



Advances in Research

19(1): 1-14, 2019; Article no.AIR.48978
ISSN: 2348-0394, NLM ID: 101666096

Disentangling and Quantifying the Functional Determinants of Species Abundance Unevenness in Ecological Communities

Jean Béguinot^{1*}

¹Société Histoire Naturelle-Bourgogne Nature, 7 bvd H. P. Schneider, 71200 Le Creusot, France.

Author's contribution

The sole author designed, analysed, interpreted and prepared the manuscript.

Article Information

DOI: 10.9734/AIR/2019/v19i130114

Editor(s):

(1) Dr. Martin Kröger, Professor, Computational Polymer Physics, Swiss Federal Institute of Technology (ETH Zürich), Switzerland.

Reviewers:

(1) Manoel Fernando Demétrio, Brazil.

(2) Junir Antonio Lutinski, Universidade Comunitária da Região de Chapecó, Brazil.

(3) João Pedro Barreiros, Universidade dos Açores, Portugal.

Complete Peer review History: <http://www.sdiarticle3.com/review-history/48978>

Received 20 February 2019

Accepted 09 May 2019

Published 14 May 2019

Method Article

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 while, yet, 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 assigned 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.

*Corresponding author: E-mail: jean-beguिनot@orange.fr;

Keywords: Distribution; evenness; broken-stick model; competition; resource partitioning; Allee effect.

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” [4-5]), then these species will not persist any more within the set of species [5].

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 these recruited species, which drives the hierarchical structuration of their relative abundances. However, a 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 [6-17]. 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 variable success among 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 (as a rule, 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). Yet, 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]:

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

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

with a_1 and a_{S_t} 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 DIRECT 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. For example, in the expression above of species unevenness (equation (1)), this trivial influence is cancelled by rationalizing $[\log(a_1/a_{S_t})]$ 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 [24,29]. As an example, this negative direct influence of species richness on abundance unevenness is empirically highlighted in Fig. 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 average trend for a monotonous decrease of abundance unevenness with increasing species richness is almost entirely explained by the continuously decelerated decreasing rate of the (log-transformed) minimal relative abundance a_{S_t} with growing species richness, while the (log-transformed) relative abundance of the dominant species a_1 remains almost constant (Fig. 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 Fig. 1. Likewise, the hyperbolic-like decrease of $\log(a_{S_t})$ with growing species richness S_t (Fig. 2) is in contradiction with the linear decrease of $\log(a_{S_t})$ with S_t that would result from an assumed independence of abundance unevenness U with respect to species richness (as shown in Fig. 3). Thus, at both (related) points of view (i.e. $U = f(S_t)$: Fig. 1 and $\log(a_{S_t}) = f(S_t)$: Figs. 2 & 3), the null hypothesis of independence between 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), two causative mechanisms, at least, may be suggested.

At first, it is likely that, as the number of recruited species (i.e. the species richness) increases, the *probability* for a growing number of ecological niches being involved will also increase more or less – as an average trend [30,31]. Accordingly, the average differential success among consecutive species along the S.A.D., $\log(a_i/a_{i+1})$ – that is the abundance unevenness (equation (1)) – is expected to decrease with higher species richness. A trend for a reduced

unevenness (i.e. for an *improved relaxation of the mean competitive intensity*) with increasing species richness is thus expected from this *statistically based, first mechanism*.

Second, when the lowest species abundances in a community end up getting weaker and weaker, as species richness becomes larger, then an *Allee-like effect* may possibly be involved, finally

