Disentangling and quantifying the functional determinants of species abundance unevenness in ecological communities

Abstract

Species richness and species abundance unevenness are two major synthetic descriptors of the internal organization within ecological communities. Yet, while the former is a simple concept in essence, the unevenness of species abundance distribution is less so, being partly linked (negatively) to species richness as a general trend but more or less deviating from this average trend according to idiosyncratic specificities of each community (a bit similar to the size among individuals of a same species, which depend on age but more or less deviates due to inter-individual differences in growth rate which singularizes each individual). I argue that for abundance unevenness it is therefore relevant to consider and quantify separately these two aspects – the overall trend on the one hand and the idiosyncratic deviation from this trend on the other hand. In particular, comparing abundance unevenness levels between communities differing in species richness requires considering separately what has to be directly assign to the difference in species richness and what can be relevantly attributed to some genuine, idiosyncratic difference in the hierarchical structuring of abundances between the compared communities. The appropriate formalism arising from this approach is detailed for practical implementation, thereby allowing for a deeper understanding of the ins and outs of the functional organization within ecological communities.

1. Introduction

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

2. General considerations

Schematically, the species that co-occur at a given time in an ecological community are those that have been successfully recruited along the time already elapsed (thanks, in particular, to sufficient dispersal abilities) and, then, that successfully cope with the ecological and syn-ecological constraints therein. Interspecific differences in competitive

success (competition being understood *sensu latissimo*, including not only biotic but also all kinds of abiotic factors *cf.* below) subsequently determine the degree of species abundance unevenness, from which proceeds, finally, the overall range of species abundances in the community and, in particular, the abundance of the rarest species (section 5). At last, if it turns out that the abundances of one or several of the rarest species fall below some minimum threshold(s) required for survival (in relation, in particular, with "Allee effect" [4-6]), then these species will not persist any more within the set of species [6].

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

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

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

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

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

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

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

4. Functional significance of species abundance unevenness

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

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

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

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

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

More precisely, this overall trend for a monotonous decrease of abundance unevenness with increasing species richness is almost entirely accommodated by the continuously decelerated decreasing rate of the minimal relative abundance a_{St} with growing species richness, while the relative abundance of the dominant species a_1 remains almost constant (Figure 2).

Accordingly, the null hypothesis assuming the lack of any *direct* influence of species richness upon abundance unevenness (as an overall average trend), already questioned previously [24, 29], is, here, clearly rejected, considering the empirical results in Figure 1. Likewise, the hyperbolic-like decrease of $\log(a_{St})$ with growing species richness S_t (Figure 2) is in contradiction with the linear decrease of $\log(a_{St})$ with S_t that would result from an assumed independence of abundance unevenness U with respect to species richness (as shown in Figure 3). Thus, at both (related) points of view (U = f(St): Figure 1 and $\log(a_{St})$ = f(St): Figure 2 & 3), the null hypothesis of independence between species abundance unevenness and species richness, (as an overall average trend), is empirically rejected with a high level of statistical significance (p < 0.0001).

As regards the possible origin(s) of this highly significant *direct* influence of species richness upon species abundance unevenness (as an overall average trend), at least two causative mechanisms may be suggested.

