Method Article

The hierarchical structuring of species abundances within communities: disentangling the intensity of the underlying structuring *process* behind the apparent unevenness *pattern*

Abstract

Besides species richness, the hierarchical structuration of species abundances is the second major characteristic that numerically specifies a community of species. However, while the meaning of species richness is simple and straightforward, the hierarchical structuration of abundances is a less simple concept, where the *pattern* – i.e. the straightforwardly observed level of unevenness of species abundance distribution – *does not* reliably mirror the genuine intensity of the structuring *process* itself. This is because the level of unevenness is also mathematically dependent upon species richness. Accordingly, when specifying numerically a community of species, I advocate not to be satisfied, as usual, by considering only the total species richness and the degree of unevenness (whatever the expression chosen to quantify unevenness). A third parameter should be further considered: the genuine intensity of the structuring *process* itself, defined *freed* from the purely mathematical influence of species richness and, thereby, accurately reflecting the *functional* contribution to the hierarchical structuration of species abundances. The level of unevenness is thus only granted a simply descriptive goal, while the intensity of the structuring process relevantly speaks for the biological background behind the apparent hierarchical structuration of species abundances in communities.

An additional requirement to warrant the reliable evaluations of these three parameters is, of course, to work with (sub-) exhaustive samplings of the studied communities or, when not possible in practice, to consider the least-biased *numerical extrapolations* of partial samplings, when only these are available.

The benefits of this renewed methodological way to quantify the internal organization of species communities, as well as the potential pitfalls to which one may be exposed by considering only species richness and abundance unevenness, are argued from a theoretical point of view and then highlighted concretely in a series of examples.

Key words: ranked abundance distribution, numerical extrapolation, species richness, diversity, evenness

1. Introduction

The number of species that co-occur in a same assemblage and, then, the distribution of their relative abundances are largely recognized as the two main descriptive features of the internal organization of species communities in the wild [1-10]. Now, moving from the mere descriptive *pattern* (i.e. the recorded level of unevenness of species abundances) towards the intensity of the underlying *process* driving the hierarchical structuration of abundances is less straightforward that may be thought at first. In fact, the recorded level of unevenness of species abundance – the pattern – *does not* uniquely mirror the intensity of the structuring *process* itself, because the degree of unevenness is *also largely modulated* mathematically by the level of species richness [11-14].

Yet, most frequently, this difficulty remains ignored in common practice, and only the crudely recorded level of unevenness is addressed, still being implicitly – but unduly – considered as reflecting faithfully the intensity of the underlying structuring process. As this is not the case indeed, the structuring intensity must then be disentangled from the crude evaluation of abundance unevenness, in order to get access to the *functionally relevant* aspects of the hierarchical structuring of species abundances in communities.

The approach developed hereafter aims, accordingly, at disentangling the intensity of the process at work behind the immediately highlighted pattern of species abundance unevenness.

2. Disentangling the genuine intensity of the structuring "process" from the observed unevenness "pattern"

The degree of unevenness of species abundance distribution may be evaluated according to many different – more or less equivalent – ways. Let consider the classical mode of representation of Species Abundance Distributions (the so-called "Whittaker plot" or "ranked abundance distribution"), according to which the (log-transformed) relative abundances a_i are plotted against their rank i of decreasing value (with, thus, a_1 and a_{St} respectively standing for the highest and the lowest abundances in an assemblage of S_t species). In this very classical mode of representation, it then goes natural to quantify the degree of abundance unevenness as the average slope of the abundance decrease along the whole range of the abundance distribution. This slope is defined as $[\log(a_1) - \log(a_{St})]/(S_t - 1) = \log(a_1/a_{St})/(S_t - 1)$ (N.B.: with untransformed abundances, the equivalent figure would become $(a_1/a_{St})^{(1/(St-1))}$.

