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3 **Disentangling and quantifying the functional determinants**
4 **of species abundance unevenness in ecological communities**
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9 **Abstract**

10 Species richness and species abundance unevenness are two major synthetic descriptors of
11 the internal organization within ecological communities. Yet, while the former is a simple
12 concept in essence, the unevenness of abundance distribution is less so, being partly linked
13 (negatively) to species richness as a general trend but more or less deviating from this
14 average trend according to idiosyncratic specificities of each community (a bit similar to
15 the size among individuals of a same species, which depend on age but more or less
16 deviates due to inter-individual differences in growth rate which singularizes each
17 individual).

18 I argue that for abundance unevenness it is therefore relevant to consider and quantify
19 separately these two aspects – the overall trend and the idiosyncratic deviation from this
20 trend. In particular, comparing abundance unevenness levels between communities
21 differing in species richness requires considering what has to be directly assign to the
22 difference in species richness and what can be relevantly attributed to some genuine
23 difference in the hierarchical structuring of abundances between the compared
24 communities. The appropriate formalism arising from this approach is detailed for
25 practical implementation, thereby allowing for a deeper understanding of the ins and outs
26 of the functional organization within ecological communities.

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28 **Key-words:** species abundance distribution, abundance evenness, broken-stick model,
29 competition, resource partitioning
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32 **1. Introduction**

33 A more or less uneven distribution of species abundances is a general characteristic of the
34 internal organization within ecological communities [1-3]. Beyond its simply descriptive
35 aspect, the abundance unevenness deserves to be analyzed more deeply by trying (i) to
36 identify the various functional factors involved in the determination of the level of
37 abundance unevenness and (ii) to quantify the respective contributions of these various
38 functional factors. Although this approach remains very synthetic and rather reductionist,
39 it proves able to provide, however, some valuable insights into how co-occurring species
40 are organized among each other, within each particular ecological community, at the local
41 scale.
42

43 **2. General considerations**

44 Schematically, the species that co-occur at a given time in an ecological community are
45 those that have been successfully recruited along the time already elapsed (thanks, in

46 particular, to sufficient dispersal abilities) and then successfully cope with the ecological
47 and syn-ecological constraints therein. Interspecific differences in competitive success
48 (competition being understood *sensu latissimo*, including not only biotic but also all kinds
49 of abiotic factors *cf.* below) subsequently determine the degree of abundance unevenness,
50 from which proceeds finally the overall range of species abundances in the community and,
51 in particular, the abundance of the rarest species (section 5). At last, if it turns out that the
52 abundances of one or several of the rarest species fall below a certain minimum threshold
53 required for survival (in relation, in particular, with the so-called “Allee effect” [4-6]), then
54 these species will not persist any more within the set of co-occurring species [6].

55 In short, the overall range of species abundance is primarily dependent upon (i) the
56 available stock of recruited species and (ii) the competitive intensity among those species,
57 which drives the hierarchical structuration of their relative abundances. However, a further
58 restriction (iii) comes from some minimum abundance threshold required for survival, in
59 particular via mate-finding Allee effect.

60 As emphasized above, “differential competitive success” among co-occurring species
61 should be understood in the broadest scope that can be assigned to the notion of
62 “competition”: not simply limited to the competitive interactions between species sharing
63 same available resource, but *unrestrictedly extended* to all factors that are, directly or
64 indirectly, influential on the differential success between co-occurring species. In
65 particular, this should include not only interspecific competitive interactions for resource
66 exploitation or differential ability to avoid predation but involves, as well, all other efficient
67 parameters, such as time-related factors leading to appreciable inter-specific differences in
68 initial colonization dates or subsequent recruitment rates, both being ultimately related to
69 various abilities regarding long-range dispersal and also to less deterministic, more
70 opportunistic events [7-17]. In short, the notion of “differential competitive success”
71 involves *all factors, either biotic or abiotic of any kind*, that contribute to sanction a more or
72 less differentiated success between co-occurring species.

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74 **3. Quantifying the degree of unevenness of the species abundance distribution**

75 The Species Abundance Distribution (S.A.D.) of a local community of species is usually
76 presented graphically, with the (usually log-transformed) relative abundances ‘ a_i ’ of
77 species plotted against the rank ‘ i ’ of these species, ordered by decreasing level of
78 abundance. S.A.D.s are a fundamental tool helping to investigate and get an overall
79 understanding of the internal organization within ecological communities, on both the
80 *descriptive* and the *functional* points of view [18-26].