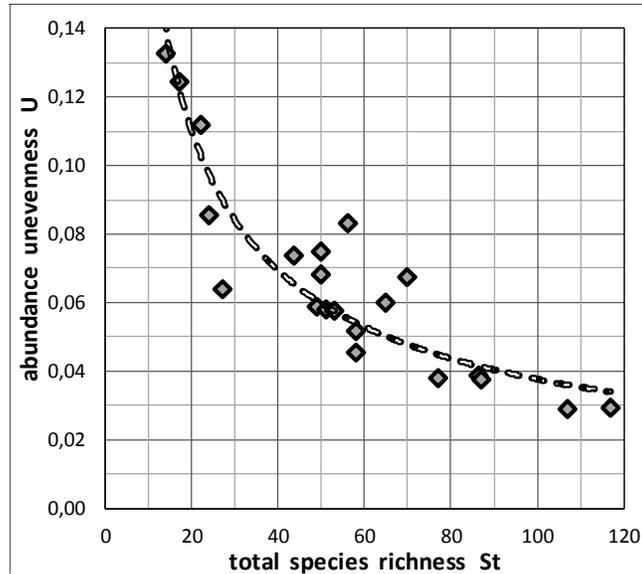


Fig. 1. The degree of abundance unevenness U plotted against total species richness in 21 marine communities. Seven gastropod communities (Andaman [32], Mannar Gulf [33], Fiji [34]); two sea-star communities (South China Sea [35]) and twelve fish communities (Caribbean [36], Columbia [37], Brazil [38],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

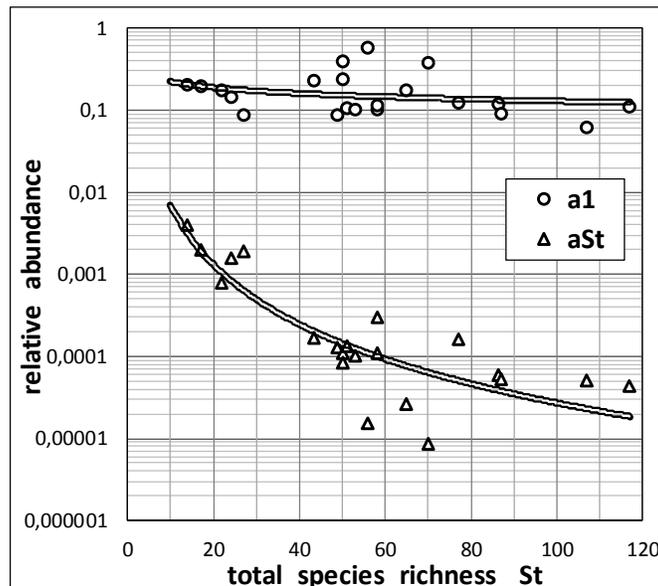


Fig. 2. The (log-transformed) relative abundances, a_1 and a_{St} , of the more abundant and the less abundant species, plotted against total species richness S_t , in 21 marine communities (same as in Fig. 1). Power regressions for a_1 and a_{St} are superimposed.
Power regressions: $n = 21$, $r = 0.846$, $p < 0.0001$ for a_{St} and $r = 0.240$, $p = 0.29$ for a_1

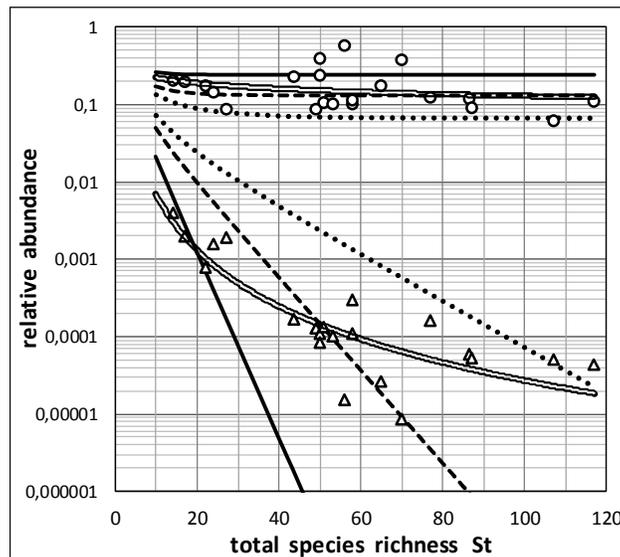


Fig. 3. Same as Fig. 2 with, in addition, the relative abundances a_1 and a_{St} computed for three geometric series each of them computed with a constant level of abundance unevenness, U , independently of species richness: $U = 0.12$ (solid line), $U = 0.06$ (dashed line), $U = 0.03$ (dotted line). The straight lines pattern, characteristic of constant level of abundance unevenness whatever species richness, does not fit at all the hyperbolic pattern of recorded values of a_{St} . Geometric series are chosen here for easier computation

