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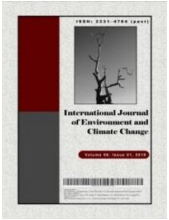
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Estimating True Species Richness and the Degree of Hierarchical Structuring of Species Abundances in Eight Frog Communities from the North-Western Ghats of India

Jean Béguinot[1*]

[1]Biogéosciences, UMR 6282, CNRS, Université Bourgogne Franche-Comté, 6, Boulevard Gabriel, 21000 Dijon, France.

Author's contribution

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

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ABSTRACT

The Distribution of Species Abundances within natural communities – when properly analysed – can provide essential information regarding general aspects of the internal organisation of these communities. In particular, true species richness on the one hand and the intensity of the process of hierarchical structuring of species abundances on the other hand may be estimated independently and, thereby, can provide truly complementary information. In turn, specific issues may thereby be addressed. For example, whether one unique dominant factor or numerous combined factors are involved in the structuring process of a community can be tested contradictorily. Although these methods are not new conceptually, their implementation in common practice remains scarce. The reason is that the relevant implementation of these methods requires to be sure that virtually all member-species in the community have been sampled. As exhaustive samplings often reveal difficult to achieve in practice, an appropriate, *least-biased* procedure of *numerical extrapolation* of incomplete inventories is imperatively required.

Considering the steadily increasing threats to the environment and biodiversity, especially facing the on-going climatic change, time has come now with ever greater urgency to go beyond the apparent limits of non-exhaustive sampling and make the most of what is available in terms of recorded field data, whatever the degree of incompleteness of species inventories.

As a modest and limited attempt to concretise this wish at the local level, I try, hereafter, to highlight the importance of additional information that may be unveiled through adequate post-analysis of a set of eight frog communities, recently inventoried by Katwate, Apte & Raut in an

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

amphibian hot-spot in the north-western Ghats of India. At last, the likely variations of both total species richness and the intensity of hierarchical structuring of species abundance are simulated as an answer to the steadily increasing influence of the ongoing climatic change.

Keywords: Species diversity; species abundance; rank abundance distribution; amphibians; anurans; incomplete sampling; numerical extrapolation; climate change.

1. INTRODUCTION

Total species richness, taxonomic composition and hierarchical structuring of species abundance distribution are three main topics that together provide a good deal of information about species communities in the wild. The Species Abundance Distribution (especially under the form of the "*Rank Abundance Distribution*") is a convenient tool for characterising species communities this way, but this requires, yet, that the sampling effort has been sufficient enough for the resulting abundance distribution being (quasi) *exhaustive*.

Exhaustive samplings, however, are difficult to obtain and rarely reached in practice, especially when having to deal with species rich communities, such as most invertebrates' assemblages. But even in some vertebrates' communities, comprehensive species inventories may occasionally require very large sampling sizes, hard to implement in practice, when one or more of the less common member species happen to be excessively rare. Hopefully, even in such case, it remains possible to extract far much information than would be expected from substantially incomplete samplings, by implementing an appropriate *numerical extrapolation* procedure [1,2]. While the taxonomic identification of the still undetected species remains, of course, impossible, two other major descriptive features of communities (total species richness and the hierarchical structuring of species abundances) can be extrapolated fairly accurately, on the *only basis* of data extracted from substantially incomplete samples.

Hereafter, I report on the analysis of the inventories of eight frogs communities originally sampled by Katwate, Apte & Raut [3] in northern-western Ghats of India. Among these eight inventories, five may be considered quasi exhaustive (since no singleton is actually subsisting in the samples), while the other three inventories remain more or less incomplete and thus require the implementation of numerical extrapolation to unveil the *complete range* of species abundance distribution.

Considering together the five exhaustive Species Abundance Distributions and the three "numerically-completed" ones, I focused on the comparison between these eight frogs' communities, regarding: (i) their respective levels of species richness and (ii) their respective patterns of abundances distribution. Beyond the mere description of abundance patterns, dealing with already *complete* or *numerically extrapolated* Species Abundance Distributions allows to relevantly address (i) the type and (ii) the strength of the process driving the hierarchical structuring of species abundances in each studied communities.