81 The S.A.D. of a community comprising a total of S_t co-occurring species provides a rich
82 source of information including $(S_t - 1)$ independent parameters (the sum of the S_t relative
83 abundances a_i , constrained to equal unity). At least in a first approach, it is more
84 convenient and manageable to focus upon two major descriptors of the S.A.D.: the *species*
85 *richness* S_t and the degree of abundance evenness – or, more evocatively [27], its opposite,
86 the degree of *abundance unevenness* U . Among the various manners of quantifying the
87 degree of abundance unevenness, the more directly related to S.A.D. is to consider the
88 average steepness of the descending slope of ranked abundances, as already suggested in
89 [28]:

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$$U = [\log(a_1) - \log(a_{S_t})]/(S_t - 1) = [\log(a_1/a_{S_t})]/(S_t - 1) \quad (1)$$

93 with a_1 and a_{S_t} standing for the highest and the lowest relative abundances in the studied
94 community comprising a total of S_t species.

95 **4. Functional significance of species abundance unevenness**

97 Thus defined, the degree of abundance unevenness U provides a rather synthetic but
98 convenient *descriptive* appreciation of the organization of species relative abundances
99 within an ecological community.

100 Now, from a *functional* point of view, it results from equation (1) that abundance
101 unevenness U represents, as well, the average value of the gap, $\log(a_i/a_{i+1})$, between the
102 abundances of two consecutive species (ranks i and $i+1$) along the S.A.D. That is, abundance
103 unevenness U highlights also the *mean differential success* between consecutive species
104 and, consequently, reflects the *overall mean competitive intensity* within community
105 (competition being, understood in its broadest sense, as already emphasized above).

106 **5. The influence of species richness upon the degree of abundance unevenness**

107 At first, a trivial source of influence of species richness on apparent (un-) evenness has
108 been accounted for, and relevantly cancelled in the various classical expressions of
109 abundance (un-) evenness [29-31]. For example, in the expression above of species
110 unevenness (equation (1)), this trivial influence is cancelled by rationalizing [$\log(a_1/a_{S_t})$] to
111 ($S_t - 1$).

112 However, this still leaves aside another additional, less obvious influence of species
113 richness on abundance unevenness, which deserves being highlighted and considered for
114 its own contribution to the degree of abundance unevenness. This second, more subtle,
115 influence of species richness on abundance unevenness had already drawn the attention of
116 several authors [24, 29]; specifically, a negative *mathematical-like* dependence of
117 abundance unevenness upon species richness has been emphasized in [24]. As an example,
118 this negative influence of species richness on abundance unevenness is empirically
119 highlighted in Figure 1, where abundance unevenness U is plotted against S_t for a set of 21
120 marine communities encompassing a wide taxonomic range, including both vertebrate
121 (reef fishes) and invertebrates (gastropods, echinoderms) and covering a large
122 geographical area.

123 More precisely, the overall trend for a monotonous decrease of abundance unevenness
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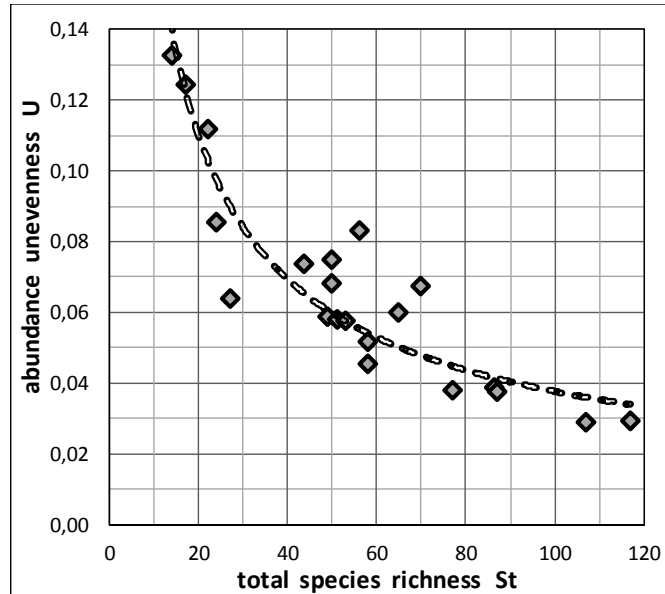
125 species richness is almost entirely due to the (continuously decelerated) decreasing rate of
126 the minimal relative abundance a_{S_t} with growing species richness, while the relative
127 abundance of the dominant species a_1 remains almost constant (Figure 2). This pattern of
128 continued deceleration in the decreasing rate of a_{S_t} with increasing species richness can be
129 explained from the general considerations proposed above in section 2.