139 At first, it is likely that, as the number of recruited species (i.e. the species richness)
140 increases, the *probability* for a growing number of ecological niches being involved will also
141 increase more or less, as an average trend. Accordingly, the average differential success
142 among consecutive species along the S.A.D., $\log(a_i/a_{i+1})$ – that is the abundance unevenness
143 (equation (1)) – is expected to decrease with higher species richness. A trend for reduced
144 unevenness (i.e. improved relaxation of the mean competitive intensity) with species
145 richness is thus expected from this first, *statistically* based, mechanism.
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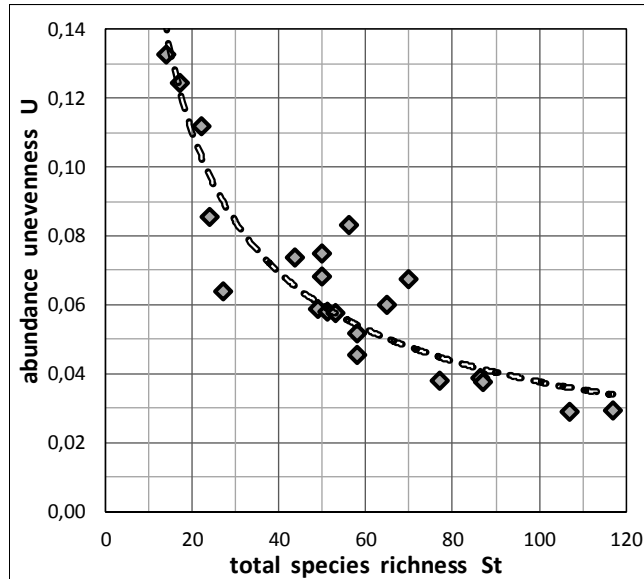
147
148 **Figure 1** – The degree of abundance unevenness U plotted against total species richness in 21 marine
149 communities. Seven gastropod communities (Andaman [32], Mannar Gulf [33], Fiji [34]); two sea-star
150 communities (South China Sea [35]) and twelve fish communities (Caribbean [36], Columbia [37], Brazil
151 [38], Red Sea (unpublished results)). Power regression, n = 21, r = 0.902, p < 0.0001.
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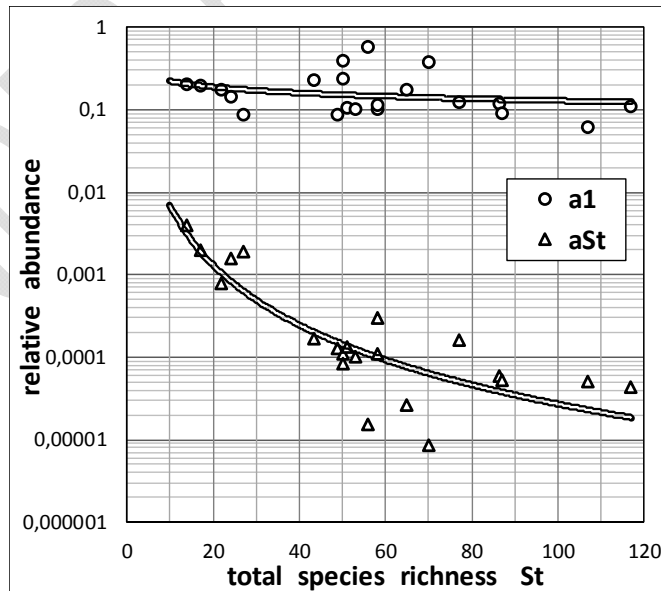
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154 **Figure 2** – The (log-transformed) relative abundances, a_1 and a_{St}, of the more abundant and the less
155 abundant species, plotted against total species richness S_t, in 21 marine communities (same as in Figure
156 1). Power regressions for a_1 and a_{St} are superimposed. Power regression, n = 21, r = 0.846, p < 0.0001 for
157 a_{St} and r = 0.240, p = 0.29 for a_1.

