characteristics and/or an isolated
4 phylogenetic position. As such, the assemblage-level rarity of a species' functional and
5 phylogenetic characteristics (that we name 'effective originality') results from both the rarity
6 and the distinctiveness of this species. The functional and phylogenetic diversity of an
7 assemblage then results from a compromise between the abundances and the effective
8 originalities of the species it contains. Although the distinctiveness of a species itself depends
9 on the abundance of the other species in the assemblage, distinctiveness indices that are
10 available in the ecological literature scarcely consider abundance data. We develop a unifying
11 framework that demonstrates the direct connections between measures of diversity, rarity,
12 distinctiveness and effective originality. While developing our framework, we discovered a
13 family of distinctiveness indices that permit a full control of the influence one wants to give to
14 the strict uniqueness of a species (=its smallest functional or phylogenetic distance to another
15 species in the assemblage). Illustrating our framework with bat phylogenetic diversity along a
16 disturbance gradient in Mexico, we show how each component of rarity, distinctiveness and
17 originality can be controlled to obtain efficient indicators for conservation. Overall our
18 framework is aimed to improve conservation actions directed towards highly diverse areas
19 and/or towards species whose loss would considerably decrease biodiversity by offering
20 flexible quantitative tools where the influence of abundant versus rare, and ordinary versus
21 original, species is understood and controlled.

22

23 *Keywords:* conservation priority ranks, diversity index, equivalent number, evolutionary
24 history, functional traits, quadratic entropy

25

26 **1. Introduction**

27

28 Generally speaking, biodiversity is the range of many different characteristics of biological
29 systems (see the Convention on Biological Diversity, [https://www.cbd.int/doc/legal/cbd-](https://www.cbd.int/doc/legal/cbd-en.pdf)
30 [en.pdf](https://www.cbd.int/doc/legal/cbd-en.pdf) [accessed in August 2021], for the primary definition). In species assemblages,
31 biodiversity thus emerges because species are not equivalent in their abundance and
32 biological characteristics, their functional traits and phylogeny. To simplify the writing,
33 hereafter we use the acronym 'FP' to mean 'functional or phylogenetic'. In local assemblages,

34 often many species are rare, having small population size, and only a few species dominate in
35 abundance (e.g., Hughes, 1986). Another increasingly studied aspect of rarity (Pavoine et al.,
36 2017; Violle et al., 2017; Chapman et al., 2018; Kondratyeva et al., 2019) is the rarity of a
37 species' FP-characteristics. We consider two terms often used to designate the rarity of a
38 species' biological characteristics: distinctiveness and originality. Distinctiveness is the
39 quality of being easy to recognize because of being different from other things (Cambridge
40 Dictionary, 2021). In our context, the distinctiveness of a species can thus be defined as its
41 quality of being easy to recognize because it has some unique functional characteristics or as
42 its quality of being easily found in a phylogenetic tree because it belongs to an old, species-
43 poor clade. Originality is the quality of being special and interesting and not the same as
44 anything or anyone else (Cambridge Dictionary, 2021). This is why the originality of a
45 species can be considered as the assemblage-level rarity of the FP-characteristics associated to
46 this species (Pavoine et al., 2017). This originality depends on whether abundance data are
47 considered (Fig. 1).

48

49 In absence of abundance data, the concept of originality is equivalent to that of distinctiveness
50 (Pavoine et al., 2005). This is because the species own rarity is discarded and the rarity of a
51 species' biological characteristics is only linked to the proportion of functional traits or
52 phylogenetic history that are unshared with other species (see, e.g., the distinct species 1 and 2
53 in Fig. 1a,b,c). In global conservation studies for example abundance data are rarely
54 considered (e.g., Gaüzère et al., 2015). For more local ecological studies however, abundance
55 data are often available and often reveal meaningful to analyze ecological systems (e.g.
56 Enquist et al., 2019). Consider that a focal species j is distinct from other species in a defined
57 species pool. If in an assemblage, its few functionally sibling or close relatives "dominate" the
58 assemblage by their high abundance or if species j is itself very abundant, then the
59 assemblage-level rarity of the FP-characteristics associated to species j is actually low and the
60 originality of this species is in fact low (e.g., species 1 and 2 in Fig. 1d,e). Inversely, consider
61 that species j has low distinctiveness in the species pool (where abundance data is discarded).
62 Species j may still be effectively original in an assemblage where its abundance and those of
63 its sibling, close species are all low (e.g. species 3 to 8 in Fig. 1d,e). Hereafter, we will refer
64 to this abundance-based definition of FP-originality as the effective FP-originality.
65 Combining the different aspects of a species rarity (its low abundance; the distinctiveness of
66 its traits; its isolated position in the phylogeny), for the scope of this paper, we will thus
67 consider two intuitive conditions that a measure of effective FP-originality should respect.

68 Consider an assemblage composed of N species with relative abundances p_j
69 ($j = 1, 2, \dots, N$), with $0 < p_j \leq 1$ and $\sum_{j=1}^N p_j = 1$. The two conditions are:

70

71 C1. the effective originality of a given species j should increase with its functional or
72 phylogenetic distinctiveness with respect to the individuals of other species in the assemblage,
73 and

74

75 C2. the effective originality of a given species j should increase with its abundance-based
76 rarity, a decreasing function of p_j .

77

78 In our context, the effective originality of a species can thus be considered as its quality of
79 being of ecological interest because it is special, all both rare, unique and distinct from all
80 other species in an assemblage.

81

82 Our aim here is to develop a unifying framework that demonstrates the direct connections
83 between community-level measures of diversity, and species-level measures of rarity,
84 distinctiveness and effective originality. Thanks to this framework, we offer flexible
85 quantitative tools, as guides to conservation strategies, where the influence of abundant versus
86 rare, and ordinary versus original, species is understood and controlled. Our framework relies
87 on, and combines, three abundance-weighted measures of originality: Cadotte et al. (2010)
88 *AED* index and Kondratyeva et al. (2019) *O* index for phylogenetic originality; and Ricotta et
89 al. (2016) *K* index for functional originality. These measures of originality have the advantage
90 to be linked with standard measures of diversity: Faith phylogenetic diversity (PD; Faith
91 1992) for the measure of Cadotte et al., an abundance-weighted generalization of Faith's PD
92 (Pavoine et al., 2009) for the measure of Kondratyeva et al. and Rao's quadratic entropy
93 (hereafter more simply named quadratic diversity; Rao, 1982) for the measure of Ricotta et al.
94 We thus extend below these three originality indices and unify them in a common framework
95 on the link between community-level diversity indices, and species-level rarity,
96 distinctiveness and originality indices.

97

98 **2. Quadratic diversity as a mean of effective originalities**

99

100 Several diversity indices can be viewed as functions of distinctiveness or effective
101 originalities. For example, Isaac et al. (2017) developed the index ED of evolutionary
102 distinctiveness which is a partitioning of Faith (1992) phylogenetic diversity index into
103 individual species contributions; Ricotta et al. (2016) showed that quadratic diversity can be
104 viewed as mean species originality; Violle et al. (2017) underlined that Webb et al. (2002)
105 MPD and NNTD indices of phylogenetic diversity can be also viewed as mean species
106 distinctiveness and easily translated to the context of functional diversity (see Kondratyeva et
107 al. 2019 for a review of such relationships between distinctiveness or effective originality and
108 diversity). Our framework relies on several diversity indices that can be viewed as weighted
109 means of effective originalities, in other words as expected effective originalities. Here, we
110 start with one of such indices, the quadratic diversity, and, in the next section, consider
111 parametric extensions of it. Let d_{ij} be the FP-dissimilarity between species i and j such that
112 $d_{ij} \geq 0$ and $d_{jj} = 0$. Dealing with FP-diversity, we can define the FP-distinctiveness of species
113 j as the weighted mean FP-dissimilarity of j from all other species in the assemblage (Ricotta
114 et al., 2016):

$$116 \quad D_j = \sum_{i \neq j}^N \frac{p_i}{1 - p_j} d_{ij} \quad (1)$$

117
118 where the quantity $p_i/(1-p_j)$ is the relative abundance of species i ($i \neq j$) with
119 $\sum_{i \neq j}^N p_i/(1-p_j) = 1$. Note that D_j is equal to Ricotta et al. (2016) \bar{K}_i index and is
120 equivalent to Violle et al. (2017) D_i index as underlined by Grenié et al. (2017). We chose to
121 name it here D for "Distinctiveness". D_j satisfies condition C1 of a measure of effective
122 originality but not condition C2, as it does not depend on the abundance-based rarity of
123 species j (only on the relative abundance of other species and on the FP-dissimilarity with
124 other species). A community-level measure of expected FP-distinctiveness defined as

$$125 \quad D = \sum_{j=1}^N p_j \times D_j$$

would not behave as an index of diversity (see Appendix A for details).