Accordingly, the *degree of unevenness* "U" of the distribution of species abundances in a community is:

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

$$[\ \text{or, alternatively, } U^* = (a_1/a_{St})^{(1/(St-1))} \qquad (2)\ ]$$

One important (although too often overlooked) issue regards the unavoidable mathematical influence of the species richness S_t of the community on the degree of unevenness. Several authors [11-14] have already call attention to a consistent trend for the level of species dominance to decrease with increasing total species richness: all other things remaining equal, the degree of dominance tends to be all the more "diluted" than the number of co-occurring species increases. This intuitive influence of species richness on the degree of unevenness U of the distribution of abundances may further be demonstrated by considering the "broken-stick" model [15]. This model, which involves the random apportionment of relative abundances among co-occurring species, thus calls upon a *constant process* of hierarchical structuration, so that all "broken-stick" distributions depend *only on* (and are only parametrized by) the level of species richness S_t. Accordingly, the variation of the degree of unevenness of the "broken-stick" distribution with S_t characterizes numerically the mathematical trend for the degree of unevenness to decrease with increasing species richness, as shown graphically in Figures 1, 2, 3.

Thus, comparing the Species Abundance Distribution under study to the corresponding "broken-stick" distribution (i.e. the "broken-stick" computed for the *same* species richness) would reveal especially relevant because using this comparison makes possible to *get rid from* the direct mathematical influence of the number of co-occurring species on the unevenness level [12]. Similarly, *standardizing* the degree of unevenness U (the average slope of the S.A.D.) to the degree of unevenness U' of the corresponding "broken-stick" model is a relevant way to *get rid from* the direct influence of species richness on U and, thereby, to retain only what makes the intensity of the structuring process *functionally specific* to the community under study [16].

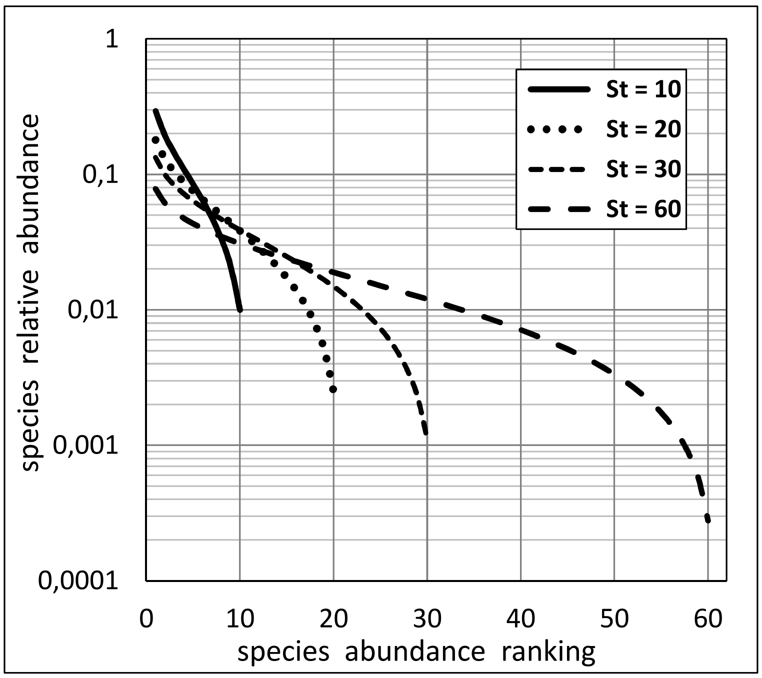

Figure 1 – The "broken-stick" distributions computed for increasing species richness S_t = 10, 20, 30, 60. Although the theoretical structuring process involved in the "broken-stick" model remains unchanged (the random apportionment of relative abundances among the S_t member-species), the average slope of the species abundance distribution strongly depends upon (and monotonously decreases with) S_t.