This complementary, *functional*-type approach stands out by its particular interest in the context of the on-going *climate change*. Indeed, even before climatic change is expected to significantly affect the taxonomic composition within animal communities, it is the *functional* aspects of these communities – such as the hierarchical structuring of species abundances – that are likely to be *impacted first*. And frog communities, especially sensitive to climatic parameters, are among the priorities to be addressed in this respect [4,5].

2. MATERIALS AND METHODS

2.1 Materials

Katwate, Apte & Raut [3] reported on the inventories of eight frogs communities (Amphibians, anurans) from *Phansad Wildlife Sanctuary*, located in the Northern Western Ghats of India. Five of these inventories (labelled A, C, D, E, G) show no subsisting singletons (i.e. species sampled only once) and, accordingly, may be considered virtually exhaustive [6-8]. The other three inventories (labelled B, F, H) all retain, on the contrary, one or more singletons and, thus, likely remain more or less incomplete (as actually confirmed subsequently).

Details on the sites location where these frog communities were sampled, the local ecological conditions and constraints peculiar to these sites,

the lists of species identities and the numbers of recorded individuals per species, are provided in the aforementioned reference [3].

2.2 Numerical Extrapolation Procedures Applied to the Three Incomplete Inventories

* *Total species richness*: the least-biased estimation of the number of still undetected species at the end of partial sampling and the resulting estimation of the total species richness of the partially sampled community are derived according to the procedure defined in [9,10] and briefly summarised in Appendix 1. Estimates are based on the numbers f_x of species observed x-times during partial sampling (x = 1 to 5: Figs. A1.1 to A1.3 in Appendix 1).
* *Species Abundance Distribution*: to accurately exploit their full potential, the as-recorded Species Abundance Distributions ("S.A.D.s") require [1,11]:

  - First, to be *corrected* for statistical sampling bias, resulting from the finite size of samplings and,
  - Second, and still more importantly, to be *completed* by numerical extrapolation to the extent that sampling is suspected to be incomplete, as revealed by the subsistence of singletons.

The appropriate procedure of correction and the *least-biased* numerical extrapolation of the as-recorded S.A.D.s, described in details in [1], is briefly recalled in Appendix 2.

After being *corrected* and *extrapolated* accordingly, the S.A.D.:

- Not only provides an overview of both the true (total) species richness of the sampled community and the diversity of the respective abundances of member species,
- But, also, can help addressing several important questions regarding the *kind of process driving the hierarchical structuration* of the community (Fig. 1).

More precisely, these questions may relate to:

- The *process of structuration* of a community of species: for example, does *only one* (or very few) dominant factor is (are) at work to structure the community or, on the contrary, does *many independent* factors are contributing together. This may be tested by checking the conformity of the corresponding S.A.D. to either the *log-series* model or the *log-normal* model respectively [12–16];
- The *degree of structuration* of a community of species, which broadly refers to the level of unevenness between species abundances within the community. This may be appropriately tested by comparing the slope of the corresponding S.A.D. to either the "ideally even" model or the