4

158
159 Second, when the lowest species abundances in a community end up getting weaker and
160 weaker, as species richness becomes larger, then an *Allee-like effect* may finally be involved
161 (section 2) which, in turn, would allow to persist (i.e. would "select") those communities
162 only having an increasingly lower level of unevenness of species abundance, as species
163 richness becomes larger. This second mechanism also results, mathematically, in a negative
164 direct dependence between species richness and abundance unevenness. However, this
165 mechanism may be involved later, postponed when the weaker abundances eventually
166 approach the minimum threshold levels for Allee effect becoming effective.
167 Both alternative or complementary mechanisms above result in an apparently *mathematic-*
168 *like* trend for a direct negative dependence of species abundance unevenness upon species
169 richness, as originally pointed in [24] and reiterated in [32-38, 40]. And this, even if
170 *biological causes* are, at least partly, involved in the process.
171 Yet, whatever the causal contribution(s) involved, the constraining character of this direct
172 influence of species richness is limited to the overall average trend, since considerable
173 deviations from this trend can occur and, thereby, more or less *singularize each community*
174 *in particular*, as shown in Figure 1. This highlights the involvement of *complementary,*
175 *idiosyncratic contributions* to abundance unevenness, which deserve specific attention and
176 justify to *consider separately* the *"genuine" deviations* from the *overall average trend*: see
177 following section.
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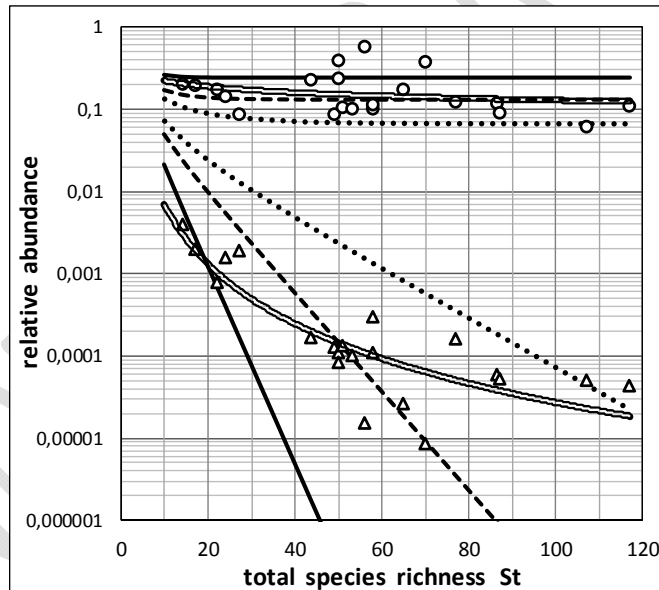
179
180 **Figure 3** – Same as Figure 2 with, in addition, the relative abundances a_1 and a_{St} computed for three
181 geometric series each of them computed with a constant level of abundance unevenness, U,
182 independently of species richness: U = 0.12 (solid line), U = 0.06 (dashed line), U = 0.03 (dotted line). The
183 straight lines pattern, characteristic of constant level of abundance unevenness whatever species
184 richness, does not fit at all the hyperbolic pattern of recorded values of a_{St}. Geometric series are chosen
185 here for easier computation.
186

## 6. An appropriate standardization for the degree of species abundance unevenness, highlighting the "genuine" part, *unrelated* directly to species richness

189 Beyond the average decreasing trend highlighted above, the abundance unevenness can
190 still appreciably differ between communities having a same species richness, as obvious

191 from Figure 1. Difference in unevenness at a same level of species richness can be very
192 important, reaching a factor of two at least, in $\log_{10}$. That is, in un-transformed abundances,
193 at least *two orders of magnitude* (Figure 1). And these deviations from the "standard" trend
194 are all the more important to consider that they highlight the *"genuine" ecological*
195 *specificity* of each particular community, beyond the general trend, as emphasized above.
196 One way to quantify these deviations is to compare the rough abundance unevenness U to
197 the value taken by the empirical regression of U against S_t (derived above, Figure 1) at the
198 same level of species richness.
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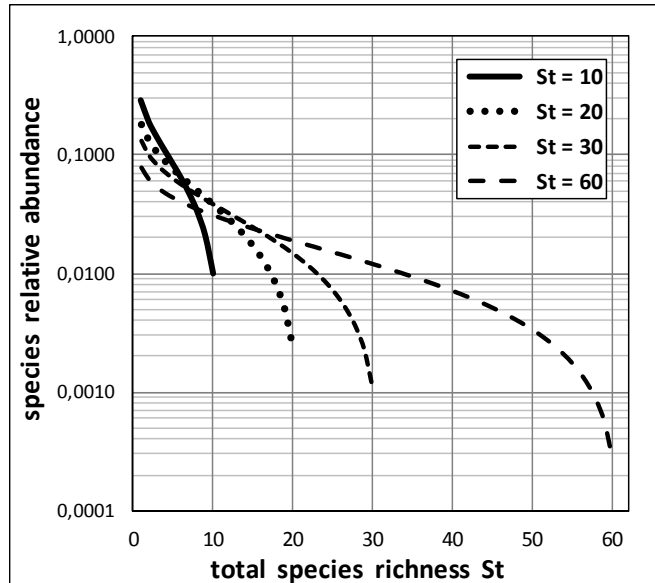
201 **Figure 4** – "Broken-stick" distributions computed for increasing species richness S_t = 10, 20, 30, 60.
202 Although the theoretical structuring process involved in the "broken-stick" model remains unchanged,
203 regardless of species richness, the slope of the species abundance distribution – and thus the abundance
204 unevenness – strongly depend upon (and monotonously decrease with) the level of species richness S_t
205 (the relative abundance of the species of rank 'i' is computed as: $(1/S_t).\Sigma_n (1/n)$, with the summation Σ_n
206 on the integer n being extended from n = i to n = S_t, see reference [1].
207
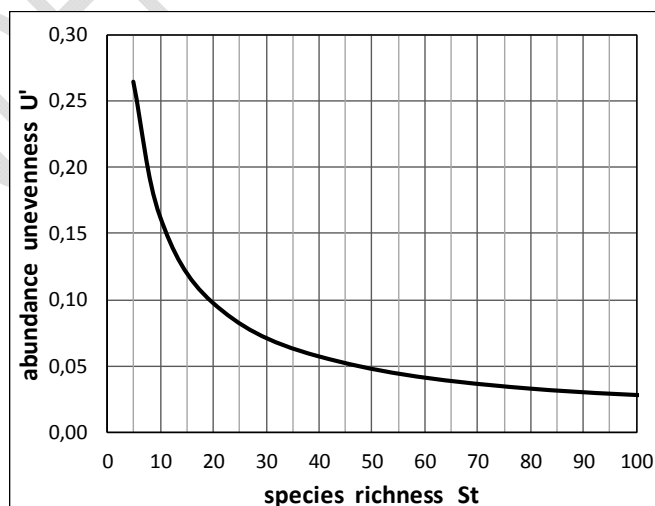
209 **Figure 5** – The abundance unevenness U' for the "broken-stick" distribution plotted against species
210 richness S_t. U' is steadily decreasing monotonously with increasing species richness and varies
211 approximately as U' ≈ 0.944 $S_t^{-0.767}$.
212

