# 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 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 and the idiosyncratic deviation from this trend. In particular, comparing abundance unevenness levels between communities differing in species richness requires considering what has to be directly assign to the difference in species richness and what can be relevantly attributed to some genuine 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.

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## 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

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.
73
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]:
90
91      $$U = [\log(a_1) - \log(a_{S_t})]/(S_t - 1) = [\log(a_1/a_{S_t})]/(S_t - 1) \qquad (1)$$
92

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

## 4. Functional significance of species abundance unevenness

Thus defined, the degree of abundance unevenness U provides a rather synthetic but convenient *descriptive* appreciation of the organization of species relative abundances 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 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 deserves being highlighted and considered for its own contribution to the degree of abundance unevenness. This second, more subtle, influence of species richness on abundance unevenness had already drawn the attention of several authors [24, 29]; specifically, a negative *mathematical-like* dependence of abundance unevenness upon species richness has been emphasized in [24]. As an example, this negative influence of species richness on abundance unevenness is empirically highlighted in Figure 1, where abundance unevenness U is plotted against $S_t$ for a set of 21 marine communities encompassing a wide taxonomic range, including both vertebrate (reef fishes) and invertebrates (gastropods, echinoderms) and covering a large geographical area.

More precisely, the overall trend for a monotonous decrease of abundance unevenness with
species richness is almost entirely due to 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). This pattern of continued deceleration in the decreasing rate of $a_{St}$ with increasing species richness can be explained from the general considerations proposed above in section 2.

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

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

  (ii) an expansion of abundance range $R_a$ (mostly accommodated by a decrease of the minimum abundance $a_{St}$). The asymptotically decelerating rates in the decrease of both $a_{St}$ and U likely resulting from the gradual approach of some unavoidable minimum thresholds for both the lowest abundance $a_{St}$ (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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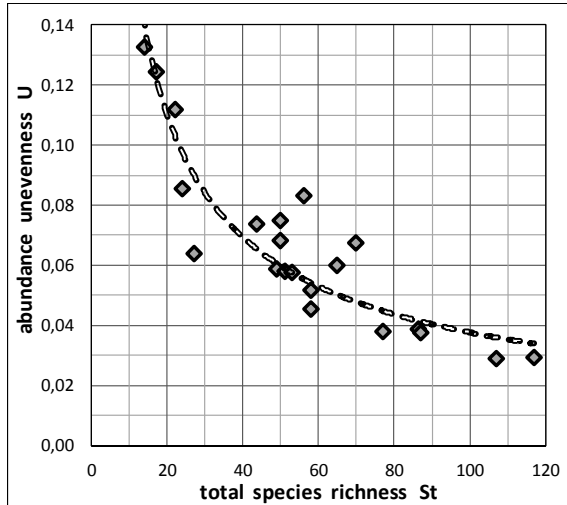


142
143  **Figure 1** – The degree of abundance unevenness U plotted against total species richness in 21 marine
144  communities. Seven gastropod communities (Andaman [32], Mannar Gulf [33], Fiji [34]); two sea-star
145  communities (South China Sea [35]) and twelve fish communities (Caribbean [36], Columbia [37], Brazil
146  [38], Red Sea (unpublished results)). Power regression, n = 21, r = 0.902, p < 0.0001.

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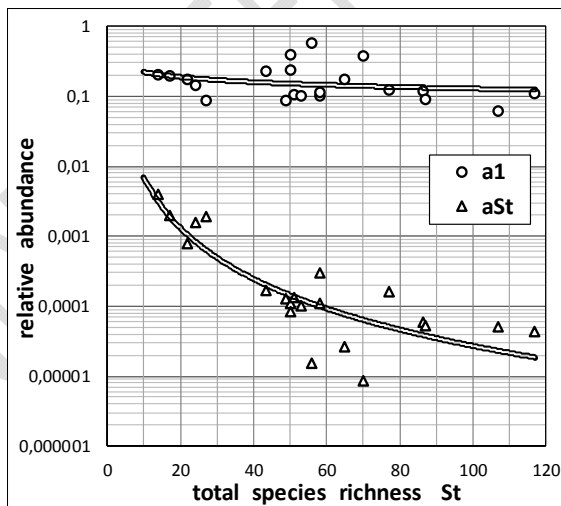


149
150  **Figure 2** – The (log-transformed) relative abundances, $a_1$ and $a_{St}$, of the more and the less abundant
151  species, plotted against total species richness $S_t$, in 21 marine communities (same as in Figure 1). Power
152  regressions for $a_1$ and $a_{St}$ are superimposed. Power regression, 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