126
127 An index of FP-diversity can however be obtained by combining a species abundance-based
128 rarity with its FP-distinctiveness. For d_{ij} in the range $[0, 1]$, consider s_{ij} , the similarity

129 between species i and j calculated as $s_{ij} = 1 - d_{ij}$. Let $\omega_j = \sum_{i=1}^N p_i s_{ij}$ be the ordinariness of
 130 species j , i.e., the expected similarity between an individual of species j and an individual
 131 chosen at random in the assemblage, including the individuals of species j itself. According to
 132 Leinster and Cobbold (2012), ω_j can be thus interpreted as the relative abundance of all
 133 species that are FP-similar to j . Since $\sum_{i \neq j}^N p_i d_{ij} = 1 - \omega_j$, we have:

134

$$135 \quad D_j = \frac{1 - \omega_j}{1 - p_j} \quad (2)$$

136

137 The denominator of Eq. 2, $\rho_j = 1 - p_j$, is the rarity of species j according to the well-known
 138 Simpson diversity (Simpson, 1949; Patil and Taillie, 1982). The numerator of Eq. 2,
 139 $O_j = 1 - \omega_j$ is identical to the species-level originality index K of Ricotta et al. (2016) that
 140 we mentioned in the Introduction section. O_j satisfies both conditions C1 and C2 of an index
 141 of effective originality. The corresponding community-level measure of expected effective
 142 originality equals the quadratic diversity:

143

$$144 \quad Q = \sum_{j=1}^N p_j \times O_j = \sum_{j=1}^N p_j \sum_{i=1}^N p_i d_{ij} \quad (3)$$

145

146 the abundance-weighted average FP-dissimilarity between any two species in the assemblage.
 147 In contrast to FP-distinctiveness D_j , effective FP-originality O_j accounts for the abundance of
 148 species j itself: to evaluate the rarity of the biological characters of a focal species when
 149 abundance data are considered, then the abundance of the focal species itself has to be
 150 considered. For example, in Fig. 1d, according to index D_j , species #1 is distinct because,
 151 among the 9 other species, each represented by one individual, only one species share its
 152 morphological aspects. However according to O_j , the effective originality of species #1 is low
 153 because this species is represented in the assemblage by 30 individuals, which amounts to
 154 77% of the size of the assemblage. D_j and O_j thus drive different points of view on a species:
 155 its distinctiveness and its effective originality, respectively.

156

157 **3. Parametric generalizations**

158

159 As regards the measurement of community-level diversity, we consider below two possible
 160 parametric extensions of quadratic diversity. The parameter α of the first one controls the
 161 importance given to ordinary species in opposition to effectively original species:

162

$$163 \quad {}^\alpha K = \sum_{j=1}^N p_j \times \frac{1 - \omega_j^{\alpha-1}}{\alpha - 1} \quad (4)$$

164

165 Eq. 4 was first developed by Ricotta and Szeidl (2006). For $\alpha = 2$, ${}^2K = Q$ and for α tending
 166 to 1, it is a generalization of the Shannon index (Shannon, 1948; Ricotta and Szeidl, 2006).

167 When parameter α in ${}^\alpha K$ increases, then ordinary species (i.e. those with both low rarity and
 168 low abundance weighted distinctiveness) are given increasingly important weights in the
 169 measurement of FP-diversity. We develop in Table 1 a decomposition of ${}^\alpha K$ in terms of
 170 rarity, distinctiveness and originality (see details and proofs in Appendix A). With ${}^\alpha K$, the

171 effective originality of a species is measured by a single formula $O_j = 1 - \omega_j = \sum_{i \neq j}^N p_i d_{ij}$
 172 that conveys a single viewpoint on effective originality: the average FP-dissimilarity between
 173 a focal species j and all species from the assemblage (including the focal species itself).
 174 Knowing this unique definition of effective originality, varying α in ${}^\alpha K$ thus enables to
 175 control how much the effectively original species versus the ordinary ones drives the level of
 176 FP-diversity.

177

178 We develop here the following alternative to index ${}^\alpha K$, named ${}^\alpha K^*$, where parameter α
 179 controls species' abundance instead of ordinariness, i.e. α controls the importance given to
 180 abundant species in opposition to rare species:

181

$$182 \quad {}^\alpha K^* = \sum_{j=1}^N p_j \times \frac{\sum_{c=1}^{N-1} u_{c|j} (1 - p_{c|j}^{\alpha-1})}{\alpha - 1} \quad (5)$$

183

184 where $c|j$ indicates the c th closest species from species j ; $u_{c|j} = d_{c|j,j} - d_{c-1|j,j}$ for $c > 1$ with $0|j$
 185 $= j$ and thus $d_{0|j,j} = 0$ and $p_{0|j} = p_j$; and $p_{c|j} = \sum_{i=0}^{c-1} p_{i|j}$. Compared with ${}^\alpha K$, ${}^\alpha K^*$ does not
 186 require that the d_{ij} vary in $[0,1]$; the only necessary condition is $d_{ij} \geq 0$. For $\alpha = 2$, ${}^2K^* = Q$.

187 For α tending to 1, it is a generalization of the Shannon index different from that associated
 188 with index ${}^\alpha K$ (Appendix A). We provide in Table 1 a decomposition of ${}^\alpha K^*$ in terms of
 189 rarity, distinctiveness and originality (see details and proofs in Appendix A). With ${}^\alpha K^*$, the
 190 effective originality of a species is measured by a parametric index
 191 ${}^\alpha O_j^* = \sum_{c=1}^{N-1} u_{c|j} (1 - p_{c|j}^{\alpha-1}) / (\alpha - 1)$ that conveys different viewpoints on effective originality
 192 depending on the value of parameter α : varying α in ${}^\alpha K^*$ enables to control how much the
 193 abundant species versus the rare ones drive the levels of FP-distinctiveness, effective
 194 originality and diversity. In ${}^\alpha O_j^*$, $(1 - p_{c|j}^{\alpha-1}) / (\alpha - 1)$ represents the global rarity of the set of c
 195 species that have the smallest FP-dissimilarity with species j (including j itself) and $u_{c|j}$
 196 represents the excess of FP-dissimilarity with species j brought by the c th closest species
 197 compared to the $c-1$ th closest species. Overall, the effective originality of species j , as
 198 measured by ${}^\alpha O_j^*$, can be viewed as the rate at which the rarity of species tends to decrease
 199 with the FP-dissimilarity to the focal species j (Fig. 2). Low rate as in Scenario a of Fig. 2
 200 corresponds to high effective originality as it means that abundant species tend to be FP-
 201 distant from the focal species; inversely, high rate as in Scenario c of Fig. 2, corresponds to a
 202 low effective originality as it means that abundant species tend to be FP-close to the focal
 203 species.