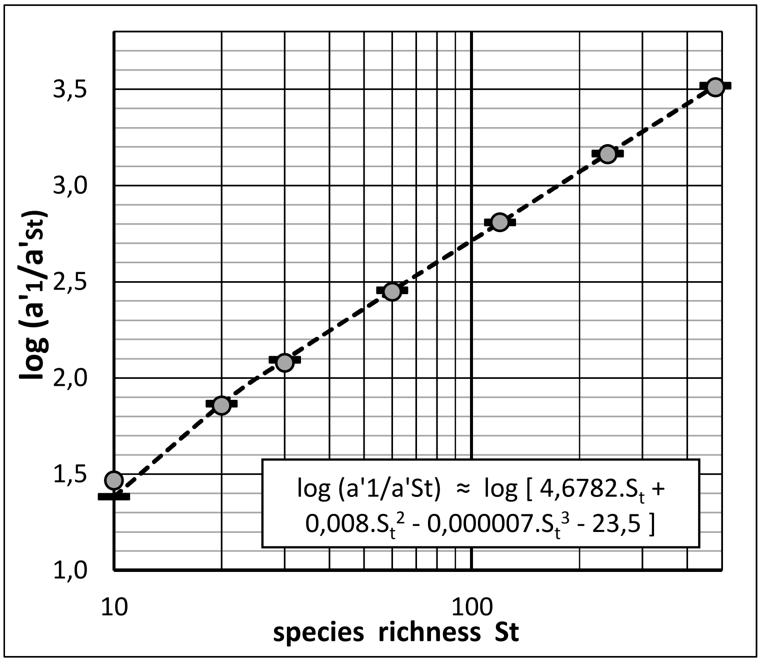

Figure 2– The variation of the degree of dominance, $\log(a'_1/a'_{St})$, computed against species richness S_t for the "broken-stick" distribution (from Figure 1): grey discs. A regression is proposed as: $\log(a'_1/a'_{St}) \approx \log[\,4{,}6782.S_t + 0{,}008.S_t^2 - 0{,}000007.S_t^3 - 23{,}5\,]$: dashed line. The range of species richness is extended up to 480 species.

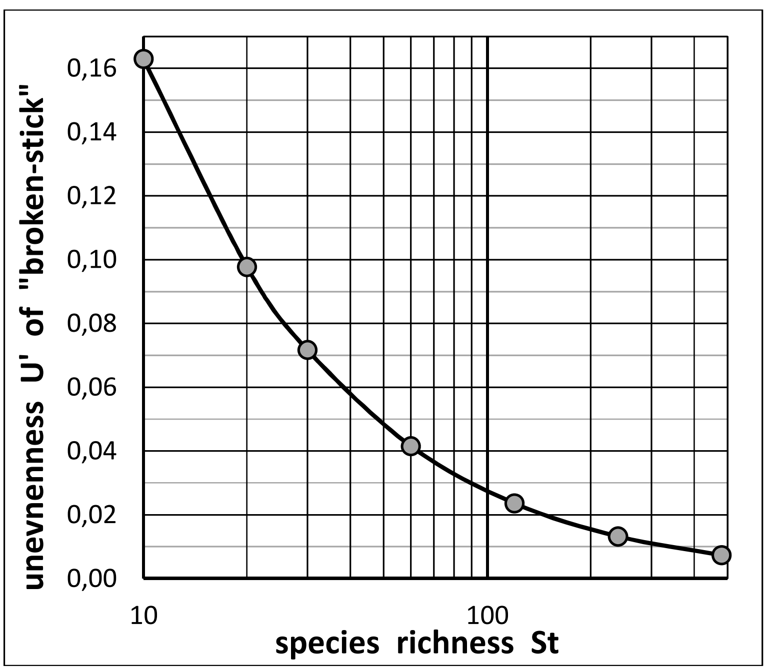

Figure 3 – The variation of the degree of unevenness, $U' = \log(a'_1/a'_{St})/(S_t - 1)$ for the "broken-stick" distribution, computed against species richness S_t (from Figure 1). The range of species richness is extended up to 480 species.