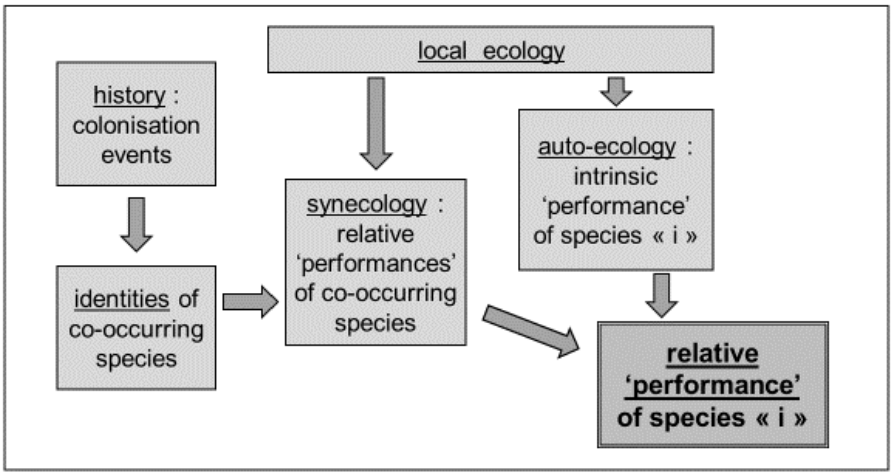


Fig. 1. Schematic sketch showing how the combination of both historical and ecological contexts peculiar to a given community of species drive the relative "performance" - *sensu latissimo* - of each member species "i", thus generating the *hierarchical structuring of species abundances in the community*

"broken-stick" model. These two models provide two reference levels of structuration, namely the "ideally even" model characterises the *zero* level of structuration while the "broken-stick" model accounts for the degree of structuration that would be obtained by a *random apportionment* of relative abundances among all co-occurring species in the community [17]. Standardising the degree of structuration (the slope of the S.A.D.) to the "broken-stick" model is particularly relevant as this allows to set apart the "mechanistic", trivial influence of species richness upon the level of unevenness of species abundances in the community [18 –20]. This "mechanistic" influence of species richness on the slope of the abundance distribution and, consequently, on the degree of community structuration, is demonstrated in Appendix 3). Thus standardised, the degree of structuration of a community becomes *truly independent* of the trivial influence of species richness.

3. RESULTS

3.1 The Recorded or Estimated Total Species Richness of the Eight Frog Communities

As regards the three incompletely sampled communities (B, F, H) and considering the values of the numbers f_x of species observed x-times in each of the three samples (see Figs. A1, A2, A3 in Appendix 1), it turns out that the *least-biased* nonparametric estimator of the number of undetected species is *Jackknife-5* (JK-5 = $5f_1 - 10f_2 + 10f_3 - 5f_4 + f_5$) in all three cases: see the selective key in Appendix 1.

Accordingly, the corresponding *least-biased* estimations of the number Δ of species remaining undetected in the inventories of B, F, H, are given by Jackknife-5 and the resulting least-biased estimation is $S_t = Ro + \Delta$, with Ro as the number of recorded species.

For the five communities A, C, D, E, G, having no remaining singletons and thus considered to be comprehensively sampled, Δ thus equals 0 and, accordingly, the total species richness S_t is equal to the number R_o of already recorded species.

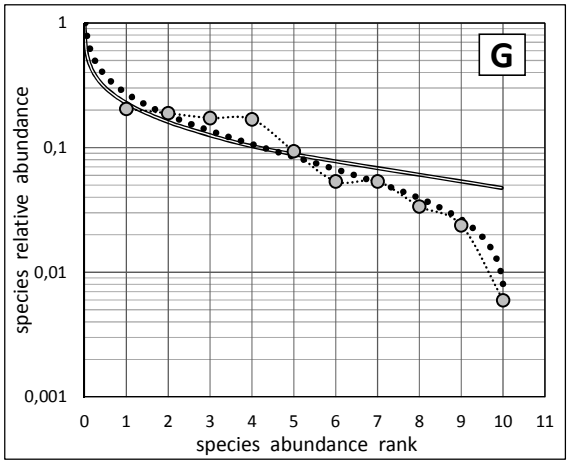
All the results are summarised in Table 1. Note, in addition that, as might have been expected, the product of sample-size No times the relative abundance a_{St} of the rarest species in each sampled community is much *less* than 1 when dealing with incomplete samplings (communities B, F, H) and much *greater* than 1 when dealing with exhaustive samplings (communities A, C, D, E, G).

3.2 Fitting Abundance Distributions to either Log-Normal or Log-Series Models

As a whole, abundance distributions best fit the corresponding "log-normal" model than the corresponding "log-series" model. Figs. 2 and 3 provide two typical examples of such close fitting of the Species Abundance Distribution to the corresponding "log-normal" distribution, for both an exhaustively sampled community (G) and an incompletely sampled community (F).