204
 205 For the specific case of species characterized by their rooted phylogenetic tree, the parametric
 206 index ${}^\alpha I$ of phylogenetic diversity proposed by Pavoine et al. (2009) (Table 2) is equivalent to
 207 ${}^\alpha K^*$ applied to d_{ij} = the sum of branch lengths on the path from tip j to its most recent
 208 common ancestor with species i . In addition, in this particular case the associated species
 209 effective originalities (Table 2) are equivalent to those introduced by Kondratyeva et al.
 210 (2019) who expressed index ${}^\alpha I$ of phylogenetic diversity as a mean of the species originalities.
 211 For $\alpha = 0$, the phylogenetic effective originality associated with ${}^\alpha I$ (Table 2) reduces to
 212 $AED_j \times n - H_j$ (Kondratyeva et al. 2019) where AED is Cadotte et al. (2010) index that we
 213 referred to in the Introduction section, n is the total number of individuals in the assemblage
 214 and H_j is the sum of branch lengths from the focal species j to the root of the tree. This links,
 215 in a unified framework, Ricotta et al. K , Kondratyeva et al. O and Cadotte et al. AED
 216 measures of abundance-weighted originality. ${}^\alpha I$ provides thus a consistent alternative to ${}^\alpha K^*$
 217 in the special case of a phylogenetic tree and we depict its writing in terms of rarity,

218 distinctiveness and effective originality in Table 2. Similarly, we introduce in Table 2 a
 219 rewriting (named ${}^\alpha Y$) of index ${}^\alpha K$ and its associated indices of distinctiveness and
 220 originality, in the special case where species are tips of a phylogenetic tree and the
 221 phylogenetic distance between species j and i is calculated as the sum of branch lengths on the
 222 path from tip j to its most recent common ancestor with species i . All functions of rarity,
 223 distinctiveness and effective originality discussed here are thus connected in a global
 224 framework in Tables 1 and 2, highlighting the strong links between different facets of rarity,
 225 distinctiveness, originality and diversity.

226

227 All these diversity indices can be easily transformed into equivalent numbers of species: the
 228 number of evenly and maximally dissimilar species needed to obtain the level of FP-diversity
 229 observed in an assemblage (Tables 1 and 2). The functions that transform the diversity indices
 230 we discussed here in terms of equivalent numbers of species do not change the way species
 231 assemblages are ranked from the least to the most diverse (Appendix A).

232

233 **4. The special case of abundance-free distinctiveness indices**

234

235 Abundance-free distinctiveness indices, particularly phylogenetic distinctiveness indices, are
 236 often used in conservation biology (Isaac et al., 2007; Redding et al., 2014). Imposing equal
 237 relative abundances for all species in our framework provides a useful family of such
 238 distinctiveness indices where abundance data is discarded as outlined below (see a complete
 239 introduction of the family in Appendix B).

240

241 In the special case of equal abundance for all species ($p_j=1/N$ for all j), the phylogenetic
 242 distinctiveness index ${}^\alpha \Delta^*$ associated with phylogenetic diversity index ${}^\alpha I$ (Table 2)
 243 becomes:

244

$$245 \quad {}^\alpha \Delta_{eq}^* = \sum_{b \in C(j, \text{root})} L_b \left(\frac{N^{\alpha-1} - N_b^{\alpha-1}}{N^{\alpha-1} - 1} \right) \quad (6)$$

246

247 where N_b stands for the number of species that descend from branch b and $C(j, \text{root})$ for the
 248 set of branches between species j , tip of the phylogenetic tree, and the root of the tree.

249

250 ${}^{\alpha}\Delta\text{eq}^*$ thus provides a parametric alternative to the most widely used index of species
 251 distinctiveness named "evolutionary distinctiveness" (ED ; Isaac et al., 2007) or "Fair-
 252 Proportion" (Redding et al., 2014) and whose formula is:

253

$$254 \quad ED_j = \sum_{b \in C(j, \text{root})} \frac{L_b}{N_b} \quad (7)$$

255

256 Both ED and ${}^{\alpha}\Delta\text{eq}_j^*$ can be seen as the sum, on the path from a tip to root, of the product of a
 257 branch length times a decreasing function of the number of species descending from that
 258 branch. While by construction, the value of ED is dominated by the length of the terminal
 259 branch that connects species j to the tree (Redding et al., 2014), the parameter α in ${}^{\alpha}\Delta\text{eq}^*$
 260 allows controlling the influence of this terminal branch (see Appendix B for more details).

261

262 Although the diversity indices of Tables 1 and 2 are meaningful only for nonnegative values
 263 of α (as otherwise rarity function rapidly tends to infinity for low values of α), negative values
 264 are meaningful for calculating ${}^{\alpha}\Delta\text{eq}_j^*$. Indeed, ${}^{\alpha}\Delta\text{eq}_j^*$ varies between the length, h_j , of the
 265 terminal branch that connects j to the rest of the tree (${}^{\alpha}\Delta\text{eq}_j^* \xrightarrow{\alpha \rightarrow -\infty} h_j$, Appendix B), and
 266 the distance, $H_j = \sum_{b \in C(j, \text{root})} L_b$, from tip j to the root of the tree (${}^{\alpha}\Delta\text{eq}_j^* \xrightarrow{\alpha \rightarrow +\infty} H_j$,
 267 Appendix B). Another notable case is obtained with $\alpha = 2$ because

268

$$269 \quad {}^2\Delta\text{eq}_j^* = \sum_{b \in C(j, \text{root})} L_b \left(\frac{N - N_b}{N - 1} \right) = \frac{\sum_{i=1}^N d_{ij}}{N - 1} \quad (8)$$

270

271 where d_{ij} is the sum of branch lengths on the path from tip j to its most recent common
 272 ancestor with species i . As a consequence, by varying parameter α between $-\infty$ and 2 in
 273 ${}^{\alpha}\Delta\text{eq}_j^*$ one can obtain a range of strongly connected indices of phylogenetic distinctiveness
 274 along a gradient that goes from a strong influence of the terminal branch to the average
 275 distance between a species and all others in phylogenetic tree. ${}^{\alpha}\Delta\text{eq}_j^*$ can be seen as a
 276 quantification of the extent to which the loss of species j would weaken/threaten phylogenetic
 277 diversity, with two extreme views: α tending to $-\infty$, where the loss of species j would imply
 278 the loss of its unique phylogenetic history (terminal branch length); and α tending to $+\infty$,

279 where the loss of species j would imply that all its phylogenetic history is threatened (length
280 of the path between j and the root of the tree). Varying α between these two extreme cases
281 controls the extent to which a phylogenetic branch from which species j descends can be
282 considered secure if one or more other species also descend from it. The parametric index of
283 distinctiveness makes it possible to study and compare all points of view in a consistent way
284 and to know according to which point of view, if any, the safeguarding of a species should be
285 considered a priority. Index ${}^{\alpha}\Delta_{eq_j}^*$ thus responds to the critical need in conservation science
286 to justify and organize indices of evolutionary distinctiveness which currently represent
287 different trade-offs between the unique evolutionary history represented by a species versus
288 its average distance to all other species, trade-offs that may impact on-the-ground decision on
289 conservation priority (Redding et al., 2014). Similarly, using even abundance in the
290 distinctiveness index ${}^{\alpha}D_j^*$ (Table 1) provides a measure of FP-distinctiveness ${}^{\alpha}Deq^*$ whose
291 values vary (by varying α) from the smallest FP-dissimilarity between j and any other species
292 ($\alpha \rightarrow -\infty$), through the average FP-dissimilarity to all other species ($\alpha = 2$), to the largest FP-
293 dissimilarity between j and any other species ($\alpha \rightarrow +\infty$) (Appendix B).