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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,
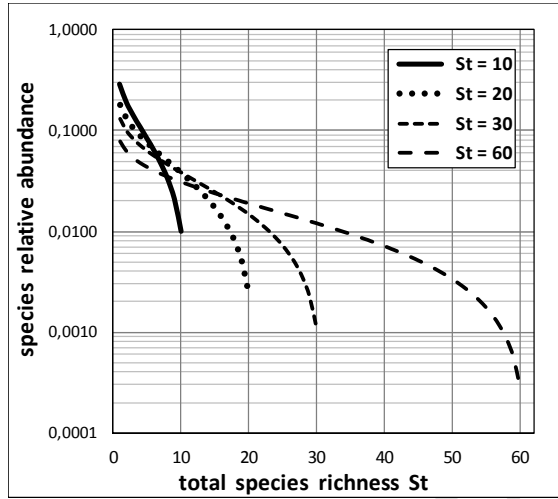160  involved in the process.
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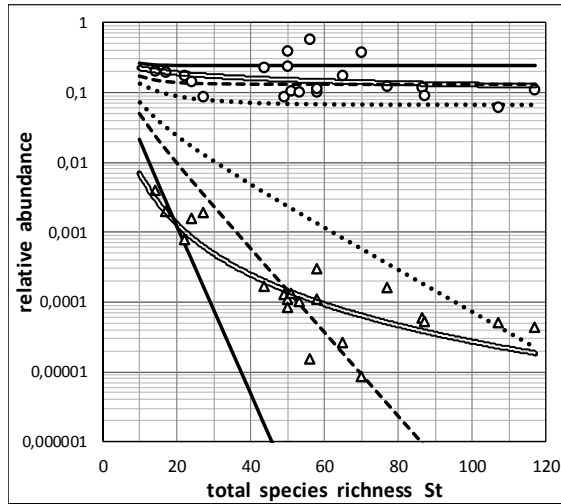


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164  **Figure 3** – Same as Figure 2 with, in addition, the relative abundances $a_1$ and $a_{St}$ computed for three
165  geometric series each of them characterized by a constant level of abundance unevenness,
166  independently of species richness: 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 $a_{St}$.
169

**6. An appropriate standardization for the degree of species abundance unevenness,**
**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):
190
191  $$U'(S_t) \approx 0.944 \, S_t^{-0.767} \qquad (2)$$

192



193

**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: $(1/S_t).\Sigma_n (1/n)$, with the summation $\Sigma_n$ on the integer n being extended from n = i to n = $S_t$, see reference [1].

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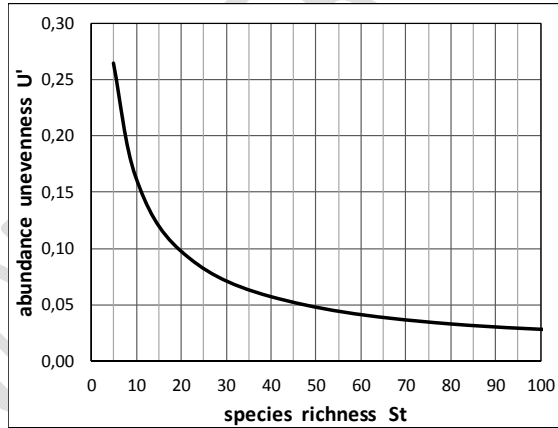
**Figure 5** – The abundance unevenness U' for the "broken-stick" distribution plotted against species richness $S_t$. U' is steadily decreasing monotonously with increasing species richness. The abundance unevenness U' of the "broken-stick" distribution varies approximately as U' ≈ 0.944 $S_t^{-0.767}$.

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 St 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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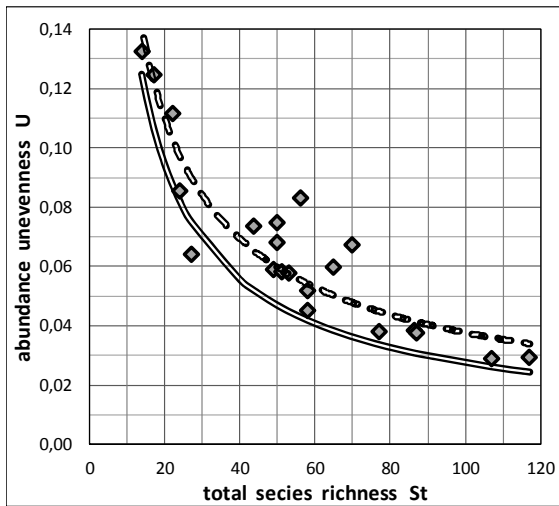