Table 1. The sample-size No, the number of recorded species Ro, the selected least-biased estimator, the number of undetected species Δ, the total species richness St (either recorded for A, C, D, E, G, or extrapolated St = Ro+Δ for B, F, H), the relative abundance a_{St} of the rarest species (rank St). As expected, the sample-size multiplying the relative abundance of the rarest species (No.a_{St}) is << 1 in each of the three incomplete inventories (B, F, H) and >> 1 for each of the other five comprehensive inventories (A, C, D, E, G)

Community	No	Ro	Selected estimator	Δ	St	a_{St}	No.a_{St}
B	468	11	JK-5	1.9	12.9	.0003	0.14
F	231	14	JK-5	2.8	16.8	.0006	0.14
H	417	10	JK-5	2.4	12.4	.0002	0.08
A	615	15	/	0	15	.0063	3.9
C	329	11	/	0	11	.0265	8.6
D	403	11	/	0	11	.0386	15.3
E	304	11	/	0	11	.0254	7.6
G	493	10	/	0	10	.0060	2.9



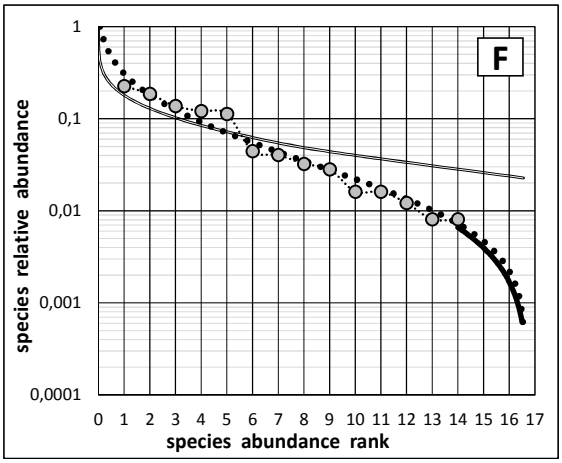


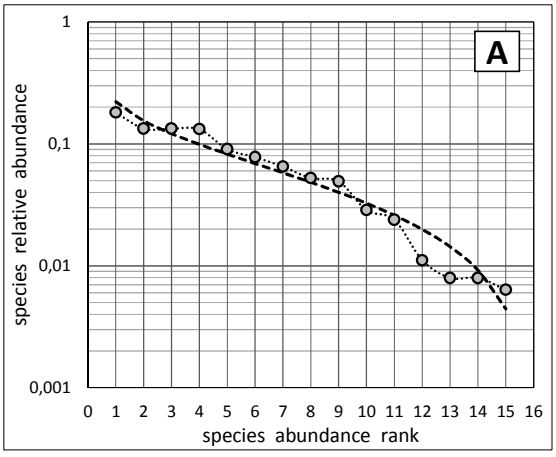
Fig. 2. The ranked Species Abundance Distribution of community "G" (coarse grey dots) compared to two associated models: the "log-normal" distribution (dotted line) and the "log-series" distribution (double line)

Fig. 3. The ranked Species Abundance Distribution of community "F" (coarse grey dots and coarse solid line for the extrapolated part: ranks > 14) compared to two associated models: the "log-normal" distribution (dotted line) and the "log-series" distribution (double line)

3.3 Quantifying the Degree of Hierarchical Structuring of Abundances in Species Communities: From Pattern to the Underlying Process

The ranked Species Abundance Distributions of the eight frog communities are plotted in Figs. 4 to 11 respectively, after all these distributions have been corrected and after the three incompletely sampled communities (B, F, H) have been duly extrapolated.