(section 2). In turn, such an Allee-effect would allow to persist (i.e. would “select”) those communities *only* having an increasingly lower level of unevenness of species abundance, as species richness becomes larger. This second mechanism also results, mathematically, in a negative, direct dependence between species richness and abundance unevenness. However, this mechanism may likely be involved later, postponed when the weakest abundances eventually approach the minimum threshold levels for an Allee effect to become effective.

Both alternative or complementary mechanisms above result in an apparently *mathematic-like* trend for a direct negative dependence of species abundance unevenness upon species richness, as originally pointed in [24,29] and reiterated in [32-39]. And this, even though *biological causes* are obviously involved, at least partly, in the process.

However, regardless of the detail of the causal contribution(s) involved, the constraining character of this direct influence of species richness is *limited* to the overall average trend, since considerable deviations from this average trend can occur and, thereby, can more or less *singularize each community in particular*, as shown in Fig. 1. This highlights the involvement of *complementary, idiosyncratic contributions* to

abundance unevenness, which deserve specific attention and justify to *consider separately* the “*genuine*” deviations from the *overall average trend*: see following section.

6. STANDARDIZING THE DEGREE OF SPECIES ABUNDANCE UNEVENNESS DOES HIGHLIGHT ITS “GENUINE” PART, FREED FROM THE DIRECT INFLUENCE OF SPECIES RICHNESS

Beyond the average decreasing trend highlighted above, the abundance unevenness can still appreciably differ between communities having a same species richness, as obvious from Fig. 1. Difference in unevenness at a same level of species richness can be very important, reaching a factor of two at least, in \log_{10} . That is, in untransformed abundances, at least *two orders of magnitude* (Fig. 1). And these deviations from the “standard” trend are all the more important to consider that they highlight the “*genuine*” *ecological specificity* of each particular community, beyond the general trend, as emphasized above.

One way to quantify these deviations is to compare the rough abundance unevenness U to the value taken by the empirical regression of U against S_t (derived above, Fig. 1) at the same level of species richness.

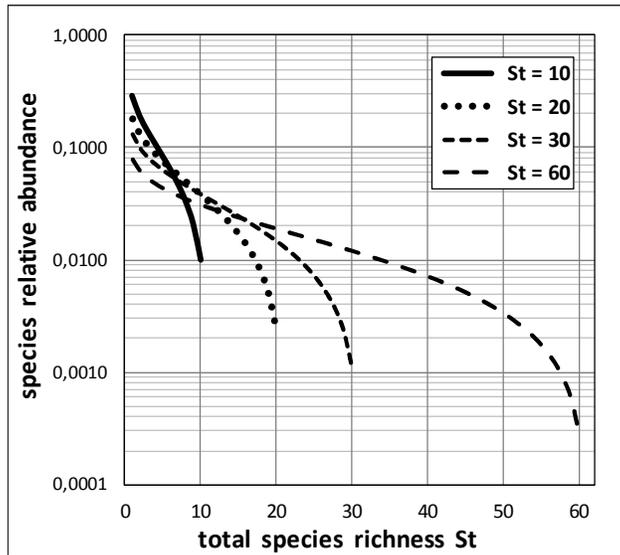


Fig. 4. “Broken-stick” distributions computed for increasing species richness $S_t = 10, 20, 30, 60$. Although the theoretical structuring process involved in the “broken-stick” model remains unchanged, regardless of species richness, the slope of the species abundance distribution – and thus the abundance 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: $(1/S_t) \cdot \sum_{n=1}^i (1/n)$, with the summation \sum_n on the integer n being extended from $n = 1$ to $n = S_t$, see reference [1])