213 Yet, an alternative choice features more appropriate, that consists in standardizing U to the
214 abundance unevenness U' of the well-known "broken-stick" theoretical distribution [39],
215 characterized by an *invariant process* of allocation of abundances to species [1] (namely, a
216 random allocation process). Despite this invariance in the process involved, regardless of
217 the level of species richness, the abundance unevenness U' in the "broken-stick"
218 distribution is *entirely determined by species richness* [1, 39] (see Figures 4 and 5), so that U'
219 *relevantly accounts* for the mathematical-like *direct* influence of species richness on
220 abundance unevenness [1].
221 This direct dependence of U' on S_t approximately answers the following equation (Figure
222 5):

223 $$U'(S_t) \approx 0.944\, S_t^{-0.767} \qquad (2)$$
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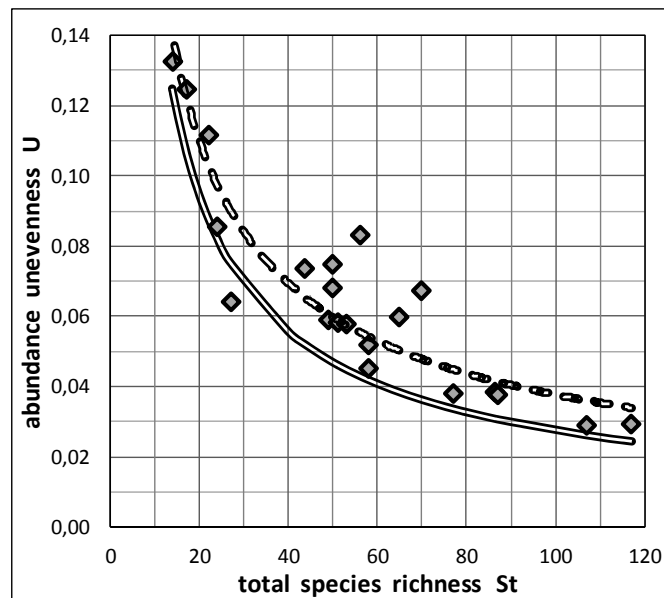
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226 **Figure 6** – Same as Figure 1, highlighting, in addition, the dependence upon species richness of the
227 abundance unevenness U' in the "broken-stick" distribution (double line). The empirical regression of
228 abundance unevenness U for the 21 marine communities (dashed line) and the abundance unevenness
229 U' for the "broken-stick" distribution are remarkably parallel to each other.
230
231 Choosing the "broken-stick" distribution as a reference to standardize abundance
232 unevenness offers several advantages:
233   (i) as just emphasized, by virtue of its very conception, the "broken-stick" distribution
234 offers the unique particularity of being entirely and exclusively parametrized in term of
235 species richness; it thereby accurately accounts for the mathematical-like trend of *direct*
236 dependence of U upon S_t, on a theoretical basis [1, 39];
237   (ii) this *theoretical basement* better establishes the *general* soundness of the "broken-
238 stick" distribution as a relevant reference (as compared to the alternative, empirically
239 derived reference evoked at first);
240   (iii) as already mentioned, the "broken-stick" distribution is one of the few *universally
241 well-known* models of abundance distribution;
242   (iv) and, from an ecological point of view, the "broken-stick" distribution offers an
243 "ideal" *concrete benchmark* reference [41, 42], likely speaking explicitly to everyone – being
244 in particular, most often associated to the level of abundance unevenness *typical for bird
245 communities*, that are much familiar to most naturalists.