The *genuine* intensity, "I_{str}", of the hierarchical structuring process is thus defined as the ratio between the slope $U = \log(a_1/a_{St})/(S_t - 1)$ of the Species Abundance Distribution and the slope $U' = \log(a'_1/a'_{St})/(S_t - 1)$ of the corresponding "broken-stick" distribution (computed for the same species richness S_t):

$$I_{str} = U/U' = [\log(a_1/a_{St})/(S_t - 1)]/[\log(a'_1/a'_{St})/(S_t - 1)] \qquad (3)$$

that is, finally:

$$I_{str} = \log(a_1/a_{St})/\log(a'_1/a'_{St}) \qquad (4)$$

with the abundances being classically log-transformed and with a_1 and a_{St} standing for the highest and the lowest abundances in the studied assemblage 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).

Nota: alternatively the intensity of the structuring process may be written as:

$$I_{str}^* = U^*/U^{*\prime} = (a_1/a_{St})/(a'_1/a'_{St}) \qquad (5)$$

The variation with S_t of the ratio of abundances (a'_1/a'_{St}) between the most and the least abundant species is approximately ruled, in the "broken-stick" distribution, by the following equation (regression for species richness between 10 and 500 species, Fig. 2):

$$(a'_1/a'_{St}) \approx 4{,}6782.S_t + 0{,}008.S_t^2 - 0{,}000007.S_t^3 - 23{,}5 \qquad (6)$$

Thus standardized, and only thus, the intensity of the process driving the hierarchical structuration of species abundances becomes *freed from the direct influence* of the species richness of the community, as required. This, in particular, means that if a dependence is actually observed between the intensity of the structuring process I_{str} and the species richness, when comparing several communities having different species richness, then this dependence is likely to have *true biological meaning* (since, in I_{str}, the purely mathematical influence of species richness has been set aside).

Besides, the *intrinsic signification* of I_{str} is that the genuine intensity of the structuring process as a whole is equal to I_{str}^* $[=(a_1/a_{St})/(a'_1/a'_{St})]$ times the intensity of the referential process of random apportionment of abundances among the same number of species S_t (or equal to $(I_{str}^*)^{(1/(St-1))}$, if considered species by species, on average).

The main further advantage of considering the genuine intensity I_{str} of the structuring process is, as already underlined, the possibility to *reliably compare* the intensities of the structuring processes at work in several communities *whatever the differences between their respective species richness* – precisely by cancelling the bias liable to the differences in species richness.

3. Dealing in practice with the three major numerical descriptors of a community of species: S_t, U, I_{str}

The total species richness S_t on the one hand and the two parameters I_{str} and U which respectively account for the genuine *process* and the descriptive *pattern* of abundance structuration on the other hand, together convey the main quantitative information characterizing a community of species. An appropriate graphical expression of this information is to plot: (i) the unevenness U versus S_t and (ii) the intensity of the structuring process I_{str} versus S_t. Yet, it results from above that while I_{str} and S_t are truly orthogonal dimensions (mutual independence), U and S_t are not, due to the argued mathematical influence of S_t on U. This *distinction is essential* and should be kept in mind when discussing the relevant significance to be given to the occurrence – or the absence – of covariance that might appear either between U and S_t or between I_{str} and S_t. To illustrate the point, let consider a first example.

The Western Ghats of India are known for the diversity of their frog assemblages; the structuration of a set of eight frog communities was addressed and the parameters S_t, U, I_{str} computed for each of them [17]. The species richness S_t of these eight communities ranges from 10 to 17 and the values of the abundance unevenness U and of the structuring intensity I_{str} are plotted against S_t in Figure 4, focusing on the two frog communities having the lowest and the highest richness (S_t = 10 and 17 respectively).