294

295 **5. Worked example**

296

297 *5.1. Data*

298

299 As a case study, we considered changes in bat phylogenetic diversity across a disturbance
300 gradient in the Selva Lacandona of Chiapas, Mexico. Medellín et al. (2000) collected the
301 abundance of bat species in four habitats (rainforests, cacao plantations, old fields and
302 cornfields). We obtained the phylogeny of 34 observed species using a consensus ultrametric
303 tree (function `consensus.edge`, R package `phytools`; Revell, 2012) on 9,999 credible birth-
304 death, tip-dated completed trees downloaded from <http://vertlife.org/phylosubsets> on
305 2021/02/12 (Upham et al., 2019). For species names, we followed Upham et al. (2019).
306 Branch lengths on the consensus tree were obtained using mean edge length, ignoring credible
307 trees in which the branch is absent (Revell, 2012).

308

309 *5.2. Analyses*

310

311 Our objective in the analysis of this dataset, in addition to simply illustrate our theoretical
312 developments, was to depict how disturbance changes the level of bat phylogenetic diversity
313 by identifying which among the rarity, distinctiveness, and effective originality of bat species
314 is/are affected. For that, we calculated, in each habitat, the phylogenetic diversity using ${}^{\alpha}Y$
315 and ${}^{\alpha}I$, for α varying between 0 and 3 with a step of 0.1. We explored then in detail the
316 patterns of phylogenetic diversity in terms of effective originality. Additionally, we analyzed
317 species distinctiveness in the species pool (using indices ED and ${}^{\alpha}\Delta_{eq}^*$ that both discard
318 abundance data).

319

320 5.3. Results

321

322 In the species pool, for values of α of 1, 2 and 3, according to ${}^{\alpha}\Delta_{eq}^*$ the two Vespertilionidae
323 species (*Bauerus dubiaquercus* and *Myotis keaysi*) are the most phylogenetically distinct,
324 being the sole members of their clade in the dataset (Fig. 3). The least distinctive species are
325 the two *Artibeus* species as they are in the most species-rich part of the phylogenetic tree,
326 where both terminal and internal branches are numerous and relatively short. For low values
327 of α , the distinctiveness is strongly influenced by the length of the terminal branches. This has
328 two main consequences: the species perceived as least distinct are the two *Carollia* species
329 that diverged recently; and the two Vespertilionidae species are no longer perceived as the
330 most distinct, as their terminal branches are shorter than those of *Thyroptera tricolor*,
331 *Pteronotus parnellii* and *Mormoops megalophylla*. The case, $\alpha = 0$ is the closest to ED
332 (Pearson correlation = 1). For ${}^0\Delta_{eq}^*$ and ED , *T. tricolor* is the most distinctive followed by
333 the two Vespertilionidae and then *P. parnellii* and *M. megalophylla*; the least distinctive are
334 the *Artibeus* species followed by the *Dermanura* species and then the *Carollia* species. A
335 more complete visualization of variation in ${}^{\alpha}\Delta_{eq}^*$ as a function of α can be found in video
336 S1.

337

338 Phylogenetic diversity decreases along the disturbance gradient (from rainforest, through
339 cacao plantation and old fields, to cornfields) whatever the value of α we considered (from 0
340 to 3 in Fig. 4) for ${}^{\alpha}I$ and for high values of α ($\alpha \geq 1.5$ in Fig. 4) for ${}^{\alpha}Y$. With ${}^{\alpha}Y$, for low
341 values of α ($\alpha < 1.5$ in Fig. 4) the phylogenetic diversity of old fields exceeds that of cacao
342 plantations; and as α approaches zero ($\alpha < 0.5$ in Fig. 4) the phylogenetic diversity of old

343 fields even exceeds that of the rainforest. This is because old fields contain both *B.*
344 *dubiaquercus* and *M. keaysi*, the two Vespertilionidae species with the highest average
345 phylogenetic distance to all other species, while only one of them was observed in the
346 rainforest and in the cacao plantation, and none in the cornfields (Fig. 5). Indeed index ${}^{\alpha}Y$, as
347 ${}^{\alpha}K$, uses the effective originality associated with the quadratic diversity and a parameter α
348 that controls the relative importance given to ordinary species compared to effectively
349 original species. For low values of α , the influence of the most effectively original species in
350 the measurement of phylogenetic diversity increases. In contrast as shown above, α in ${}^{\alpha}I$, as
351 in ${}^{\alpha}K^*$, controls the importance given to abundant compared to rare species, influencing the
352 way the effective originality of a species is perceived (with strong influence of the terminal
353 branch for low values of α). Compared to other habitats, cornfields lacked effectively original
354 species (Fig. 5; see also Video S2 for a more complete visualization of variation in species
355 originality ${}^{\alpha}\Omega^*$ as a function of α). Phylogenetic diversity in cornfields was thus always the
356 smallest (whatever α ; and even strongly lower than that of other habitats when α approaches
357 zero; Fig. 4). Species with the least effective originality were often either the *Carollia* species
358 or the *Artibeus* species depending on the habitat and the value of α considered (Fig. 5).
359 However the relatively high abundance of *P. parnelii* observed in the rainforest, made this
360 species perceived as one of the least effectively original in this habitat when rare species were
361 given high weights in the measurement of phylogenetic diversity ($\alpha = 0$, index ${}^{\alpha}I$, Fig. 5),
362 despite its high distinctiveness (Fig. 3 and 5; see also Video S3 for a more complete
363 visualization of variation in species distinctiveness ${}^{\alpha}\Delta^*$ as a function of α).

364

365 **6. Discussion**

366

367 The contribution of a given species to the biodiversity of an assemblage thus depends on its
368 rarity and on the rarity of its FP-characteristics. Starting from Ricotta et al. (2016) measure of
369 species-level originality, we have shown that quadratic diversity can be expressed as a mean
370 of effective FP-originality values over all species in an assemblage, and that Faith's (1992)
371 phylogenetic diversity index and Cadotte et al. (2010) and Kondratyeva et al. (2019) measures
372 of effective phylogenetic originality can be both related to parametric extensions of quadratic
373 diversity. This led us to develop a unified framework (summarized in Tables 1 and 2) where
374 diversity, rarity, distinctiveness and originality measures are intrinsically linked.

375

376 The parametric indices developed in this framework allow regulating the importance given to
377 abundant and ordinary species in FP-diversity measures. They include generalizations of the
378 Shannon index (for $\alpha \rightarrow 1$) and the Simpson index (for $\alpha = 2$) to functional and phylogenetic
379 data. By increasing the value of their parameter α , the weight given to abundant and ordinary
380 species in the measurement of FP-diversity increases in comparison with the weight given to
381 rare and effectively original species. Low values of α may thus indicate regions with high
382 diversity but a diversity that may be threatened by the rarity of the most effectively original
383 species. Low values of the parameter α could thus be particularly relevant to obtain
384 biodiversity indicators directed to the preservation of rare and distinct species while
385 maintaining a high level of global diversity (e.g., Hidasi-Neto, Loyola and Cianciaruso,
386 2015). Increasing α may reveal how much phylogenetic diversity depends on these rare
387 species.