These ranked Species Abundance Distributions highlight the detailed patterns of hierarchical structuring of species abundances which are specific to each studied community. In particular, the stronger the rate of abundance decrease (i.e. the steeper the slope of the ranked abundance distribution) and the more severe looks the hierarchical structuring. Yet, this descriptive approach does not relevantly account for the genuine strength of the structuring process at work in the community, because the slope of the



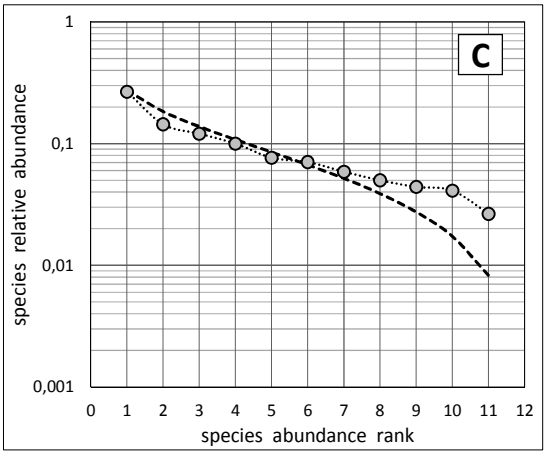
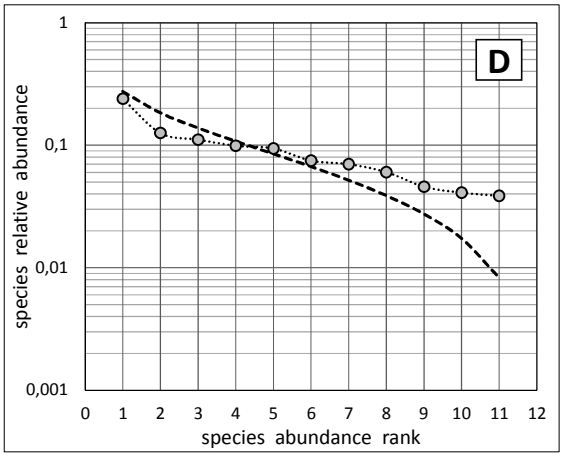


Fig. 4. The ranked Species Abundance Distribution of community "A" (coarse grey dots) and the associated "broken-stick" distribution, computed for the same species richness (dashed line)

Fig. 5. The ranked Species Abundance Distribution of community "C" (coarse grey dots) and the associated "broken-stick" distribution, computed for the same species richness (dashed line)



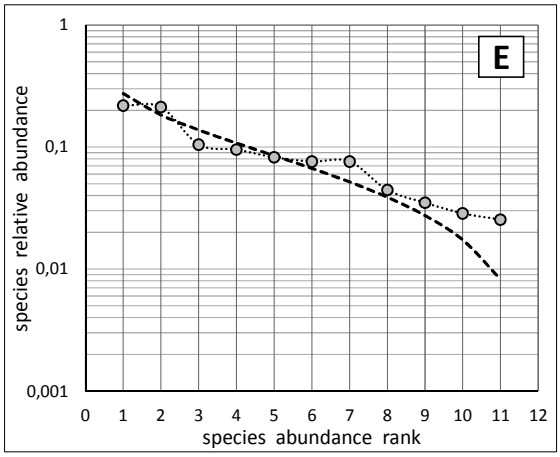
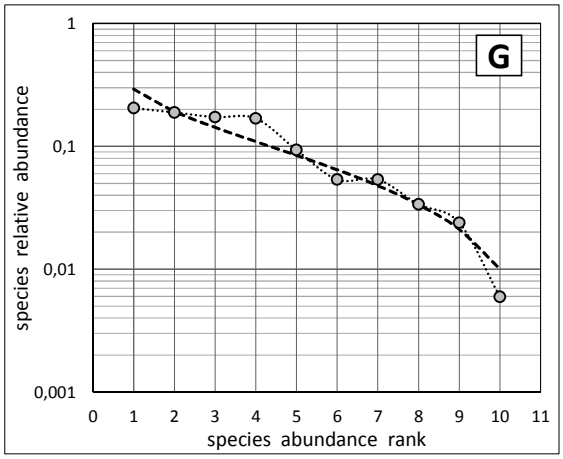


Fig. 6. The ranked Species Abundance Distribution of community "D" (coarse grey dots) and the associated "broken-stick" distribution, computed for the same species richness (dashed line)

