The Hierarchical Structuring of Species Abundances within Communities: Disentangling the Intensity of the Underlying Structuring Process behind the Apparent Unevenness Pattern

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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 the latter 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 (apparent)
abundance unevenness, are argued from a theoretical point of view and then highlighted concretely
in a series of examples.

Keywords: Ranked abundance distribution; numerical extrapolation; species richness; diversity;
evenness, feeding guild.

1. INTRODUCTION

The number of species that co-occur in a same assemblage and the distribution of their relative
abundances – especially the degree of unevenness of this distribution – 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 of abundances
unevenness towards the intensity of the underlying process driving the hierarchical
structuration of abundances is less straightforward that might have been 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 regretfully ignored in common practice. Only the crudely recorded level of unevenness is addressed, since it is 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_S respectively standing for the highest and the lowest abundances in an assemblage of S_i 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 [15]. This slope is defined as \( \log(a_1) - \log(a_{S_i})/(S_i-1) = \log(a_i/a_{S_i})/(S_i-1) \).

N.B.: with untransformed abundances, the equivalent figure would become \( (a_i/a_{S_i})^{1/(S_i-1)} \).

Accordingly, the degree of unevenness “U” of the distribution of species abundances in a community is:

\[ U = \log(a_1/a_{S_i})/(S_i-1) \]  \hspace{1cm} (1)

or, alternatively, \( U^* = (a_i/a_{S_i})^{1/(S_i-1)} \) \hspace{1cm} (2)

One important (although too often overlooked) issue regards the unavoidable mathematical
influence of the species richness S_i 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 species abundances may further be demonstrated by considering the “broken-stick” model [16]. 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 \( S_t \) purely characterizes numerically the mathematical trend for the degree of unevenness to decrease with increasing species richness, as shown graphically in Figs 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 \( S_t \) 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 unevenness \( U \) and, thereby, to retain only what makes the intensity of the structuring process functionally specific to the community under study [17].

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 \( S_t \):

\[
I_{str} = \frac{U}{U'} = \frac{[\log(a_1/a_{St})/(S_t–1)]/[\log(a’_1/a’_{St})/(S_t–1)]}{(3)}
\]

that is, finally:

\[
I_{str} = \frac{\log(a_1/a_{St})}{\log(a’_1/a’_{St})} \quad (4)
\]

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 \( S_t \)).

![Fig. 1. The “broken-stick” distributions computed for increasing values of 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) \( S_t \). This highlights and quantifies the purely mathematical influence of species richness \( S_t \) on the unevenness pattern \( U \) in any S.A.D](image-url)}
Fig. 2. The variation of the degree of dominance, $\log(a'/a'_{St})$, computed against species richness $S_t$ for the “broken-stick” distribution (from Figure 1): grey discs. A regression is proposed as: $\log (a'/a'_{St}) = \log [ 4,6782.S_t + 0,008.S_t^2 - 0,000007.S_t^3 - 23,5 ]$: dashed line. The range of species richness is extended up to 480 species.

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

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

$$I_{str}^* = U^* / U'^* = (a_1/a_{St}) / (a'_{St}/a'_{St})$$

(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):

$$a_1'/a'_{St} \approx 4,6782.S_t + 0,008.S_t^2 - 0,000007.S_t^3 - 23,5$$

(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 is required. This 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) – which is not the case with \( U \).

Besides, the intrinsic signification of \( I_{str} \) is that the genuine intensity of the structuring process as a whole is equal to \( I_{str}^* \) [\( = (a_1/a_0)/(a_1'/a_0') \)] times the intensity of the referential process of random apportionment of abundances among the same number of species \( S_t \) (or equal to \( (I_{str}^*)^{(1/(S_t-1))} \), 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 apparent unevenness pattern \( U \) 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 (i.e. mutually independent), \( U \) and \( S_t \) are not, due to the 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 any 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.

![Diagram](image_url)

Fig. 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 \( S_t \) for two tropical frog communities of Western Ghats of India (\( S_t = 10 \) 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 indeed (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 9.
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 $S$, $U$, $I_{str}$ were computed for each of them [18]. The species richness $S$ 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 $S$ in Fig. 4, focusing on the two frog communities having the lowest and the highest richness ($S = 10$ and 17 respectively).

Here, unevenness $U$ 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 $S$ grows from 10 to 17 species, thus dismissing the erroneous premature appreciation that would be based on considering the level of unevenness only, as usually practiced.

4. **Sampling Completeness (or Proper Extrapolation) Basically Required to Derive Relevant Inferences for $S$, $U$, $I_{str}$**

As is obvious, the three parameters $S$, $U$, $I_{str}$, 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” [7,19,20]. Yet, hopefully, a procedure of numerical extrapolation of substantially incomplete samplings has recently been developed, which, being applied to partial samplings, can provide reliable estimations of both (i) the number of the undetected species [21,22] and (ii) the distribution of their respective abundances [23]. This, in turn, allows the derivation of reliable inferences (i) of the true 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 (but see comment on this subject at the end of the Discussion section).