388

389 In our case study, when effectively original species were given high weights in the
390 measurement of diversity, the old fields had the highest measure of phylogenetic diversity.
391 This was due to the presence of the two species from the Vespertilionidae family. Although
392 distinct in our study area, the Vespertilionidae species represent a large family of bats at a
393 global scale. This illustrates how the measurement of a species' distinctiveness is dependent
394 on the reference species assemblage, on the data used to characterize species (here
395 phylogeny), and thus on the taxonomic, phylogenetic and spatial scales of a study. A species'
396 rarity, when measured relatively to the rarity of all other species rather than as an absolute
397 value, is also dependent on these scales. According to the International Union for the
398 Conservation of Nature (IUCN, 2021), all species of our case study are least-concern (i.e.,
399 neither threatened nor near threatened) at a global scale with either stable or unknown
400 population trends except *M. megalophylla* that is least-concern but with decreasing population
401 trends, and *B. dubiaquercus* that is near threatened (+ *Vampyressa pusilla* classified as data
402 deficient). Our results showed that *M. megalophylla* and *B. dubiaquercus* are among the most
403 phylogenetically distinct species in our study area. Only one individuals of *M. megalophylla*
404 and three individuals of *B. dubiaquercus* were observed in our case study (out of a total of
405 2405 bats). *M. megalophylla* was observed in old fields and *B. dubiaquercus* in rainforest and
406 old fields. These scarce occurrences prevented us to evaluate the possible direct effects of
407 agriculture on their population size. However, both species are aerial insectivorous species
408 (Rodríguez-Aguilar et al., 2017) and insect-eating bats are known to be affected when high
409 pesticide inputs are used in plantations (e.g., Estrada et al., 2006). Other studies showed that,

410 in addition to cave collapse and vandalism, threats on *M. megalophylla* and *B. dubiaquercus*
411 also concern their sensitivity to disturbance and habitat loss (IUCN, 2021). In an urban
412 context in the highlands of Chiapas, it was shown that abundance of *B. dubiaquercus* tends to
413 diminish outside forest; and the activity of both *M. megalophylla* and *B. dubiaquercus*
414 increases with tree density (Rodríguez-Aguilar et al., 2017).

415

416 The whole framework can thus be used in ecological studies to reveal the relative
417 contributions of each species to biodiversity, and to depict these contributions in terms of
418 abundance-based rarity, species-level FP-distinctiveness and effective FP-originality. It can be
419 applied from local to global scales provided abundance data are available and the species
420 assemblage is clearly delimited. In the context of the sixth species mass extinction (Ceballos
421 et al., 2015), our framework could be used to evaluate how changes in species contributions
422 may impact ecosystem services, via changes in biodiversity levels. It would allow following
423 changes in species contribution to biodiversity under novel environmental conditions.
424 Relative abundances may change under novel environmental conditions with rare species for
425 example benefiting from the reduction of population size of other species. If these species are
426 functionally rare, an increase in their abundance can considerably increase the functional
427 diversity of an assemblage and modify ecosystem functioning and the connected ecosystem
428 services. The bioprospecting or option value associated to a species notably advocates as a
429 precaution principle to protect species with the aim to give option to discover new uses of
430 these species in the future, especially in medicine. Here functionally and phylogenetically
431 unique species may be considered as disproportionately contributing to bioprospecting value
432 (Dee et al., 2019). Where and when they have low abundance, they might be in need of urgent
433 conservation actions (e.g., the Van Gelder's bat, *B. dubiaquercus*, of our case study). Indeed,
434 if environmental changes inversely lead to the extinction of currently effectively original
435 species with key role in the ecosystem, these changes could yield the biological system to
436 collapse, with potential drastic loss of ecosystem services. Effectively original species may
437 for example be directly threatened when they are increasingly targeted by economic activities
438 because of their combined aspects of rarity (e.g., private collections of rare, distinct
439 specimens; safaris spotting rare, distinct species; e.g., Holden and McDonald-Madden, 2017).

440

441 Links between the functional distinctiveness of a species and its abundance-based rarity have
442 for example been observed in European estuarine fish communities, with identified potential
443 consequences on the stability of these communities (Teichert et al., 2017). Links between the

444 functional distinctiveness of a species and its risk of extinction have also sometimes been
445 observed: e.g., among anurans in Ecuador (Menéndes-Guerrero et al., 2020); globally in
446 mammals and birds (Cooke et al., 2020). Species which are rare both in terms of low
447 abundance and phylogenetic distinctiveness have sometimes been found to be threatened. For
448 example, Uchida et al. (2019) observed that, in semi-natural grasslands of south west Japan,
449 low-abundance and phylogenetically distinct species were threatened by land-use
450 intensification, resulting in plant phylogenetic diversity loss.

451

452 To make our mathematical framework readily available for data analysis, we have updated
453 and added R functions in package `adiv` of R (Pavoine 2020, 2021; R Core Team, 2021) (see
454 also Appendix C). `adiv` is dedicated to the analysis of diversity in ecology and now integrates
455 a range of functions to measure both species-level originality and community-level diversity.
456 It constitutes thus a useful tool to implement our framework. Compared to previous studies
457 that connected a single index of distinctiveness or of effective originality to a single diversity
458 index (e.g. Isaac et al., 2007; Ricotta et al., 2016; Violle et al., 2017), our parametric
459 framework unifies, in a mathematical scheme, various well-used measures of diversity,
460 distinctiveness and effective originality, previously scattered in the literature and developed in
461 different contexts. It also allows disentangling the effects of rarity, distinctiveness, and
462 effective originality on biodiversity levels to better identify how species together contribute to
463 biodiversity levels. As such, it has the potential to improve studies on the mechanisms by
464 which global changes affect biodiversity levels, by identifying which aspect of biodiversity
465 they impact, be it rarity, functional distinctiveness or the global effective originality of some
466 species, which was not possible with previously published connections between diversity and
467 either rarity, distinctiveness, or effective originality. By developing it, we revealed a
468 parametric family of phylogenetic distinctiveness indices that could complement the most
469 currently used "evolutionary distinctiveness" index (e.g. Isaac et al., 2007; Ibáñez-álamo et
470 al., 2017; Potter 2018; Cooke et al., 2020) whose values are strongly dominated by the
471 independent evolutionary history of a species (length of terminal branch in a phylogenetic tree
472 with the species as tip; Redding et al., 2014). The parametric family indeed allows controlling
473 the degree of influence of this independent evolutionary history on the distinctiveness index.
474 We provide also an equivalent parametric family for functional distinctiveness. Overall, our
475 framework helps to provide justification, explanation and order when applying a quantitative
476 reasoning to biodiversity, contributing to the development of efficient biodiversity indicators
477 for conservation strategies.

478

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481 *commercial, or non-for-profit sectors.*

482

483 **Data statement**

484 *R scripts and data have been placed in Appendixes C to E. We also integrated scripts in*
485 *package 'adiv' (Pavoine 2020, 2021) into functions named 'distinctAb', 'distinctDis',*
486 *'distinctTree', 'FPdivparam', 'plot.FPdivparam' as indicated in Appendix C, and data in the*
487 *dataset named 'batcomm'.*

488

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613

Table 1

Summary of the links between rarity, distinctiveness, originality, and diversity developed in the main text with diversity indices Q , ${}^\alpha K$ and ${}^\alpha K^*$.