Fig. 7. The ranked Species Abundance Distribution of community "E" (coarse grey dots) and the associated "broken-stick" distribution, computed for the same species richness (dashed line)



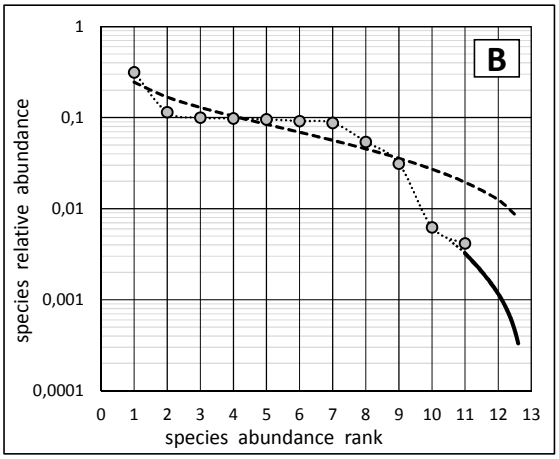


Fig. 8. The ranked Species Abundance Distribution of community "G" (coarse grey dots) and the associated "broken-stick" distribution, computed for the same species richness (dashed line)

Fig. 9. The ranked Species Abundance Distribution of community "B" (coarse grey dots and coarse solid line for the extrapolated part: ranks > 11) and the associated "broken-stick" distribution, computed for the same species richness (dashed line)

abundance distribution depends not only upon the structuring process itself but also depends on the level of species richness of the community. Indeed, all other things being equal, the rate (i.e. the slope) of abundance decrease is negatively dependent upon the level of species richness of the community, as highlighted in Appendix 3. Accordingly, the Species Abundance Distribution should relevantly be compared to the corresponding "broken-stick" model (i.e. the "broken-stick" model computed for the same level of species richness), in order to cancel the trivial influence of species richness level and, thus, unveil the *genuine intensity* of the structuring process. Thus, in Figs. 4 to 11, each complete (or completed) Species Abundance Distribution is plotted together with its corresponding "broken-stick" distribution. This straightforwardly provides a *reliable appreciation of the degree of hierarchical structuring* of species abundances in each community.

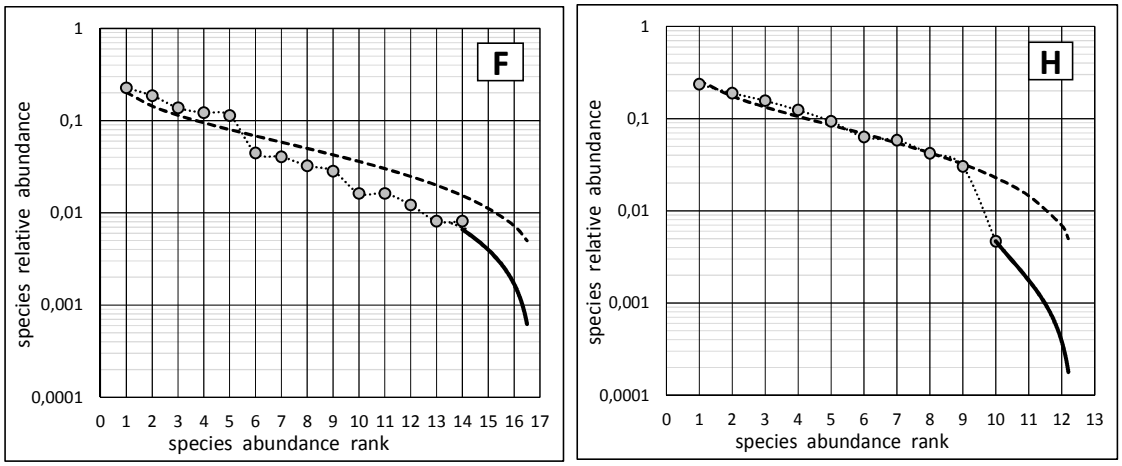


Fig. 10. The ranked Species Abundance Distribution of community "F" (coarse grey dots and coarse solid line for the extrapolated part: ranks > 14) and the associated "broken-stick" distribution, computed for the same species richness (dashed line)