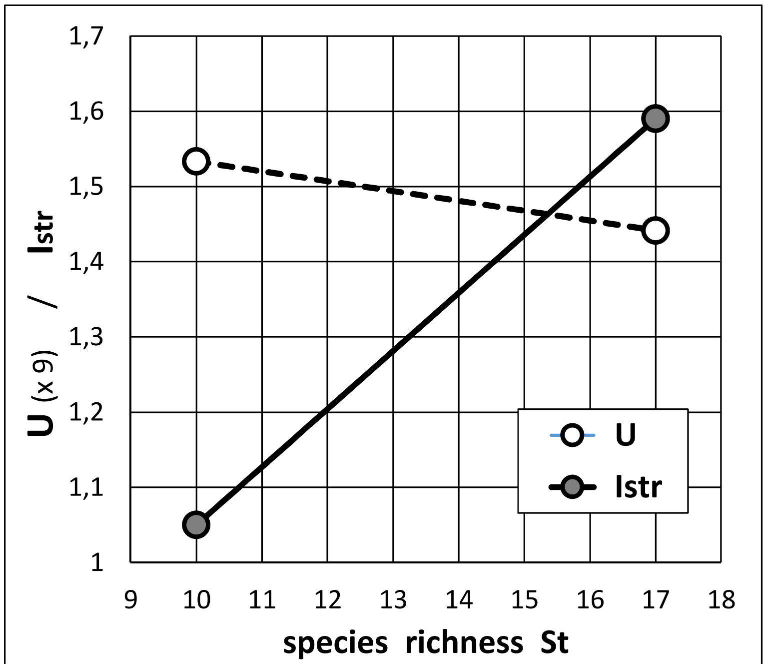

Figure 4 – The degree U of unevenness of species abundances (*dashed* line) and the intensity I_{str} of the underlying structuring process (*solid* line) plotted against the total species richness St, for two tropical frog communities of Western Ghats of India (St = 10 and 17 respectively). While the unevenness of species abundances slightly decreases with enlarging species richness, the intensity of the structuring process, functionally driving this unevenness, strongly increases (as expected from the negative mathematical dependence of U upon S_t). *Note that, for commodity of graphical comparison between U and I_{str}, the degrees of unevenness are uniformly multiplied by a same factor 9.*

Here, unevenness slightly decreases with species richness, so that the classical approach, relying on recorded unevenness only, would incite to conclude the same for the intensity of the structuring process itself. In fact, the structuring intensity I_{str} does not decrease at all but, on the contrary, increases by more than 50% when S_t grows from 10 to 17 species, thus dismissing the erroneous premature appreciation that would be based on considering, as usually practiced, the level of unevenness only.

4. Sampling completeness (or proper extrapolation) basically required to derive relevant inferences for S_t, U, I_{str}

As is obvious, the three parameters S_t, U, I_{str}, can be reliably evaluated only if the complete Species Abundance Distribution is available. Unfortunately, this is not always the case in practice. Indeed, partial, incomplete inventories are doomed to become even more frequent with the inevitable generalization of "rapid assessments" and "quick surveys" [7, 18, 19]. Yet, hopefully, a procedure of *numerical extrapolation* of substantially incomplete samplings has recently been developed, which, when applied to partial samplings, can provide reliable estimations of both (i) the number of the undetected species [20, 21] and (ii) the distribution of their respective abundances [22]. This, in turn, allows the derivation of reliable inferences (i) of the *total* species richness and (ii) of the *complete* distribution of species abundances (i.e. including the set of the still undetected species). Only the taxonomic identities of the latter escape, of course, any attempt of extrapolation.

Thus, after being numerically *completed* (and *only* when it is so: [17, 22-24, 25]), the distribution of species abundances becomes appropriate for addressing both the pattern and the underlying process of the hierarchical structuring of species abundances.

As obvious as it is in principle, the importance of funding conclusions on the sole basis of exhaustive, or numerically extrapolated, samplings yet deserves to be highlighted a little bit further, by considering concrete examples.

Marine gastropod communities in tropical shallow waters are usually species rich and, thus, often sampled only *partially*, with substantial degree of sampling incompleteness.

A partially inventoried intertidal marine gastropod community along rocky shore of middle Andaman Island (India) provides the *recorded* data in the second line of Table 1 (see [25] for details). Then, the values of S_t, U, I_{str}, based on the least-biased numerical extrapolation of this partial sampling, are provided in the third line of Table 1. Due to partial sampling, the *crude* evaluations of S_t, U, I_{str} reveal *strongly underestimated*, by 45%, 26% and 55% respectively.