| | Quadratic diversity ^a | First parametric extension ^a | Second parametric extension ^a |
|----------------------------------|--|--|---|
| Species-level | | | |
| FP-distinctiveness | $D_j = \sum_{i \neq j}^N \frac{p_i}{1-p_j} d_{ij}$ | ${}^\alpha D_j = \frac{1 - \left(\sum_{i=1}^N p_i s_{ij} \right)^{\alpha-1}}{1-p_j^{\alpha-1}}$ | ${}^\alpha D_j^* = \frac{\sum_{c=1}^{N-1} u_{clj} (1-p_{clj}^{\alpha-1})}{(1-p_j^{\alpha-1})}$ |
| abundance-based rarity | $\rho_j = (1-p_j)$ | ${}^\alpha \rho_j = \frac{1-p_j^{\alpha-1}}{\alpha-1}$ | ${}^\alpha \rho_j = \frac{1-p_j^{\alpha-1}}{\alpha-1}$ |
| effective originality | $O_j = U_j \times \rho_j$ | ${}^\alpha O_j = {}^\alpha D_j \times {}^\alpha \rho_j$ | ${}^\alpha O_j^* = {}^\alpha D_j^* \times {}^\alpha \rho_j$ |
| Community-level | | | |
| species diversity ^b | $S = \sum_{j=1}^N p_j \rho_j$ $= 1 - \sum_{i=1}^N p_i^2$ | ${}^\alpha S = \sum_{j=1}^N p_j ({}^\alpha \rho_j)$ $= \frac{1 - \sum_{j=1}^N p_j^\alpha}{\alpha-1}$ | ${}^\alpha S = \sum_{j=1}^N p_j ({}^\alpha \rho_j)$ $= \frac{1 - \sum_{j=1}^N p_j^\alpha}{\alpha-1}$ |
| FP-diversity | $Q = \sum_{j=1}^N p_j O_j$ $= \sum_{i=1}^N \sum_{j=1}^N p_i p_j d_{ij}$ | ${}^\alpha K = \sum_{j=1}^N p_j ({}^\alpha O_j)$ $= \sum_{j=1}^N p_j \times \frac{1 - \left(\sum_{i=1}^N p_i s_{ij} \right)^{\alpha-1}}{\alpha-1}$ | ${}^\alpha K^* = \sum_{j=1}^N p_j ({}^\alpha O_j^*)$ $= \sum_{j=1}^N p_j \times \frac{\sum_{c=1}^{N-1} u_{clj} (1-p_{clj}^{\alpha-1})}{\alpha-1}$ |
| Species equivalents ^c | $E = 1 / \sum_{i=1}^N \sum_{j=1}^N p_i p_j s_{ij}$ | ${}^\alpha E = \left(\sum_{j=1}^N p_j \left(\sum_{i=1}^N p_i s_{ij} \right)^{\alpha-1} \right)^{\frac{1}{(1-\alpha)}}$ | ${}^\alpha E^* = \left(\sum_{j=1}^N p_j \left(1 - \frac{\max_i (d_{ij})}{d_{\max}} + \sum_{c=1}^{N-1} \frac{u_{clj}}{d_{\max}} p_{clj}^{\alpha-1} \right) \right)^{\frac{1}{(1-\alpha)}}$ |

^a $Q = {}^2K = {}^2K^*$; FP-components are expressed in terms of dissimilarities ($d_{ij} \geq 0$) or similarities ($s_{ij} = 1 - d_{ij} / d_{\max}$, with $d_{\max} \geq \max_{ij}(d_{ij})$) between species; Notations are identical as in the main text; see Table 2 for the special case of phylogenetic dissimilarities.

^b S = Simpson index (Simpson, 1949; Patil and Taillie, 1982); ${}^\alpha S$ = HCDT index (see e.g., Kondratyeva et al., 2019).

^c See Leinster and Cobbold (2012) who first developed a function similar to ${}^\alpha E$.

Table 2

Adaptation of Table 1 in the case where species are tips of a phylogenetic tree.

| | First parametric extension ^a | Second parametric extension ^a |
|----------------------------------|--|---|
| Species-level | | |
| distinctiveness | ${}^{\alpha}\Delta_j = \frac{1 - \left(\sum_{b \in C(j, \text{root})} \frac{L_b}{H} p_b \right)^{\alpha-1}}{1 - p_j^{\alpha-1}}$ | ${}^{\alpha}\Delta_j^* = \frac{\sum_{b \in C(j, \text{root})} L_b (1 - p_b^{\alpha-1})}{1 - p_j^{\alpha-1}}$ |
| effective originality | ${}^{\alpha}\Omega_j = {}^{\alpha}\Delta_j \times {}^{\alpha}\rho_j$ | ${}^{\alpha}\Omega_j^* = {}^{\alpha}\Delta_j^* \times {}^{\alpha}\rho_j$ |
| Community-level | | |
| FP-diversity ^b | ${}^{\alpha}Y = \sum_{j=1}^N p_j ({}^{\alpha}\Omega_j)$ $= \sum_{j=1}^N p_j \times \frac{1 - \left(1 - \frac{H_j}{H} + \sum_{b \in C(j, \text{root})} \frac{L_b}{H} p_b \right)^{\alpha-1}}{\alpha - 1}$ | ${}^{\alpha}I = \sum_{j=1}^N p_j ({}^{\alpha}\Omega_j^*)$ $= \sum_{j=1}^N p_j \left[\sum_{b \in C(j, \text{root})} L_b \frac{1 - p_b^{\alpha-1}}{\alpha - 1} \right]$ |
| Species equivalents ^c | ${}^{\alpha}E = \left[\sum_{j=1}^N p_j \left(1 - \frac{H_j}{H} + \sum_{b \in C(j, \text{root})} \frac{L_b}{H} p_b \right)^{\alpha-1} \right]^{\frac{1}{1-\alpha}}$ | ${}^{\alpha}E^* = \left[\sum_{j=1}^N p_j \left(1 - \frac{H_j}{H} + \sum_{b \in C(j, \text{root})} \frac{L_b}{H} p_b^{\alpha-1} \right) \right]^{\frac{1}{1-\alpha}}$ |

^a Phylogenetic diversity is here expressed in terms of the length (L_b) and relative abundance (p_b) associated with each branch b of the phylogenetic tree with species as tips. Notations are identical as in the main text; $H \geq \max_j(H_j)$. Abundance-based rarity (${}^{\alpha}\rho_j$) and species diversity (${}^{\alpha}S$) are here identical as in Table 1.

^b ${}^{\alpha}Y = {}^{\alpha}K$ and ${}^{\alpha}I = {}^{\alpha}K^*$ (described in Table 1) if ${}^{\alpha}K$ and ${}^{\alpha}K^*$ are applied to d_{ij} , the sum of branch lengths on the path from tip j to its most recent common ancestor with species i . ${}^{\alpha}I$ was first developed by Pavoine et al. (2009) and expressed in terms of species originalities by Kondratyeva et al. (2019).

^c See Chao et al. (2010) for functions related to ${}^{\alpha}E^*$.