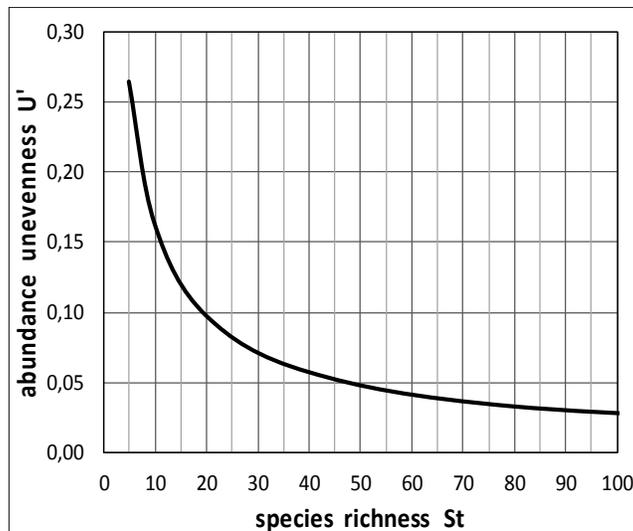


Fig. 5. The abundance unevenness U' for the “broken-stick” distribution plotted against species richness S_t . U' is steadily decreasing monotonously with increasing species richness and varies approximately as $U' \approx 0.944 S_t^{-0.767}$

Yet, an alternative choice features more appropriate [29], that consists in standardizing U to the abundance unevenness U' of the well-known “broken-stick” theoretical distribution [40], characterized by an *invariant process* of

allocation of abundances to species [1] (namely, a random allocation process). Despite this invariance in the process involved regardless of the level of species richness, the abundance unevenness U' in the “broken-stick” distribution is

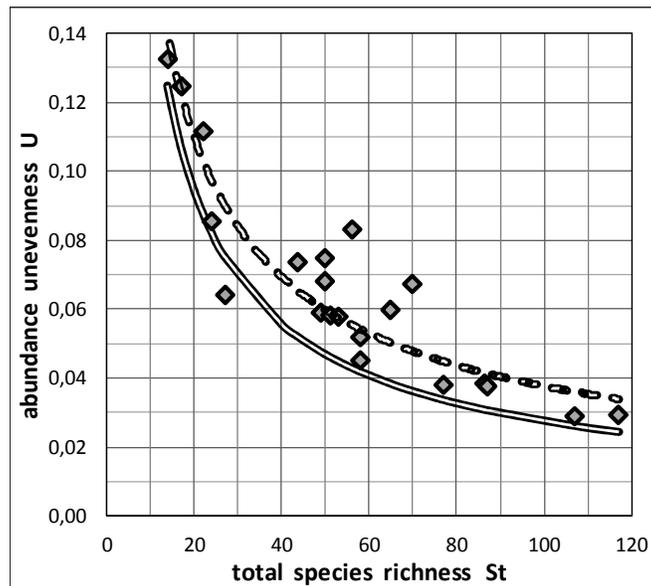


Fig. 6. Same as Fig. 1, highlighting, in addition, the dependence upon species richness of the abundance unevenness U' in the “broken-stick” distribution (double line). The empirical regression of abundance unevenness U for the 21 marine communities (dashed line) and the abundance unevenness U' for the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

entirely determined by species richness [1,40] (see Figs. 4 and 5), so that U' *relevantly accounts* for the mathematical-like trend for a *direct* influence of species richness on abundance unevenness [1].