7

246 Note that, non-surprisingly, the empirical regression of the abundance unevenness for the
247 21 marine communities stands remarkably parallel to the abundance unevenness U' of the
248 "broken-stick" model (Figure 6), being just shifted upwards to a near constant value ≈ 0.01.
249 Finally, it looks therefore appropriate to *standardize* the species abundance unevenness U
250 to the level of unevenness U' of the "broken-stick" distribution computed at the same
251 species richness (as already suggested in [32-38, 40]). A "*standardized*" index "I_{str}", is thus
252 defined as:

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

254 that is:

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

256 with a_1 and a_{St} standing for the highest and the lowest abundances in the studied
257 community and a'_1 and a'_{St} standing for the highest and the lowest abundances in the
258 corresponding "broken-stick" distribution, computed for the same species richness S_t.
259 To summarize, considering the *"standardized"* unevenness "I_{str}", alongside the *"rough"*
260 unevenness U, offers two major advantages:
261   (i) I_{str} allows for *direct*, *unbiased* comparisons between communities regardless of the
262 difference in their respective levels of species richness and,
263   (ii) I_{str} is, by construction, "self-benchmarked" and, thereby, is *explicitly evocative*, thus
264 contrasting with rough unevenness U, whose value remains hardly meaningful in itself, due
265 to lack of clear evocative reference.
266 Daring a metaphorical comparison, the situation with *unevenness* is somewhat similar to
267 that with the *size* of individuals within a same species: the size, while being, on average,
268 biologically related directly to the age, yet deviates more or less from this "standard", for
269 each individual in particular. So that the size of a given individual is expressed more
270 evocatively when its rough size is standardized to this referential benchmark, the latter
271 conveying only the "mathematical-like", direct influence of age.
272
273   **7. The "functional" meanings of the rough and the standardized unevenness**
274 As already emphasized above, the "*standardized*" index I_{str} has a major syn-ecological
275 significance in that it specifies to what extent the mean competitive intensity (*sensu*
276 *latissimo*) within the considered community actually differs from that in the broken-stick
277 distribution having the same level of species richness. That is, to what extent the
278 considered community differs, in term of mean competitive intensity, from, say, a typical
279 bird community with the same level of species richness – taken as an evocative benchmark.
280 With the "*standardized*" index I_{str} differing all the more from unity (by positive or negative
281 values) that the deviation from this reference is stronger (positively or negatively).
282 Thereby, I_{str} highlights to what extent the focused community is *genuinely distinct* – in term
283 of *mean competitive intensity* – from the standard trend.
284 In particular, relevantly comparing the average intensities of interspecific competition
285 between two communities having *different species richness* imperatively requires to
286 consider not only the rough unevenness U but, *also*, the standardized unevenness I_{str}, in
287 order to be able to disentangle and *clearly quantify* what, in the comparison, is the mere,
288 direct consequence of the difference in species richness from what is *genuinely distinctive*
289 between these communities specifically. It is in this sense that the standardized index I_{str}
290 has been considered as highlighting the *"genuine"* part of the hierarchical structuring
291 process within community [32-38, 40]. In short, from a functional point of view, the
292 structuring index I_{str} reflects "the mean competitive intensity (*sensu latissimo*), normalized
293 to what it is in the broken-stick distribution at the same level of species richness".
294

8. Species richness and mean competitive intensity broken down into their functional components

Equation (1) can be rearranged as:

$$S_t = (1/U).\log_{10}(a_1/a_{St}) + 1 = (1/U).R_a + 1 = (1/U').(1/I_{str}).R_a + 1 \qquad (4)$$

with "R_a" as the overall range of species abundances, measured on logarithmic scale: $\log_{10}(a_1) - \log_{10}(a_{St}) = \log_{10}(a_1/a_{St})$. This expression highlights the respective contributions to total species richness of its three "components": U, I_{str}, R_a.