130 All this, together, leads to the pattern highlighted in Figures 1 and 2: increasing species
131 richness S_t may be accommodated by both:

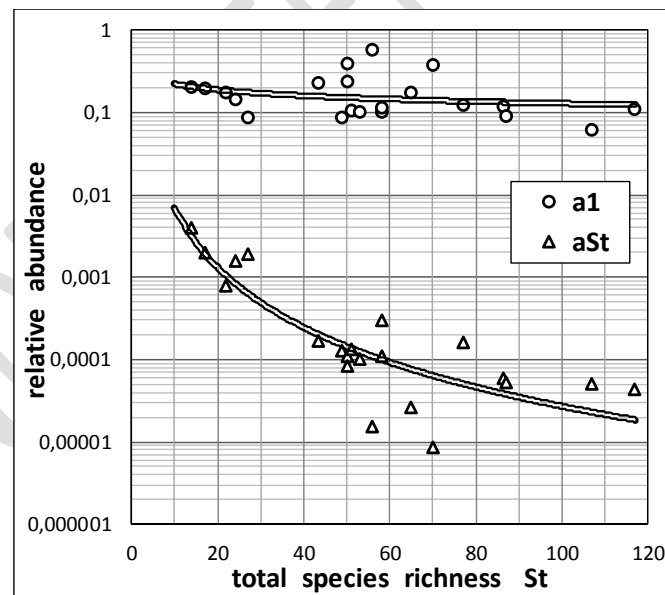
132 (i) a decrease of U (through relaxed mean competitive intensity resulting in a reduced
133 gap in differential success, $\log(a_i/a_{i+1})$) and

134 (ii) an expansion of abundance range R_a (mostly accommodated by a decrease of the
135 minimum abundance a_{S_t}). The asymptotically decelerating rates in the decrease of both a_{S_t}
136 and U likely resulting from the gradual approach of some unavoidable minimum thresholds
137 for both the lowest abundance a_{S_t} (Allee effect already mentioned) and the mean
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139 competitive intensity U (i.e. the mean gap $\log(a_i/a_{i+1})$), hence the quasi-hyperbolic decrease
 140 of U with S_t (Figure 3).
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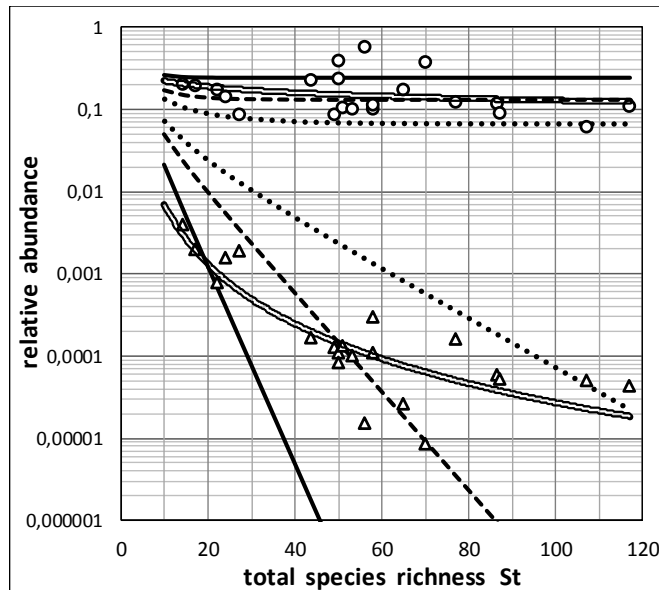
142
 143 **Figure 1** – The degree of abundance unevenness U plotted against total species richness in 21 marine
 144 communities. Seven gastropod communities (Andaman [32], Mannar Gulf [33], Fiji [34]); two sea-star
 145 communities (South China Sea [35]) and twelve fish communities (Caribbean [36], Columbia [37], Brazil
 146 [38], Red Sea (unpublished results)). Power regression, $n = 21$, $r = 0.902$, $p < 0.0001$.
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 150 **Figure 2** – The (log-transformed) relative abundances, a_1 and a_{St} , of the more and the less abundant
 151 species, plotted against total species richness S_t , in 21 marine communities (same as in Figure 1). Power
 152 regressions for a_1 and a_{St} are superimposed. Power regression, $n = 21$, $r = 0.846$, $p < 0.0001$ for a_{St} and r
 153 $= 0.240$, $p = 0.29$ for a_1 .
 154

155 Finally, this quasi “ideally” hyperbolic decrease of U with S_t , as well as its fairly good fit
 156 (see below) with the well-known, mathematically generated “broken-stick” distribution [1,
 157 39], both invited to emphasized the *mathematic-like* character of the direct, average