This direct dependence of U' on S_t approximately answers the following equation (Fig. 5):

$$U'(S_t) \approx 0.944 S_t^{-0.767} \quad (2)$$

Choosing the “broken-stick” distribution as a relevant reference to standardize abundance unevenness [29] offers several advantages:

- (i) as just emphasized, by virtue of its very conception, the “broken-stick” distribution offers the unique particularity of being entirely and exclusively parametrized in term of species richness; it thereby accurately accounts for the mathematical-like trend of *direct* dependence of U upon S_t , on a theoretical basis [1,40];
- (ii) this *theoretical basement* better establishes the *general soundness* of the “broken-stick” distribution as a relevant reference (as compared to the alternative, empirically derived reference evoked at first);
- (iii) as already mentioned, the “broken-stick” distribution is one of the few *universally*

well-known models of abundance distribution;

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

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

Finally, it looks therefore quite appropriate to *standardize* the species abundance unevenness U to the level of unevenness U' of the “broken-stick” distribution computed at the same species richness (as already suggested in [32-39]). A “standardized” index “ I_{str} ”, is thus defined as:

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

that is:

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

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

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

- (i) I_{str} allows for *direct, unbiased* comparisons between communities, *regardless* of the difference in their respective levels of species richness and,
- (ii) I_{str} is, by construction, “self-benchmarked” and, thereby, is *explicitly evocative*, contrasting in this respect with rough unevenness U , whose value remains hardly meaningful in itself, due to lack of clear evocative reference.

Daring a metaphorical comparison, the situation with *unevenness* is somewhat similar to that with the *size* of individuals within a same species: the size, while being, on average, biologically related directly to the age, yet deviates more or less from this “standard”, for each individual in particular. So that the size of a given individual is expressed *more evocatively* when its rough size is standardized to this referential benchmark, the latter conveying only the “mathematical-like”, direct influence of age.

7. THE “FUNCTIONAL” MEANINGS OF ROUGH AND STANDARDIZED ABUNDANCE UNEVENNESS

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

In particular, relevantly comparing the average intensities of interspecific competition between two communities having *different species richness* imperatively requires to consider not only the rough unevenness U but, *also*, the standardized unevenness I_{str} , in order to be able to disentangle and *clearly quantify* what, in the comparison, is the mere, direct consequence of the difference in species richness from what is *genuinely distinctive* between these communities specifically. It is in this sense that the standardized index I_{str} has been considered as highlighting the “*genuine*” part of the hierarchical structuring process within community [32-39]. In short, from a functional point of view, the structuring index I_{str} reflects “the mean competitive intensity (*sensu latissimo*), normalized to what it is in the broken-stick distribution at the same level of species richness”.

8. SPECIES RICHNESS AND MEAN COMPETITIVE INTENSITY BROKEN DOWN INTO THEIR FUNCTIONAL COMPONENTS

Equation (1) can be rearranged as:

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

$$S_t = (1/U') \cdot (1/I_{str}) \cdot R_a + 1 \quad (4)$$

with “ R_a ” as the overall range of species abundances, measured on logarithmic scale: $R_a = \log_{10}(a_1) - \log_{10}(a_{st}) = \log_{10}(a_1/a_{st})$. This expression (4) 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:

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

Then, further splitting the rough abundance unevenness $U = U' \cdot I_{str}$ 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 see section 5) and (ii) the “*genuine*” contribution of $-\partial I_{str}/I_{str}$, to the relaxation of the competitive intensity, *apart from the overall trend*:

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

Accordingly:

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

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:

- 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} (Fig. 2) and / 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 each of 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 (i.e. the relaxation of competitive intensity) will be favored to accommodate a larger number of co-occurring species. 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 meet 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.

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 $-\partial U/U$ of the mean competitive intensity U [relaxation being split, in turn, into its two components, $-\partial U'/U'$ and $-\partial I_{str}/I_{str}$] and (ii) the extension $\partial R_a/R_a$ 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%

* 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.

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 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 still 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, as well, for unrecorded rare species is important since at least some of them can 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 implementing such procedures is strongly recommended, as far as necessary.