Thus, after being numerically completed (and only when it is so: [18,23-26]), 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 [26] for details). Then, the values of $S$, $U$, $I_{str}$, 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 $S$, $U$, $I_{str}$ reveal strongly underestimated, by 45%, 26% and 55% respectively.

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

| marine Gastropods Andaman Isl. | $S$ | $U$ | $I_{str}$ |
|------------------------------|-----|-----|---------|
| Partial inventory: recorded data | $S = 42$ | 0.028 | 0.50 |
| Completed by extrapolation | $S = 77$ | 0.038 | 1.11 |
| Underestimation by partial inventory | 45% | 26% | 55% |
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

5.1 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 $S_t$ [27] and, then, numerically extrapolated to infer the complete Species Abundance Distribution (BEGUINOT 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 Fig. 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 might have been 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.

5.2 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.

![Image of Fig. 5](image-url)  

Fig. 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 $S_t$, 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.
(carnivores) [28]. Yet, beyond considering the apparent unevenness only, 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 in Andaman, already considered above, at section 4. This community comprises two feeding guilds with 30 species as primary consumers and 47 species as secondary consumers [26]. 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: Fig. 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 [28]. But, as expected, the structuring intensity $I_{str}$ 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 $I_{str} = 1.03$. Once again, relying only on the recorded unevenness would have provided an erroneous appreciation of the genuine structuring intensity.

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 in their community. Thereby, common practice unduly ignores the mathematical influence of species richness on the unevenness level [11-14,29].

Fig. 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 $S_t$, 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) [26]. Note that for commodit of graphical comparison between $U$ and $I_{str}$, unevenness levels are uniformly multiplied by a same factor 16.
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 \( U \) to the unevenness \( U' \) of the “broken-stick” distribution, computed for the same species richness (equation (4)). 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 are indeed 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 traditionally referred to.

The third parameter, the intensity \( I_{str} \) of the structuring process, is defined as freed 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 \( S_i \), while the unevenness level, \( U \), is not, due to its intrinsic sensitivity to species richness.

In turn, this intrinsic independence between \( I_{str} \) and \( S_i \) 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 it is impossible to separate, in such an observed dependence, which part corresponds to the mathematical contribution of species richness to unevenness level. In this respect, a relevant biological interpretation can be given only to an observed dependence between the species richness and the intensity \( I_{str} \) of the structuring process. While limiting oneself to consider unevenness pattern alone would actually remain inconclusive.

The concrete involvements of these limitations, at the moment of interpreting observations, are emphasized in the series of case studies proposed above as illustrative examples (Figs 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 a second, more general recommendation (obvious but still too frequently ignored or neglected) demanding to build proper analysis on (sub-) exhaustive sampling of the studied communities [23,30]. And, when sampling completeness cannot be reached (as is often the case in practice), then, relevant conclusions can be derived only when the available partial sampling is duly “completed” by proper numerical extrapolation [23].

Numerically completing partial samplings features all the more appropriate that some among the rare species may have disproportionately large contributions to the functional structure of species communities, as emphasized by [31]. Of course, one may arguably consider that the (unavoidable) lack of taxonomic identification within the set of unrecorded species remains frustrating and may limit to some extent the ecological interpretation derived from the pure numerical extrapolation of incomplete inventories. Yet, although acknowledging this point of view to a certain extent, it should be emphasized that taxonomic identities of species often matter less than had been traditionally thought previously: high taxonomic variability is often recorded even when stable functional structure is yet maintained [32 - 34]. Accordingly, implementing least-biased numerical extrapolations of both Species Accumulation Curves and Species Abundance Distributions, according to [21-22,23] is particularly relevant, especially when addressing the functional characteristics of species communities.
7. CONCLUSION

Three quantitative parameters altogether provide a rather synthetic, but yet comprehensive overview of the internal organization within species communities. Two of them are already referred to classically: the total species richness, and the as-observed unevenness of species abundance distribution. But a third, newly defined parameter, must be considered in addition: the “genuine intensity of the structuring process” accounting exclusively for the true functional contribution to the hierarchical structuration of species abundances. Thus, taken 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 observed level of unevenness of species abundances).

It should be also emphasized, following [35], that it is well the unevenness, rather than the evenness itself, which is likely to be preferred, as being a more expressive, functionally relevant, descriptor of abundances inequalities among co-occurring species in a community. In other words, while evenness is primarily focused on the result, unevenness is more specifically oriented towards the biological and ecological causes involved in the hierarchical structuration of species abundances.

Finally, it is only once this distinction between the apparent pattern and the functionally significant process is clearly recognized and duly taken into account, that relevant interpretations can be derived, regarding the internal organization of species distribution in their communities.

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COMPETING INTERESTS

Author has declared that no competing interests exist.

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