158 influence of species richness on species abundance unevenness, as originally pointed in
 159 [24] and reiterated in [32-38, 40]. And this, even though *biological causes* are, indeed,
 160 involved in the process.
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164 **Figure 3** – Same as Figure 2 with, in addition, the relative abundances a_1 and a_{St} computed for three
 165 geometric series each of them characterized by a constant level of abundance unevenness,
 166 independently of species richness: $U = 0.12$ (solid line), $U = 0.06$ (dashed line), $U = 0.03$ (dotted line). The
 167 straight lines pattern, characteristic of constant level of abundance unevenness whatever species
 168 richness, does not fit at all the hyperbolic pattern of recorded values of a_{St} .
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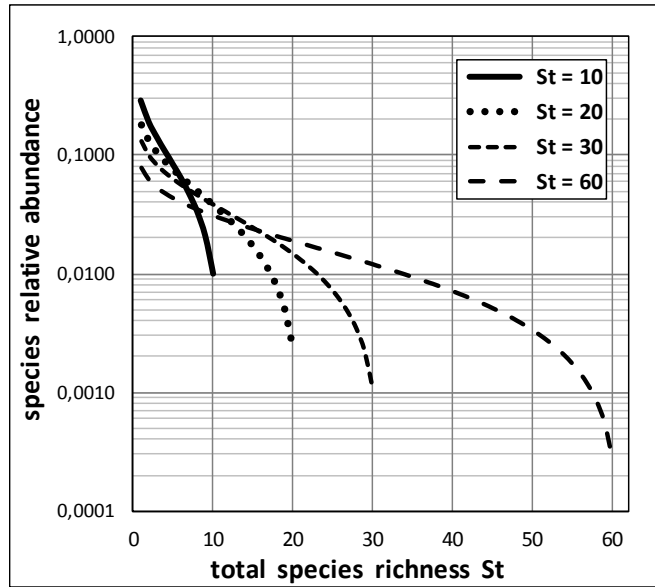
170 **6. An appropriate standardization for the degree of species abundance unevenness,**
 171 **highlighting the part *unrelated* directly to species richness**

172 Beyond the average decreasing trend with species richness, the abundance unevenness can
 173 still appreciably differ between communities having a same species richness, as obvious
 174 from Figure 1. Difference in unevenness at a same species richness can be very important,
 175 reaching a factor of two at least, in \log_{10} . That is, in un-transformed abundances, up to *two*
 176 *orders of magnitude* at least. And these deviations from the “standard” trend are all the
 177 more important to consider that they highlight the *genuine ecological specificity* of each
 178 particular community as compared to the general trend.

179 One way to quantify these deviations is to compare (i.e. to standardize) the rough
 180 abundance unevenness U to the value taken by the empirical regression of U against S_t
 181 (derived above, Figure 1) for the same species richness. Yet, an alternative choice seems
 182 more appropriate, that consists in standardizing U to the abundance unevenness U' of the
 183 well-known “broken-stick” theoretical distribution [39], characterized by an *invariant*
 184 *process* of allocation of abundances to species [1] (namely, a random allocation process).
 185 Despite this invariance in the process involved, whatever the level of species richness, the
 186 abundance unevenness U' in the “broken-stick” distribution is *entirely determined by*
 187 *species richness* [1, 39] (see Figures 4 and 5), so that U' *relevantly accounts* for the *direct*
 188 influence of species richness on abundance unevenness [1]. The mathematical-like, *direct*
 189 dependence of U' on S_t approximately answers the following equation (Figure 5):
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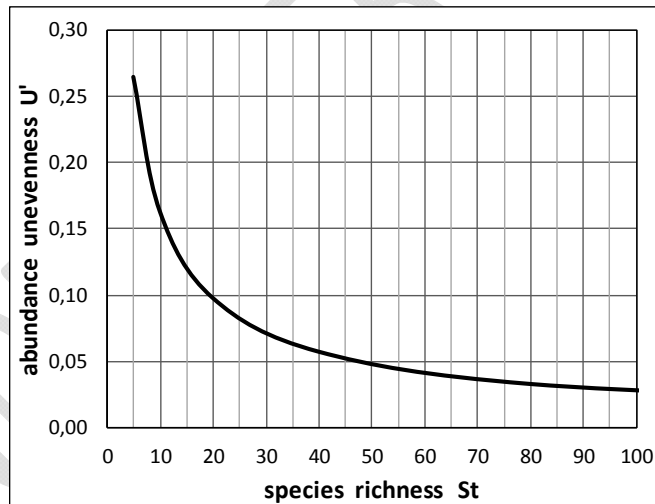
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$$U'(S_t) \approx 0.944 S_t^{-0.767} \quad (2)$$