Figure legends

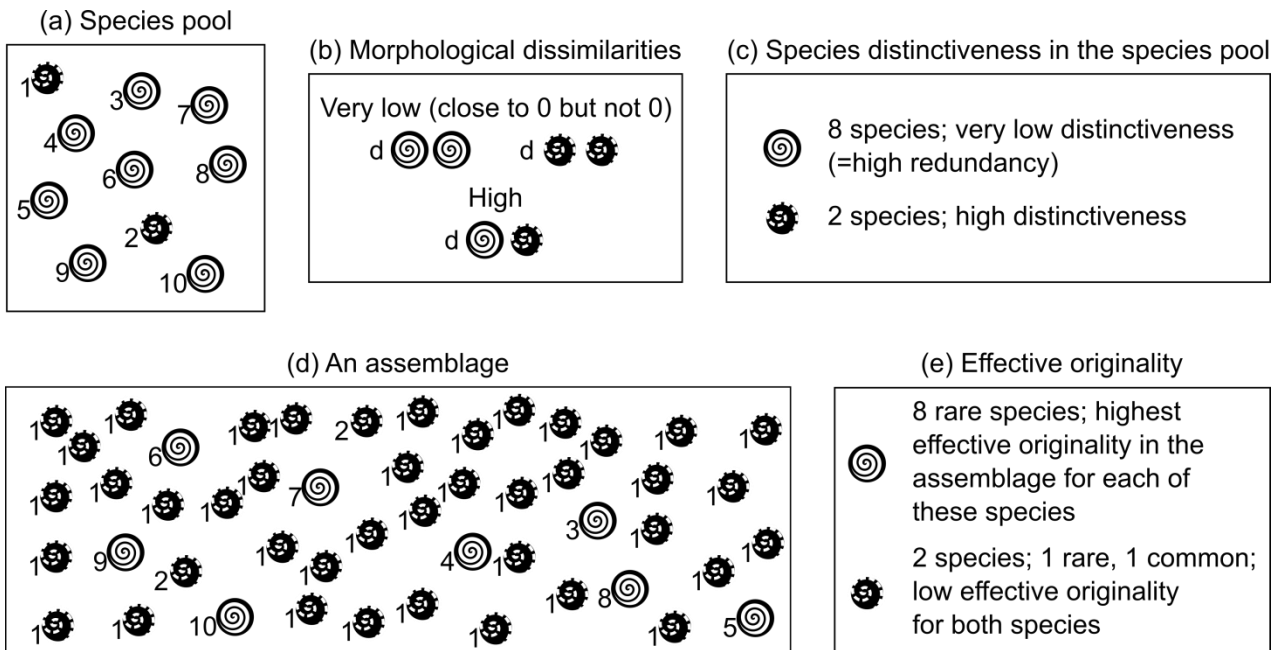


Fig. 1. Theoretical illustration of the concept of effective originality. We considered 10 theoretical species that form the species pool (panel a). We considered the morphological aspects of the species, imposing (panel b) that none of the species is exactly similar to another in the pool but that the species represented by the same symbols share many morphological characteristics. Two species are black with white broken lines and have the most distinct morphology in the species pool (panel c). We considered an assemblage where species numbered 1 is 30 times more abundant than all other species (panel d). Due to the skewed distribution of abundance, in this assemblage the white species with black lines have the highest effective originality (panel e).

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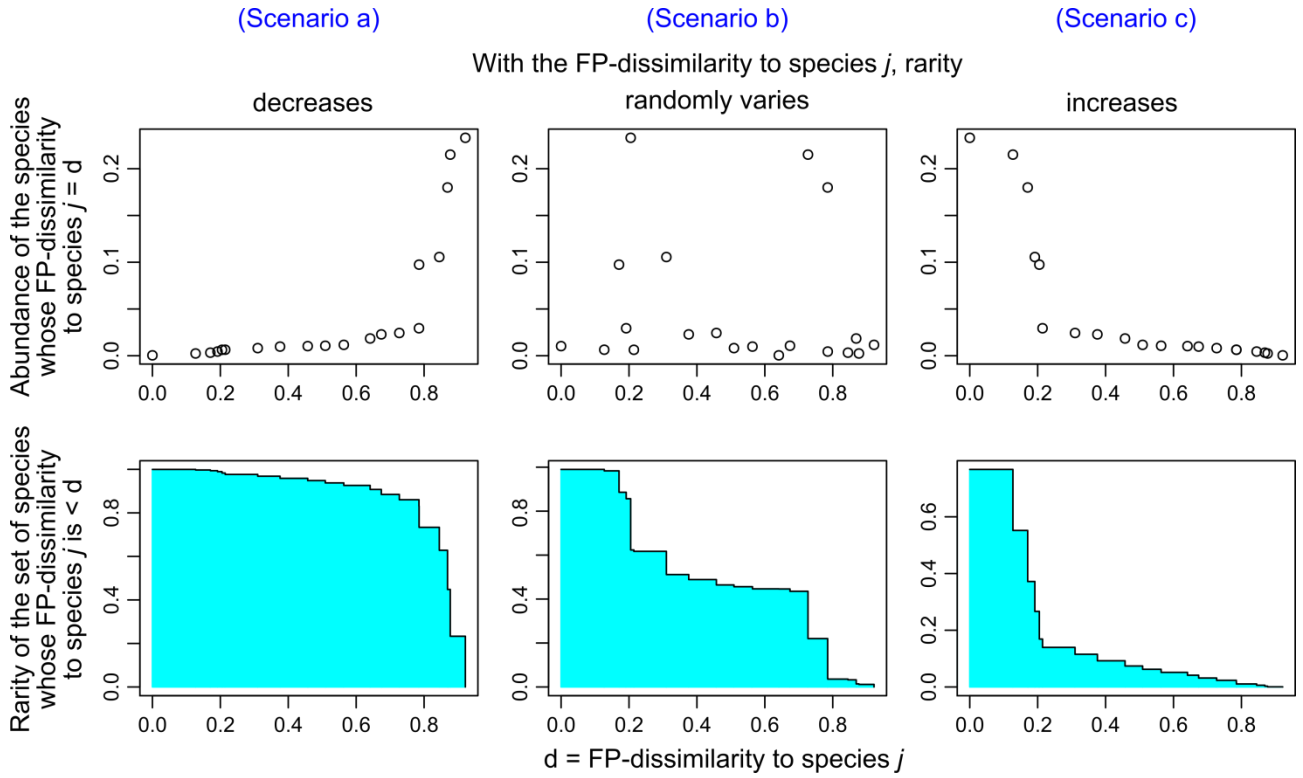


Fig. 2. Illustration of the measurement of effective originality of a species j according to index ${}^{\alpha}O_j^*$. We simulated a set of 20 species, with a standard lognormal distribution for their abundance and a uniform distribution (between 0 and 1) to define the FP-dissimilarities with a focal species j (one of the 20 species). Here we considered $\alpha = 2$ in ${}^{\alpha}O_j^*$ formula but our reasoning is valid for any nonnegative value of α . In Scenario a, species rarity tends to increase with the FP-dissimilarity with species j , while in Scenario c, it tends to decrease. Scenario b is a random scenario (where rarity is independent from the FP-dissimilarity with species j). In each scenario, the top graph provides each species' relative abundance (p_i) as a function of its FP-dissimilarity to species j and the curve in the bottom graph shows how fast the rarity of the set of species whose FP-dissimilarity to species j is lower than a nonnegative value d (as measured by $(1 - p_{c|j}^{\alpha-1})/(\alpha - 1)$ in Eq. 5) decreases with d . In these bottom graphs, ${}^{\alpha}O_j^*$ amounts to the surface of the shaded area below the curve. As expected, the effective originality of species j thus decreases from Scenario a, through Scenario b, to Scenario c.

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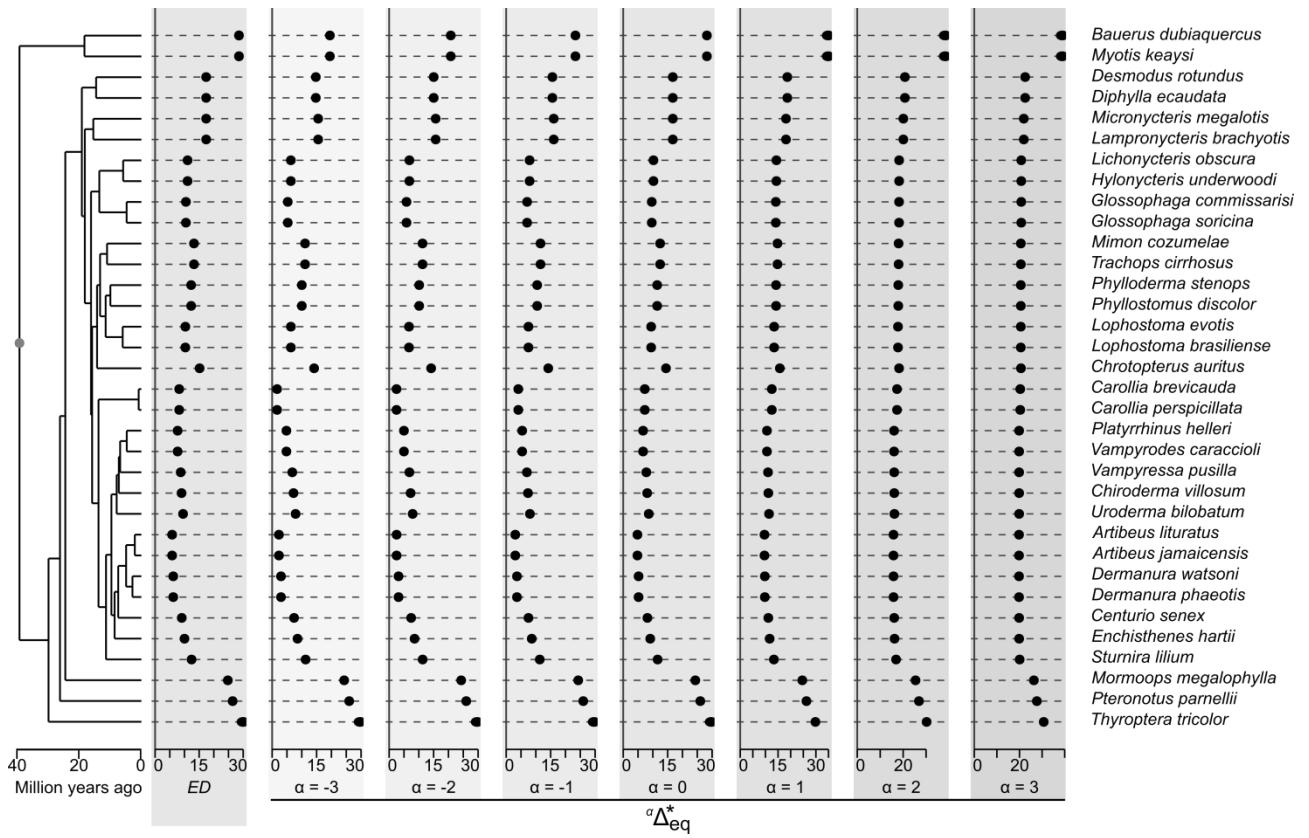