Equation (4) thus allows to quantify how a relative increase, $\partial S_t/S_t$, of species richness is "accommodated" by (i) the relative degree of relaxation, $-\partial U/U$, of the mean competitive intensity U and (ii) the extension ∂R_a of the overall range R_a of species abundances:

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

Then, further splitting the rough abundance unevenness $U = U'.I_{str}$ into its two components allows to quantify how the relative relaxation $-\partial U/U$ of the mean competitive intensity U results from (i) the "standard" contribution $-\partial U'/U'$ of the overall trend of variation of the mean competitive intensity with species richness (attributed to statistical causes and (or) Allee effect) and (ii) the "*genuine*" contribution of $-\partial I_{str}/I_{str}$ to the relaxation of the competitive intensity, *apart from the overall trend*:

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

Accordingly:

$$\partial S_t/S_t = -(\partial U'/U' + \partial I_{str}/I_{str}) + \partial R_a/R_a \qquad (7)$$

an expression which quantifies, in more detail, how a relative variation $\partial S_t/S_t$ in species richness is accommodated by the respective relative variations of its three functional components, U', I_{str} and R_a.

9. Examples of accommodation of increased / decreased species richness

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

- an *expansion* of the *overall range of species abundance*, $R_a = \log(a_1/a_{St})$, mainly allowed by the decrease of the lowest abundance a_{St} (Figure 2) or,

- a *decrease* of the *mean level of differential success*, $\log(a_i/a_{i+1})$, among co-occurring species, resulting from some degree of *relaxation*, $-\partial U/U$, of the *mean competitive intensity* U within community. This relaxation indeed allows more species to occupy a given interval of abundance. In turn, the relaxation $-\partial U/U$ of the mean competitive intensity is accommodated, for part, by the contribution, $-\partial U'/U,'$ directly linked to the variation $\partial S_t/S_t$ in species richness itself and for part by a specific contribution, $-\partial I_{str}/I_{str}$, unrelated directly to the variation in species richness and, thus, singularizing the compared communities, independently from the general trend of variation of unevenness with species richness.

Owing to the paramount tendency for any species to develop its numerical incidence, it is logically expected that the second path will be favored to accommodate a larger number of co-occurring species (i.e. the relaxation of competitive intensity). For example, some relaxation of the mean competitive intensity may be obtained by an improved resource partitioning (food, shelter, etc…) among co-occurring species [43-47]. Yet, this favored path will arguably meet some limitation so that the second alternative – expanding abundance range R_a through decreasing minimum abundance a_{St} – is expected to complement the first one. Being understood that, at last, the decrease of a_{St} can also meets ultimately some limitation, like Allee effects (or similar functional cause), as already pointed in section 2.

   * example A

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

   * **example B**

Two *marine gastropods communities* in shallow waters are considered, along the coast of Andaman Island (India) [32] and along the coast of Suva Island (Fiji archipelago) [34]. These communities appreciably differ in species richness, increasing from 77 species (Andaman) to 117 species (Fiji). The contribution of the enlargement of the range of species abundance R_a is more significant than in the previous case (36%), with 64% complementary contribution due to relaxed mean competitive intensity. The latter, in turn, breaks down in a 84% positive contribution directly related to the increase in species richness itself and a 20% negative genuine contribution. This negative contribution highlights the difficulty to further reduce competition intensity when an important relaxation has already been reached: here, unevenness U at Fiji has already fallen down as low as 0.0288.