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Figure 4 – “Broken-stick” distributions computed for increasing species richness $S_t = 10, 20, 30, 60$. Although the theoretical structuring process involved in the “broken-stick” model remains unchanged, whatever the level of species richness, the slope of the species abundance distribution – and thus the abundance unevenness – strongly depend upon (and monotonously decrease with) the level of species richness S_t (the relative abundance of the species of rank ‘i’ is computed as: $(1/S_t) \cdot \sum_n (1/n)$, with the summation \sum_n on the integer n being extended from $n = i$ to $n = S_t$, see reference [1]).



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Figure 5 – The abundance unevenness U' for the “broken-stick” distribution plotted against species richness S_t . U' is steadily decreasing monotonously with increasing species richness. The abundance unevenness U' of the “broken-stick” distribution varies approximately as $U' \approx 0.944 S_t^{-0.767}$.

Choosing the “broken-stick” distribution as a referential to standardize abundance unevenness offers several advantages:

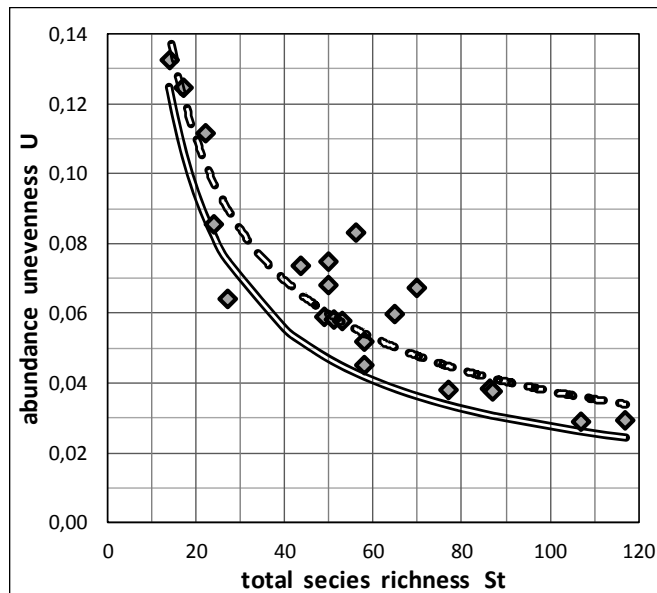
- (i) as just emphasized, by virtue of its very conception, this distribution offers the unique particularity of being entirely and exclusively parametrized in term of species richness; it thereby accurately accounts for the direct mathematical-like dependence of U upon S_t on a *theoretical* basis [1, 39];

212 (ii) this theoretical basement better establishes the *general* soundness of the “broken-
 213 stick” distribution as a reference (as compared to the alternative, empirically derived
 214 reference evoked at first);

215 (iii) as already mentioned, the “broken-stick” distribution is one of the few *universally*
 216 *well-known* models of abundance distribution;

217 (iv) and, from an ecological point of view, the “broken-stick” distribution offers an
 218 “ideal” *concrete benchmark* reference [41, 42], likely speaking explicitly to everyone – being
 219 in particular, most often associated to the level of abundance unevenness *typical for bird*
 220 *communities*, that are familiar to most naturalists.

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223 **Figure 6** – Same as Figure 1, highlighting, in addition, the dependence upon species richness of the
 224 abundance unevenness U' in the “broken-stick” distribution (double line). The empirical regression of
 225 abundance unevenness U for the 21 marine communities and the abundance unevenness U' for the
 226 “broken-stick” distribution are remarkably parallel to each other.

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228 Note that, non-surprisingly, the empirical regression of abundance unevenness for the 21
 229 marine communities stands remarkably parallel to the abundance unevenness U' of the
 230 “broken-stick” model (Figure 6), being just shifted upwards to a near constant value ≈ 0.01 .

231 Finally, it looks therefore appropriate to *standardize* the species abundance unevenness U
 232 to the level of unevenness U' of the “broken-stick” distribution computed at the same
 233 species richness (as already suggested in [32-38, 40]). A “standardized” index “ I_{str} ”, is thus
 234 defined as:

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$$I_{str} = U/U' = [\log(a_1/a_{St})/(S_t-1)]/[\log(a'_1/a'_{St})/(S_t-1)]$$

236

that is:

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$$I_{str} = U/U' = \log(a_1/a_{St})/\log(a'_1/a'_{St}) \quad (3)$$

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239 with a_1 and a_{St} standing for the highest and the lowest abundances in the studied
 240 community and a'_1 and a'_{St} standing for the highest and the lowest abundances in the
 241 corresponding “broken-stick” distribution computed for the same species richness S_t .