Table 1 – The species richness S, the abundance unevenness U and the intensity I_{str} of the structuring process computed for a community of marine Gastropods along a rocky shore at Andaman Islands (India), considering (i) the recorded data from a partial inventory (species number S = 42) and (ii) the numerically completed inventory, based on least-biased extrapolation [25]: species richness S_t = 77.

marine Gastropods **Andaman Isl.**	**S**	**U**	$\mathbf{I_{str}}$
partial inventory	S = 42	0.028	0.50
completed by extrapolation	S_t = 77	0.038	1.11
underestimation by **partial inventory**	45 %	26 %	55 %

More generally, a *systematic underestimation* is, of course, the obvious consequence of under-sampling as regards species richness. However, for U and I_{str}, things are less simple, as no systematic rule applies: here, the expected trend is dependent upon the particular shape of the Species Abundance Distribution. In particular, underestimations of U and I_{str} are expected when the Species Abundance Distribution conforms to the "log-normal" model, (due to its characteristic sigmoidal shape), while slight overestimations might be expected when conformity is to the "log-series" model (due to its characteristic "J" shape).

5. Two additional illustrative examples

**** Gastropod communities associated to coral reefs in Mannar Gulf Reserve (India)***

Partial samplings of three Gastropod communities associated to coral-reefs surrounding small islands in Mannar Gulf were numerically extrapolated for evaluation of total species richness S_t [26] and, then, numerically extrapolated to infer the complete Species Abundance Distribution (BÉGUINOT *unpublished*). Derived from this inference, the degree U of abundance unevenness and the intensity I_{str} of the structuring process are plotted against the species richness S_t in Figure 5, for each of the three communities. Although unevenness is decreasing with growing species richness, the genuine intensity of the structuring process is, on the contrary, varying the *opposite*, increasing with species richness, as indeed was expected from the negative contribution of increasing species richness to the level of abundance unevenness.
Once again, relying on the level of unevenness only, as is still usually made, leads to a quite erroneous deduction regarding the genuine intensity of the structuring process itself.

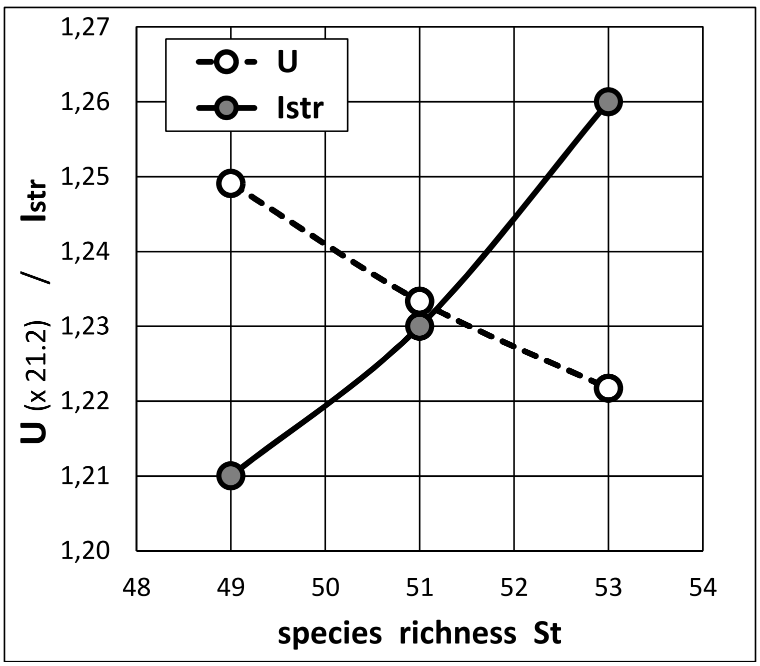

Figure 5 – The degree U of unevenness of species abundances (*dashed* line) and the intensity I_{str} of the underlying structuring process (*solid* line) plotted against the total species richness St, for three communities of coral reef associated Gastropod communities in Mannar Gulf (India). The degree of abundance unevenness decreases with increasing species richness of communities. Yet, the opposite holds true for the intensity of the structuring process driving this uneven distribution of species abundances: I_{str} increases with increasing species richness of communities, due to the negative mathematical dependence of U upon S_t. *Note that for commodity of graphical comparison between U and I_{str}, the degrees of unevenness are uniformly multiplied by a same factor 21.2.*