11. DISCUSSION AND CONCLUSION

Contrary to what is still too often assumed, total species richness S_t and species abundance unevenness U in a community are *not* truly mutually-independent descriptors [24, 9]: As an average trend, abundance unevenness is partly influenced *directly* (and negatively) by species richness. This trend results from a “mathematical-like” – although biologically rooted – constraint, being the likely consequence of, first, a statistical determinism (section 5) and

second, some possible additional Allee-effect. This average trend had already been admitted empirically in the pioneering work of MacArthur [40] with its “broken-stick” theoretical distribution, a model explicitly and exclusively mathematically dependent on species richness. Hence the relevance [29] 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 this broken-stick model, taken as the standard reference.

Indeed, if numerous bird communities fairly conform to this standard reference, as rightly advocated by MacArthur, other kinds of ecological communities most often deviate, more or less, from the broken-stick distribution. 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 – to highlight separately the part of unevenness *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*: see § 2) and in term of the resulting intensity of abundance structuring – once the *direct* influence of species richness on these intensities has been already accounted first.

ACKNOWLEDGEMENTS

Three anonymous Reviewers are acknowledged for their useful suggestions.

COMPETING INTERESTS

Author has declared that no competing interests exist.

REFERENCES

1. May RM. Patterns of species abundance and diversity. In Cody ML, Diamond JM. Ecology and evolution of communities. The Belknap Press of Harvard University. 1975; 81-120.
2. Bowler GM, Kelly CK. The general theory of species abundance distribution. *ArXiv*. 2010;1002:5008.
3. Ochiaga EO, Hui C. Forms and genesis of species abundance distributions. *Computational Ecology and Software*. 2015; 5(4):340-353.
4. Zhou SR, Zhang DY. Allee effects and the neutral theory of biodiversity. *Functional Ecology*. 2006;20:509-513.
5. Gascoigne J, Berec L, Gregory S, Courchamp F. Dangerously few liaisons: A review of mate-finding Allee effects. *Population Ecology*. 2009;51:355-372.
6. Grange SW, Stier AC. Order of arrival affects competition in two reef fishes. *Ecology*. 2009;90(10):2868-2878.
7. Huston M. A general hypothesis of species diversity. *The American Naturalist*. 1979; 113:81-101.
8. Robertson DR. Interspecific competition controls abundance and habitat use of territorial Caribbean damselfishes. *Ecology*. 1996;77:885-899.
9. Pulliam HR. On the relationship between niche and distribution. *Ecology Letters*. 2000;3:349-361.
10. Moore KA, Elmendorf SC. Propagule vs. niche limitation: Untangling the mechanisms behind plant species' distributions. *Ecology Letters*. 2006;9:797-804.
11. Peng Z, Zhou S, Zhang DY. Dispersal and recruitment limitation contribute differently to community assembly. *Journal of Plant Ecology*. 2012;5(1):89-96.
12. Mora C, Chittaro Pm, Sale PF, Kritzer JP, Ludsins SA. Patterns and processes in reef fish diversity. *Nature*. 2003;421:933-936.
13. Doherty PJ, Williams DMcB. The replenishment of coral reef populations. *Oceanographic and Marine Biology Annual Review*. 1988;26:487-551.
14. Warner RR, Chesson PJ. Coexistence mediated by recruitment fluctuations: A field guide to the storage effect. *The American Naturalist*. 1985;125:769-787.
15. Tupper M, Hunte W. Recruitment dynamics of coral reef fishes in Barbados. *Marine Ecology Progress Series*. 1994; 108:225-235.
16. Jones GP. The importance of recruitment to the dynamics of a coral reef fish population. *Ecology*. 1990;71:1691-1698.
17. Jones GP. Post-recruitment processes in the ecology of coral reef fish populations: A multi-factorial perspective. In: Sale PF. (ed.) *The ecology of fishes on coral reefs*. Academic Press, San Diego. 1991;294-330.
18. Connolly SR, Hughes TP, Bellwood DR, Karlson RH. Community structure of corals and reef fishes at multiple scales. *Science*. 2005;309:1363-1365.
19. Sanjit L, Bhatt D. How relevant are the concepts of species diversity and species richness. *Journal of Bioscience*. 2005; 30(5):557-560.
20. McGill BJ, Etienne RS, Gray JS, et al. Species abundance distributions: Moving beyond single prediction theories to integration within an ecological framework. *Ecology Letters*. 2007;10:995-1015.
21. Alonso D, Ostling A, Etienne RS. The implicit assumption of symmetry and the species abundance distribution. *Ecology Letters*. 2008;11:93-105.
22. Mac Nally R, McAlpine CA, Possingham HP, Maron M. The control of rank-abundance distributions by a competitive despotic species. *Oecologia*. 2014;176(3): 849-857.
23. Matthews TJ, Whittaker RJ. On the species abundance distribution in applied ecology and biodiversity management. *Journal of Applied Ecology*. 2015;52:443-454.
24. Loiseau N, Gaertner JC. Indices for assessing coral reef fish biodiversity: The need for a change in habits. *Ecology and Evolution*. 2015;5(18):4018-4027.
25. Connolly SR, Hughes TP, Bellwood DR. A unified model explains commonness and rarity on coral reefs. *Ecology Letters*. 2017; 20:477-486.
26. McCarthy JK, Mokany K, Ferrier S, Dwyer JM. Predicting community rank-abundance distribution under current and future climates. *Ecography*. 2017;40:1-11.
27. Strong WL. Assessing species abundance unevenness within and between plant communities. *Community Ecology*. 2002; 3(2):237-246.
DOI: 10.1556/COMEC.3.2002.2.9
28. Grzès IM. Ant species richness and evenness increase along a metal pollution