242 To summarize, considering the “standardized” unevenness “ I_{str} ”, alongside “rough”
 243 unevenness U , offers two major advantages:

244

245 (i) I_{str} allows for *direct, unbiased* comparisons between communities that differ in their
 246 respective levels of species richness and

247 (ii) I_{str} is, by construction, “self-benchmarked” and, thereby, is *explicitly evocative*, by
248 contrast with the value taken by the rough unevenness U , hardly meaningful in itself, for
249 lack of clear reference.

250 Daring a metaphorical comparison, the situation with *unevenness* is somewhat similar to
251 that with the *size* of individuals within a same species: the size, while being, on average,
252 biologically related directly to the age – in a mathematical-like manner – yet deviates more
253 or less from this “standard”, for each individual. So that the size of a given individual is
254 expressed more evocatively when its rough size has been standardized to this referential
255 benchmark, the latter conveying only the mathematical-like, direct influence of age.
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257 **7. The “functional” meanings of the rough and the standardized unevenness**

258 As already emphasized above, the “standardized” index I_{str} has a major syn-ecological
259 significance in that it specifies to what extent the mean competitive intensity (*sensu*
260 *latissimo*) within the considered community actually differs from that in the broken-stick
261 distribution, at the same level of species richness. That is, to what extent the considered
262 community differs, in term of mean competitive intensity, from, say, a typical bird
263 community having the same level of species richness – taken as an evocative benchmark.
264 The deviation from this reference being all the stronger as I_{str} differs more from unity (by
265 positive or negative values). Thereby, I_{str} highlights to what extent the focused community
266 is *genuinely distinct* – in term of *mean competitive intensity* – from the standard trend.

267 In particular, relevantly comparing the average intensities of interspecific competition
268 between two communities having *different species richness* imperatively requires to
269 consider not only the rough unevenness U but, *also*, the standardized unevenness I_{str} , in
270 order to be able to disentangle and clearly quantify what, in the comparison, is the mere
271 direct consequence of the difference in species richness from what is *genuinely distinctive*
272 between these communities specifically. It is in this sense that the standardized index I_{str}
273 has been considered as highlighting the “*genuine*” part of the hierarchical structuring
274 process within community [32-38, 40].

275 From a functional point of view, I therefore propose to consider the structuring index I_{str} as
276 reflecting “the mean competitive intensity (*sensu latissimo*), normalized to what it is in the
277 broken-stick distribution at the same level of species richness”. This index can be
278 appropriately used not only for characterizing the structuring and mean competitive
279 intensity within any particular ecological community but it also directly allows unbiased
280 comparisons between communities, regardless of their difference in species richness, since
281 the broken-stick model, to which I_{str} is standardized, reliably integrates the direct average
282 influence of species richness on abundance unevenness.

283 **8. The species richness broken down into its functional components**

284 Equation (1) can be rearranged as:

$$285 \quad S_t = (1/U) \cdot \log_{10}(a_1/a_{st}) + 1 = R_a/U + 1 \quad (4)$$

286
287 - “ R_a ” denotes the overall range of species abundances, measured on a logarithmic
288 scale: $\log_{10}(a_1) - \log_{10}(a_{st}) = \log_{10}(a_1/a_{st})$;

289 - $(1/U)$, as the inverse of U , stands for the *degree of relaxation of the mean competitive*
290 *intensity* within community.

291 Equation (4) thus allows to quantify how the level of species richness S_t is “accommodated”
292 by (i) the degree of relaxation of interspecific competition $(1/U)$ and (ii) the extent of the
293 overall range of species abundances R_a .

294 In turn, the corresponding differential form of equation (4),

$$295 \quad \partial S_t / S_t = - \partial U / U + \partial R_a / R_a \quad (5)$$

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299 allows to quantify how a relative variation $\partial S_t/S_t$ in species richness S_t is accommodated by
 300 the relative variations $[-\partial U/U]$ and $[\partial R_a/R_a]$ of its functional components U and R_a
 301 respectively.
 302 Then, further splitting rough abundance unevenness U into its two components U' and I_{str} ,
 303 yields:
 304

$$\partial S_t/S_t = -\partial U'/U' - \partial I_{str}/I_{str} + \partial R_a/R_a \quad (6)$$