**** Comparing the intensity of abundance structuring between two feeding guilds***

It has been recently argued, on both theoretical and empirical basis, that within most marine and terrestrial communities, the guild of primary consumers (herbivores) exhibits a *more uneven* abundance distribution than does the corresponding guild of secondary consumers (carnivores) [27]. Yet, beyond the observed unevenness, the trend requires to be further tested by considering the *genuine intensity* of the structuring process I_{str}. Keeping in mind the influence of species richness on unevenness, the expected trend for I_{str} may be either reinforced or, on the contrary, weakened (as compared to unevenness), depending on whether the primary guild is less species-rich or more species-rich than is the secondary guild. At the extreme, if the species richness of the secondary guild is high enough, as compared to that of the primary guild, the trend might even go up to reverse, with I_{str} becoming larger for the secondary than for the primary consumers.

As an example, let coming back to the marine Gastropod community already considered above, at section 4. This community comprises two feeding guilds with 30 species as primary consumers and 47 species as secondary consumers [25]. Thus, we are here in the case where the guild of primary consumers as a distinctly lower species richness and, accordingly, the structuring intensity I_{str} is expected to show lesser difference between the two guilds than unevenness does. Indeed, the results are fully in line with this expectation: Figure 6. The guild of primary consumers shows a 87% stronger unevenness of species abundances than the guild of secondary consumers: U = 0.097 against U = 0.052, in accordance with the general trend hypothesized in [27]. As expected, the structuring intensity exhibits a quite lesser difference, with the abundance distribution of primary consumers being *only* 31% more uneven than the abundance distribution of secondary consumers: I_{str} = 1.35 against 1.03. Once again, relying only on the recorded unevenness would have provided an erroneous appreciation of the genuine structuring intensity.

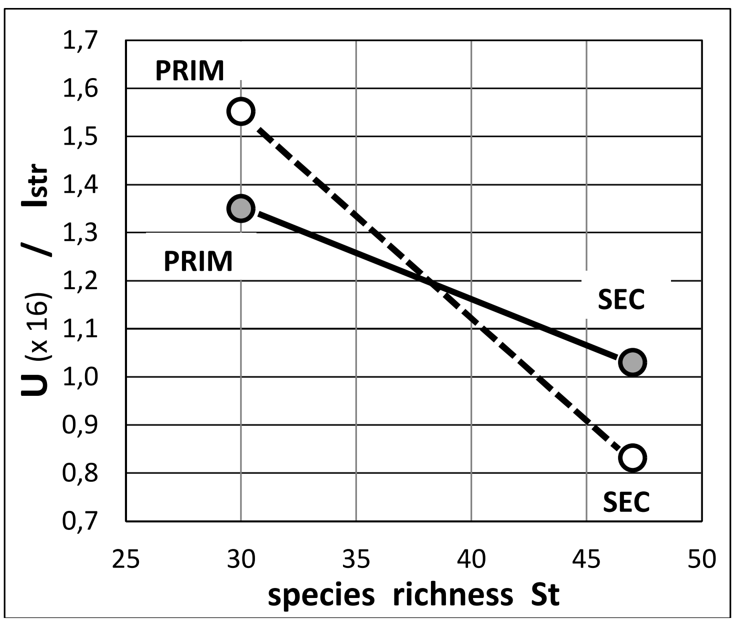

Figure 6 – The degree U of unevenness of species abundances (*dashed* line) and the intensity I_{str} of the underlying structuring process (*solid* line) plotted against the total species richness St, for the two feeding guilds – *primary* consumers (30 species) and *secondary* consumers (47 species) in a community of marine Gastropods along a rocky shore at Andaman Islands (India) [25]. *Note that for commodity of graphical comparison between U and I_{str}, unevenness levels are uniformly multiplied by a same factor 16.*