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223 **Figure 6** – Same as Figure 1, highlighting, in addition, the dependence upon species richness of the
224 abundance unevenness U' in the "broken-stick" distribution (double line). The empirical regression of
225 abundance unevenness U for the 21 marine communities and the abundance unevenness U' for the
226 "broken-stick" distribution are remarkably parallel to each other.
227
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 $\approx 0.01$.
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:
235
236          $I_{str} = U/U' = [\log(a_1/a_{St})/(S_t-1)]/[\log(a'_1/a'_{St})/(S_t-1)]$
237 that is:
238          $I_{str} = U/U' = \log(a_1/a_{St})/\log(a'_1/a'_{St})$          (3)
239
240 with $a_1$ and $a_{St}$ standing for the highest and the lowest abundances in the studied
241 community and $a'_1$ and $a'_{St}$ standing for the highest and the lowest abundances in the
242 corresponding "broken-stick" distribution computed for the same species richness $S_t$.
243 To summarize, considering the *"standardized"* unevenness "$I_{str}$", alongside *"rough"*
244 unevenness U, offers two major advantages:
245     (i) $I_{str}$ allows for *direct, unbiased* comparisons between communities that differ in their
246 respective levels of species richness and

7

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.
256
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
284     **8. The species richness broken down into its functional components**
285 Equation (1) can be rearranged as:
286
287 $$S_t = (1/U).\log_{10}(a_1/a_{St}) + 1 = R_a/U + 1 \qquad (4)$$
288   - "$R_a$" denotes the overall range of species abundances, measured on a logarithmic
289 scale: $\log_{10}(a_1) – \log_{10}(a_{St}) = \log_{10}(a_1/a_{St})$;
290   - $(1/U)$, as the inverse of U, stands for the *degree of relaxation of the mean competitive*
291 *intensity* within community.
292 Equation (4) thus allows to quantify how the level of species richness $S_t$ is "accommodated"
293 by (i) the degree of relaxation of interspecific competition $(1/U)$ and (ii) the extent of the
294 overall range of species abundances $R_a$.
295 In turn, the corresponding differential form of equation (4),
296
297 $$\partial S_t/S_t = – \partial U/U + \partial R_a/R_a \qquad (5)$$
298

8

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
305  $$\partial S_t/S_t = - \partial U'/U' - \partial I_{str}/I_{str} + \partial R_a/R_a \qquad (6)$$
306
307  which quantifies in more detail, how a relative variation $\partial S_t/S_t$ in species richness is
308  accommodated by the respective variations of its three functional components, $U'$, $I_{str}$ and
309  $R_a$, which contribute respectively for $[- \partial U'/U']$, for $[- \partial I_{str}/I_{str}]$ and for $[\partial R_a/R_a]$ to the
310  accommodation of the relative variation $\partial S_t/S_t$ of species richness.
311
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**

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 third 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 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 to 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 fourth 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 difference in species richness are provided in the three last columns. The range of species abundance $R_a$ does not significantly contribute to accommodation (with an even slight negative contribution – 4%) and, accordingly, only the relaxation of the mean competitive intensity is involved in the accommodation of 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 itself and a 32% genuine contribution.

**Table 1** – How the increase in total species richness ($S_{t\,2} - S_{t\,1}$) between two communities is accommodated by the corresponding variations of (i) the relaxation of the mean competitive intensity (1/U) [split in its two components, (1/U') and (1/$I_{str}$)] and (ii) the extension 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 requires, as far as possible, a *complete sampling* of the focused community, and this stands all the more so for the subsequent analysis of unevenness in terms of the standard reference value U' and the deviation to this standard estimated by the deviation of $I_{str}$ from unity. Unfortunately, incomplete inventories are doomed to become even more frequent with the inevitable generalization of "rapid assessments" and "quick surveys", especially for species-rich communities comprising a lot of rare species. And accounting for unrecorded rare species, as well, is important since at least some of them can yet disproportionately contribute to the functional structuring of communities in the wild [48–53]. Recently developed procedures of numerical extrapolation of incomplete samplings

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

## 11. Discussion and Conclusion

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

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

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

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

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

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

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

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**Comment [J3]:** Update references, less than half of the last five years

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