305 which quantifies in more detail, how a relative variation $\partial S_t/S_t$ in species richness is
 306 accommodated by the respective variations of its three functional components, U' , I_{str} and
 307 R_a , which contribute respectively for $[-\partial U'/U']$, for $[-\partial I_{str}/I_{str}]$ and for $[\partial R_a/R_a]$ to the
 308 accommodation of the relative variation $\partial S_t/S_t$ of species richness.
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312 **9. Accommodation of increased / decreased species richness**

313 A higher level of species richness, i.e. the subsistence of a larger number of recruited
 314 species can thus be accommodated by either:

- 315 - an *expansion* of the *overall range of species abundance*, $R_a = \log(a_1/a_{st})$, mainly
 316 allowed by the decrease of the lowest abundance a_{st} , or,
- 317 - a *decrease* of the *mean differential success* $\log(a_i/a_{i+1})$, among co-occurring species,
 318 resulting from some degree of *relaxation* ($1/U$) of the *mean competitive intensity* U within
 319 community. This relaxation allows more species to occupy a given interval of abundance.

320 In turn, the relaxation ($1/U$) of the mean competitive intensity is accommodated for part by
 321 the contribution ($1/U'$) directly linked to species richness itself and for part by a specific
 322 contribution ($1/I_{str}$) unrelated to species richness and, thus, singularizing the studied
 323 community with respect to the general trend of variation of unevenness with species
 324 richness.

325 Owing to the paramount tendency for any species to develop its numerical incidence, it is
 326 logically expected that the second path to accommodate a larger number of co-occurring
 327 species will be favored. For example, some relaxation of the mean competitive intensity
 328 may be obtained by an improved resource partitioning (food, shelter, ...) among co-
 329 occurring species [43-47]. Yet, this favored path will arguably meet some limitation so that
 330 the second alternative - expanding abundance range R_a through decreasing minimum
 331 abundance a_{st} - is expected to complement the first one. Being understood, at last, that the
 332 decrease of a_{st} can also ultimately meets some limitation, due in particular to Allee effect, as
 333 already pointed in section 2.

334 *** example A**

335 Two *marine gastropods communities* in shallow waters are considered, around the islet of
 336 Hare (Mannar Gulf, India) [33] and along the coast of Andaman Island (India) [32]. These
 337 communities appreciably differ in species richness, increasing from 49 species (Hare) to 77
 338 species (Andaman). How is this increase in species richness accommodated, in terms of the
 339 relative contributions of (i) an extension of the overall range of species abundances and (ii)
 340 a relaxation of interspecific competition? The second line of Table 1 provides the respective
 341 values of U , U' , I_{str} and R_a in each two communities. The derived contributions to
 342 accommodate the increase in species richness are provided in the three last columns. The
 343 enlargement of the range of species abundance R_a plays almost no role (4% only); the 96%
 344 contribution of relaxed mean competitive intensity being in majority (78%) the direct
 345 consequence of species richness increase, while the genuine relaxation contributes for
 346 18%.

347 *** example B**

348 Two *marine gastropods communities* in shallow waters are considered, along the coast of
 349 Andaman Island (India) [32] and along the coast of Suva Island (Fiji archipelago) [34].
 350 These communities appreciably differ in species richness, increasing from 77 species
 351 (Andaman) to 117 species (Fiji). The third line of Table 1 provides the respective values of
 352 U , U' , I_{str} and R_a in each two communities. The derived contributions to accommodate the
 353 increase in species richness are provided in the three last columns. The contribution of the
 354 enlargement of the range of species abundance R_a is more significant than in the previous
 355 case (36%), with 64% complementary contribution due to relaxed mean competitive
 356 intensity. The latter, in turn, breaks down in a 84% positive contribution directly related to
 357 the increase in species richness itself and a 20% negative genuine contribution. This
 358 negative contribution highlights the difficulty to further reduce competition intensity when
 359 an important relaxation has already been reached (here, unevenness U at Fiji has already
 360 fallen down to 0.0288).

361 * **example C**

362 Two *sea-stars communities* in shallow Malaysian waters (Central South China Sea) are
 363 considered [35]. These communities appreciably differ in species richness: 17 species and
 364 24 species respectively. The fourth line of Table 1 provides the respective values of U , U' ,
 365 I_{str} and R_a in each two communities. The derived contributions to accommodate the
 366 difference in species richness are provided in the three last columns. The range of species
 367 abundance R_a does not significantly contribute to accommodation (with an even slight
 368 negative contribution – 4%) and, accordingly, only the relaxation of the mean competitive
 369 intensity is involved in the accommodation of species richness increase (104%). In turn,
 370 this 104% contribution of relaxed competition breaks down in a 72% positive contribution
 371 directly related to the increase in species richness itself and a 32% genuine contribution.
 372