6. Discussion

Usually, no explicit distinction is made between the *observed unevenness* of the species abundance distribution in a community and the *intensity of the process* driving the hierarchical structuring of species abundances. Indeed, it is usually implicitly understood that the *pattern* (the observable degree of unevenness) faithfully mirrors the intensity of the underlying *process* that drives the differential allocation of abundances among co-occurring species. Thereby unduly ignoring the already mentioned mathematical influence of species richness on the unevenness level [11-14].

Here, I have highlighted the importance of giving full account to this distinction between the underlying process and the recorded pattern. Accordingly, I have suggested to consider a new index, the *genuine intensity* I_{str} *of the process* which actually drives the hierarchical distribution of species abundances, *once deducted the mathematical influence of species richness* on abundance unevenness. In practice, this influence of species richness is appropriately cancelled, in the expression of I_{str}, by standardizing the recorded unevenness to the unevenness of the "broken-stick" distribution, computed for the same species richness. Standardization to this particular reference is justified by the fact that the "broken-stick" distribution accounts exclusively for this mathematical, negative influence of species richness on unevenness level.

Thus, three (instead of only two) main parameters feature necessary to synthetize the numerical information characterizing a community of species. The first two, the true *total species richness* of the community and the *degree of unevenness* U of species abundances are, of course, traditionally referred to. The third parameter, the *intensity* I_{str} of the *structuring process*, is defined free from the purely mathematical influence of species richness on unevenness and, as such, relevantly represents the *functional* contribution to the degree of unevenness of species abundance distribution. Thanks to what, the intensity of the structuring process, I_{str}, becomes *intrinsically independent* from the species richness S_t, while the unevenness level, U, *is not*, due to its intrinsic sensitivity to species richness.

In turn, this *intrinsic independence* between I_{str} and S_t has important consequences, to be remembered at the time of *interpreting results*:

- not *only* the mere unevenness level does not mirror faithfully the purely *functional* (i.e. biologically significant) contribution made to the hierarchical structuration of species abundances within communities ;

- but also, an observed dependence between the unevenness level and the species richness (if any) cannot be given a biological meaning since, in this observed dependence, it is impossible to separate the mathematical contribution of species richness to unevenness level. In this respect, only an observed dependence upon species richness of the intensity I_{str} of the structuring process can relevantly receive a biological interpretation.

The concrete involvements of these limitations, at the moment of interpreting observations, are emphasized in the series of case studies proposed above as examples (Figures 4, 5, 6 and Table 1). In each case study, the conclusion based on *recorded unevenness only* proves being seriously biased and the recourse to the intensity of the structuring process, I_{str}, is required to highlight the true *functional* meaning of observations.

This specific precaution adds to the more general recommendation (obvious but still too frequently ignored or neglected) to build analysis on (sub-) *exhaustive* sampling of the studied communities [22, 28]. And, when sampling completeness cannot be reached in practice (as is often the case), then, relevant conclusions can be derived only when the available partial sampling is duly "completed" by proper *numerical extrapolation* [22].

7. Conclusion

Three quantitative parameters – the total species richness, the unevenness of species abundances (already classically referred to) and also the newly defined "intensity of the structuring process" driving the hierarchical structuration of species abundances – altogether feature appropriate in providing a rather synthetic, but yet comprehensive overview of the internal organization within species communities. Together, these three parameters account not only for the descriptive aspect, *but also* for the *functional origin* of the distribution of species in their communities. This, however, requires first disentangling the intensity of the structuring *process* – that singularizes the differential allocations of abundances among co-occurring species – from the resulting *pattern*, i.e. the level of unevenness of species abundances.

It is only once this distinction has been recognized and properly taken into account, that relevant interpretations can be derived, regarding the internal organization of species distribution in their communities.

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