- gradient in the Boleslaw zinc smelter area. *Pedobiologia*. 2009;53:65-73.
29. DeBenedictis PA. On the correlations between certain diversity indices. *The American Naturalist*. 1973;107:295-302.
 30. Petchey L, Gaston KJ. Functional diversity (FD), species richness and community composition. *Ecology Letters*. 2002;5:402-411.
 31. Halpern BS, Floeter SR. Functional diversity responses to changing species richness in reef fish communities. *Marine Ecology Progress Series*. 2008;364:147-156.
 32. Béguinot J. Numerical extrapolation of the species abundance distribution unveils the true species richness and the hierarchical structuring of a partially sampled marine gastropod community in the Andaman Islands (India). *Asian Journal of Environment and Ecology*. 2018;6(4):1–23. DOI: 10.9734/AJEE/2018/41293
 33. Béguinot J. The full hierarchical structuration of species abundances reliably inferred from the numerical extrapolation of still partial samplings: A case study with marine snail communities in Mannar Gulf (India). *Asian Journal of Environment and Ecology*. 2018;7(3):1-27. DOI: 109734/AJEE/2018/36831
 34. Béguinot J. Analyzing the role of environmental stresses on species richness and the process of hierarchical structuring of species abundances in marine Gastropods communities at Suva (Fiji Islands). *International Journal of Environment and Climate Change*. 2018; 8(3):200-233.
 35. Béguinot J. Inferring total species richness and the exhaustive hierarchical structuring of species abundances in tropical Sea-Stars communities (Asteroidea), using numerical extrapolation of partial inventories. *Asian Journal of Environment and Ecology*. 2018;8(2):1-25. DOI: 109734/AJEE/2018/46272
 36. Béguinot J. Comparing the complete hierarchical structuration of species abundances in reef fish communities according to coral morphology, using the numerical extrapolation of only incomplete inventories. *Asian Journal of Environment and Ecology*. 2018;8(1):1-20. DOI: 109734/AJEE/2018/45402
 37. Béguinot J. Influence of coral architecture on species richness and the hierarchical structuration of species abundances in reef fish communities: A case study in the eastern tropical pacific. *Asian Journal of Environment & Ecology*. 2018;8(3):1-21. Available: <https://doi.org/10.9734/ajee/2018/v8i330075>
 38. Béguinot J. Influence of fishing activity on the total species richness and the abundance unevenness in reef fish communities: A case study in a Brazilian tropical coral complex. *International Journal of Environment and Climate Change*. 2019;9(1):58-76.
 39. Béguinot J. The hierarchical structuring of species abundances within communities: disentangling the intensity of the underlying structuring process behind the apparent unevenness pattern. *Advances in Research*. 2018;16(1):1-12. DOI: 10.9734/AIR/2018/43918
 40. MacArthur RH. On the relative abundance of bird species. *Proceedings of the National Academy of Sciences U.S.A.* 1957;43:293-295.
 41. Gotelli NJ. Relative abundance. In Gotelli NJ, Graves GR. *Null models in ecology*. Smithsonian Institution Press, Washington DC; 1996.
 42. Fattorini S, Rigal F, Cardoso P, Borges PAV. Using species abundance distribution models and diversity indices for biogeographical analyses. *Acta Oecologica*. 2016;70:21-28.
 43. Pianka EC. Niche overlap and diffuse competition. *Proceedings of the National Academy of Sciences USA*. 1974;71(5): 2141-2145.
 44. Schoener TW. Resource partitioning in ecological communities. *Science*. 1974; 185:27-39.
 45. Pianka EC. Niche relations of desert Lizards. In Cody ML, Diamond JM. *Ecology and evolution of communities*. The Belknap Press of Harvard University. 1975; 292-314.
 46. Roughgarden J. Resource partitioning among competing species – A coevolutionary approach. *Theoretical Population Biology*. 1976;9(3):388-424.
 47. Pacala S, Roughgarden J. Resource partitioning and interspecific competition in two two-species insular Anolis Lizard communities. *Science*. 1982;217:444-446.
 48. Bracken M, Low N. Realistic losses of rare species disproportionately impact higher