Fig. 3. Phylogenetic species distinctiveness. (measured considering the 34 species of the dataset by *ED* and then ${}^\alpha \Delta_{eq}^*$, from $\alpha = -3$ to $\alpha = 3$ with an increment of 1; the grey dot on the phylogenetic tree indicates the root).

Figure size: Double-column

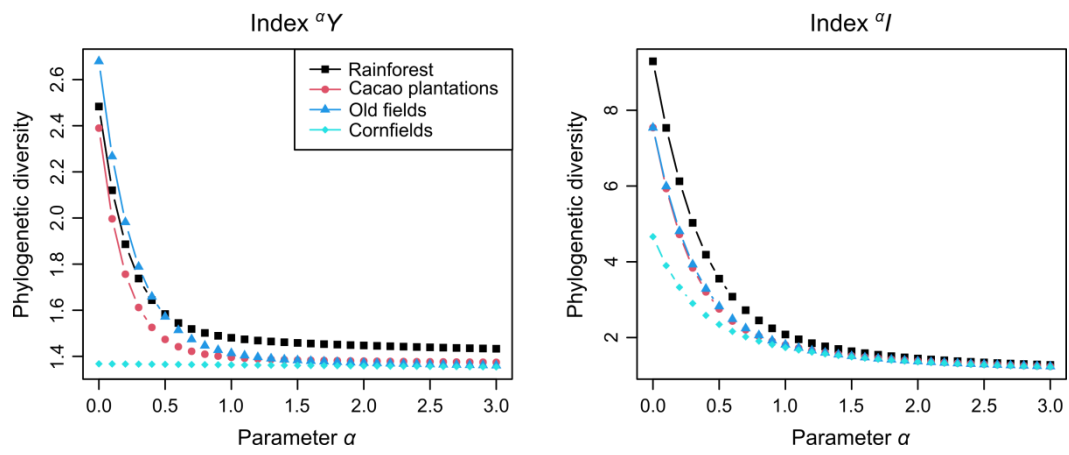


Fig. 4. Phylogenetic diversity of the four habitats. (Indices are here expressed as equivalent numbers of species).

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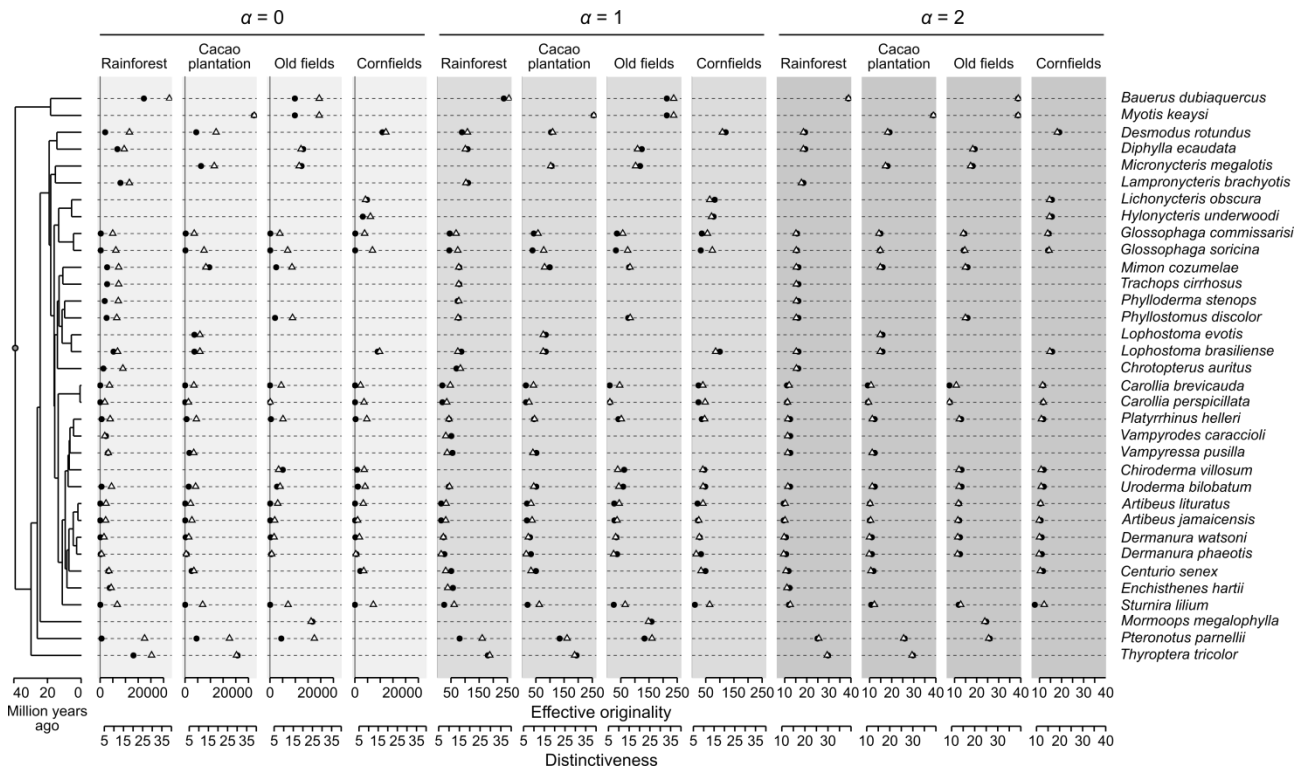


Fig. 5. Species effective originality and distinctiveness in rainforest, cacao plantation, old fields, and cornfields. (Effective originality (black circles) and distinctiveness (white triangles) were measured here with indices ${}^{\alpha}\Omega^*$ and ${}^{\alpha}\Delta^*$, respectively, considering from left to right, $\alpha = 0$, $\alpha = 1$, and $\alpha = 2$. The parameter value $\alpha = 2$ corresponds to the case where measurements for ${}^{\alpha}I$, ${}^{\alpha}Y$ and Q merge. For the effective originality and distinctiveness measures associated with ${}^{\alpha}Y$, varying the α parameter does not change the ranking of species from the least to the most effectively original species, which corresponds here to the ranking obtained with $\alpha = 2$.)

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