373 **Table 1** – How the increase in total species richness ($S_{t\ 2} - S_{t\ 1}$) between two communities is
 374 accommodated by the corresponding variations of (i) the relaxation of the mean competitive intensity
 375 ($1/U$) [split in its two components, ($1/U'$) and ($1/I_{str}$)] and (ii) the extension of the range of species
 376 abundances R_a . Case **A**: from Hare island (Mannar Gulf) $S_t = 49$ to Andaman island $S_t = 77$. Case **B**: from
 377 Andaman island $S_t = 77$ to Fiji archipelago $S_t = 117$. Case **C**: from Terumbu Peninjau islet $S_t = 17$ to
 378 Terumbu Siput $S_t = 24$. Comments in text
 379

	$S_{t\ 1}$	$S_{t\ 2}$	$U\ 1$	$U\ 2$	$U'\ 1$	$U'\ 2$	$I_{str\ 1}$	$I_{str\ 2}$	$R_a\ 1$	$R_a\ 2$	accom by U'	accom by I_{str}	accom by R_a
A	49	77	0,0589	0,0378	0,0487	0,0339	1,21	1,12	2,83	2,87	78%	18%	4%
B	77	117	0,0378	0,0288	0,0339	0,0238	1,12	1,21	2,87	3,34	84%	-20%	36%
C	17	24	0,1246	0,0854	0,1104	0,0851	1,13	1,00	1,99	1,96	72%	32%	- 4%

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381 **10. Numerical extrapolation required when dealing with incomplete samplings**

382 Any reliable evaluations of both species richness and species abundance unevenness
 383 obviously requires, as far as possible, a *complete sampling* of the focused community, and
 384 this stands all the more so for the subsequent analysis of unevenness in terms of the
 385 standard reference value U' and the deviation to this standard estimated by the deviation of
 386 I_{str} from unity. Unfortunately, incomplete inventories are doomed to become even more
 387 frequent with the inevitable generalization of “rapid assessments” and “quick surveys”,
 388 especially for species-rich communities comprising a lot of rare species. And accounting for
 389 unrecorded rare species, as well, is important since at least some of them can yet
 390 disproportionately contribute to the functional structuring of communities in the wild [48–
 391 53]. Recently developed procedures of numerical extrapolation of incomplete samplings

392 can yet compensate to a certain extent for partial samplings [54–56], so that such
393 procedures have to be considered, as far as necessary.

394

395

11. Discussion and Conclusion

396 Species richness and the more or less uneven distribution of species abundances are,
397 admittedly, considered as the two main synthetic descriptors of the internal structuration
398 within ecological communities. Yet, contrary to what is still too often assumed, these two
399 descriptors are not truly independent from each other, since abundance unevenness is, for
400 an important part, directly influenced by species richness, as an average trend. This
401 average trend had already been made explicit in the pioneering work of MacArthur [39],
402 highlighting the good fit of various bird communities with its “broken-stick” theoretical
403 distribution, a model explicitly and exclusively *mathematically dependent on species*
404 *richness*. This could, at least, instill some doubt as to the fundamental independence
405 between abundance unevenness and species richness. A doubt later confirmed by several
406 authors, as pointed above. Hence the relevance of *considering separately*:

407 (i) the part U’ of unevenness directly dependent upon species richness, aptly accounted
408 for by the broken-stick model and

409 (ii) the more or less strong deviation of each particular community from the broken-
410 stick model, taken as a standard reference.

411 For, if numerous bird communities fairly conform to this standard reference, as rightly
412 advocated by MacArthur, this is far from being the case when enlarging the scope to other
413 kinds of ecological communities.

414 Hence the “oscillating” popularity of the broken-stick model: initially put forward and then
415 refuted by the same MacArthur (precisely for its lack of generality [20, 57]); this model can
416 now find a renewed value, no longer aiming at reaching an inaccessible universality, but
417 rather serving as a useful landmark for separating what part of abundance unevenness is
418 directly dependent on species richness from what part is not.

419 Standardizing the rough abundance unevenness U to the broken-stick distribution – the
420 latter accounting only for the part directly influenced by species richness – allows a deeper
421 and more accurate appreciation of what ultimately determine the level of abundance
422 unevenness. And, thereby, avoids making biased comparisons, regarding abundance
423 unevenness, between communities differing in species richness.

424 Defined accordingly, the standardized index I_{str} , highlights to what extent a given
425 community of species is *genuinely distinct* – in term of mean competitive intensity (*sensu*
426 *latissimo*) – once the direct influence of species richness on this intensity has been
427 accounted first.

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