   * **example C**

Two *sea-stars communities* in shallow Malaysian waters (Central South China Sea) are considered [35]. These communities appreciably differ in species richness: 17 species and 24 species respectively. The range of species abundance R_a does not contribute to accommodation (with an even slightly negative contribution – 4%) and, accordingly, only the relaxation of the mean competitive intensity is involved in the accommodation of the species richness increase (104%). In turn, this 104% contribution of relaxed competition breaks down in a 72% positive contribution directly related to the increase in species richness and a 32% genuine contribution.

Table 1 – How the increase in total species richness ($S_t2 − S_t1$) between two communities is accommodated by the corresponding variations of (i) the relaxation $−∂U/U$ of the mean competitive intensity U [relaxation being split, in turn, into its two components, $−∂U'/U'$ and $−∂ I_{str}/I_{str}$] and (ii) the extension $∂R_a/R_a$ of the range of species abundances R_a. Case **A**: from Hare island (Mannar Gulf) $S_t = 49$ to Andaman island $S_t = 77$. Case **B**: from Andaman island $S_t = 77$ to Fiji archipelago $S_t = 117$. Case **C**: from Terumbu Peninjau islet $S_t = 17$ to Terumbu Siput $S_t = 24$. Comments in text

	$S_t 1$	$S_t 2$	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%**

   10. Numerical extrapolation required when dealing with incomplete samplings

Any reliable evaluations of both species richness and species abundance unevenness obviously require, as far as possible, a *complete sampling* of the focused community, and

387 this stands all the more so for the subsequent analysis of unevenness in terms of the
388 standard reference value U' and the deviation to this standard, estimated by the deviation
389 of I_{str} from unity. Unfortunately, *incomplete* inventories are doomed to become still more
390 frequent with the inevitable generalization of "rapid assessments" and "quick surveys",
391 especially for species-rich communities comprising a lot of rare species. And accounting, as
392 well, for unrecorded rare species is important since at least some of them can
393 disproportionately contribute to the functional structuring of communities in the wild [48–
394 53]. Recently developed procedures of numerical extrapolation of incomplete samplings
395 can, yet, compensate to a certain extent for partial samplings [54–56], so that
396 implementing such procedures is strongly recommended, as far as necessary.
397

11. Discussion and Conclusion

399 Contrary to what is still too often assumed, total species richness S_t and species abundance
400 unevenness U in a community are *not* truly mutually-independent descriptors: as an
401 average trend, abundance unevenness is partly influenced *directly* by species richness. This
402 trend results from a "mathematical-like" – although biologically rooted – constraint,
403 limiting the product $U.S_t$ of these two descriptors, as the likely consequence of statistical
404 determinism and (or) Allee-effect. This average trend had already been admitted
405 empirically in the pioneering work of MacArthur [39] with its "broken-stick" theoretical
406 distribution, a model explicitly and exclusively mathematically dependent on species
407 richness. Hence the relevance of *considering separately*:
408   (i) the part U' of unevenness *directly* dependent upon species richness, aptly accounted
409 for by the *broken-stick* model and
410   (ii) the more or less strong *deviation of each particular community* from the broken-
411 stick model, taken as the standard reference.
412 For, if numerous bird communities fairly conform to this standard reference, as rightly
413 advocated by MacArthur, this is far from being the case when enlarging the scope to other
414 kinds of ecological communities. Hence the "oscillating" popularity of the broken-stick
415 model: initially put forward and then refuted by the same MacArthur (precisely for its lack
416 of generality [20, 57]); this model can now find a renewed value, no longer aiming at
417 reaching an inaccessible universality, but rather serving as a *useful "landmark"* for
418 separating what part of abundance unevenness is *directly* dependent on species richness
419 from what part is *not*.
420 Standardizing the rough abundance unevenness U to the broken-stick distribution – to
421 highlight separately the part of unevenness *directly* influenced by species richness – allows
422 a deeper and more accurate appreciation of what ultimately determine the level of
423 abundance unevenness. And, thereby, avoids making biased comparisons, regarding
424 abundance unevenness, between communities differing in species richness. Defined
425 accordingly, the standardized index I_{str}, highlights to what extent a given community of
426 species is *genuinely distinct* – in term of mean competitive intensity (*sensu latissimo*) – once
427 the *direct* influence of species richness on this intensity has been already accounted first.
428

429 **Competing interests**
430 Author has declared that no competing interests exist.
431
432   **References**
433

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