- trophic levels. Ecology Letters. 2012;15: 461-467.
49. Moullot D, Bellwood DR, Baraloto C, Chave J, et al. Rare species support vulnerable functions in high-diversity ecosystems. PLoS Biol. 2013;11(5): e1001569.
50. Jain M, Flynn DFB, Prager CM, Hart GM, DeVan CM, et al. The importance of rare species: A trait-based assessment of rare species contribution to functional diversity and possible ecosystem function in tall-grass prairies. Ecology and Evolution. 2014;4(1):104-112.
51. Low-Decarie E, Kolber M, Homme P, Lofano A, Dumbrell A, Gonzalez A, Bell G. Community rescue in experimental communities. Proceedings of the National Academy of Sciences USA. 2015;112(46): 14307-14312.
52. Leitao RP, Zuanon J, Villéger S, Williams SE, Baraloto C, et al. Rare species contribute disproportionately to the functional structure of species assemblages. Proceedings of the Royal Society B. 2016;283:0084.
53. Violle C, Thuillier W, Mouquet N, Munoz F, et al. Functional rarity: The ecology of outliers. Trends in Ecology; 2017. DOI: 10.1016/j.tree.2017.02.002
54. Béguinot J. Theoretical derivation of a bias-reduced expression for the extrapolation of the Species Accumulation Curve and the associated estimation of total species richness. Advances in Research. 2016;7(3):1-16. DOI: 10.9734/AIR/2016/26387
55. Béguinot J. Extrapolation of the species accumulation curve associated to “Chao” estimator of the number of unrecorded species: A mathematically consistent derivation. Annual Research & Review in Biology. 2016;11(4):1-19. DOI: 10.9734/ARRB/2016/30522
56. Béguinot J. How to extrapolate species abundance distributions with minimum bias when dealing with incomplete species inventories. Advances in Research. 2018; 13(4):1-24. DOI: 10.9734/AIR/2018/39002
57. MacArthur RH. Note on Mrs Pielou’s comments. Ecology. 1966;47:1074.

© 2019 Béguinot; This is an Open Access article distributed under the terms of the Creative Commons Attribution License (<http://creativecommons.org/licenses/by/4.0>), which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.

Peer-review history:

*The peer review history for this paper can be accessed here:
<http://www.sdiarticle3.com/review-history/48978>*