Fig. 11. The ranked Species Abundance Distribution of community "H" (coarse grey dots and coarse solid line for the extrapolated part: ranks > 10) and the associated "broken-stick" distribution, computed for the same species richness (dashed line)

In a less detailed (and thus more reductionist) approach, the *average* slope of the Species Abundance Distribution provides a convenient, concise appreciation of the degree of hierarchical structuring. A "structuring index", based on the *average* slope, can be defined accordingly. As aforementioned, to reliably reflect the *genuine strength* of the structuring process, this index must be stantardised to the average slope of the corresponding "broken-stick" distribution. Accordingly, an appropriate *structuring index* is relevantly defined as the ratio between the average slope of the actual abundance distribution and the average slope of the corresponding "broken-stick" distribution. To conform to the usual, conventional mode of plotting abundance distributions, the abundances will be classically log-transformed. Thus defined, the structuring index I_{str} is equal to:

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

that is:

$$I_{str} = \log(a_1/a_{St})/\log(a'_1/a'_{St}) \quad (1)$$

where a_1 and a_{St} stand for the highest and the lowest abundances in the studied community and a'_1 and a'_{St} stand for the highest and the lowest abundances in the corresponding "broken-stick" distribution (i.e. computed for the same level of species richness S_t). Results are given in Table 2.

4. DISCUSSION

Although the present study aims, first, at a general methodological purpose, rather than being focused toward a particular taxonomic target, a brief argumentation is provided however, supporting the choice of frogs as an appropriate illustrative taxonomic group for the application of the method. Amphibians in general, and frogs in particular, are among animal groups which are most sensitive to environmental changes, especially climatic modifications involving temperature and hygrometry [4,5]. More specifically, amphibians in general and frogs in particular are typically stenothermic species, as such directly affected by the on-going climate changes, *via* the increase of temperature and resulting imposed shifts in local distributions, especially altitudinal increase when possible and, otherwise, local extinction [21–23]. Often connected to temperature evolution are more or less drastic changes in precipitation with resulting risks of shortage of water availability which is so important for most amphibians' survival. Severe declines of various kinds of amphibians are already reported for this reason [24–26]. And both temperature and hygrometry are major drivers of reproductive activities which may thus be strongly affected by global climate change [27–29]. The issue is all the more acute when considering amphibians "hot-spots" having a high proportion of particularly fragile endemic species,

Table 2. The degree of hierarchical structuration (*true* unevenness) of species abundances, relevantly quantified by the structuring index 'I_{str}' defined as the average slope of the Species Abundance Distribution standardised to the average slope of the corresponding "broken-stick" distribution (data from Figs. 4 to 11)

Community	S_t	Sp. Abund. Distr.		"broken-stick"		structuring index
		a_1	a_{St}	a'_1	a'_{St}	$\log[a_1/a_{St}] / \log[a'_1/a'_{St}]$
A	15	.1810	.0063	.2212	.0044	**0.86**
C	11	.2676	.0265	.2745	.0083	**0.66**
D	11	.2391	.0386	.2745	.0083	**0.52**
E	11	.2190	.0254	.2745	.0083	**0.62**
G	10	.2048	.0060	.2929	.0100	**1.05**
B	12.9	.3146	.00033	.2448	.0080	**2.01**
F	16.8	.2266	.00062	.2024	.0050	**1.59**
H	12.4	.2360	.00018	.2586	.0050	**1.82**

as is the case in the western-Ghats of India [3]. Hence, the importance of assessing, and further analysing in detail, the current state of frog communities in this region. This implies not only drawing up species-lists as complete as possible *but also* to record (and if necessary to extrapolate numerically) the Species Abundance Distributions in each of these frog communities [16,30–35]. Species Abundance Distributions are not only of descriptive interest as a *pattern*, but also ought to be considered as a mean to address the *process* governing the hierarchical structuring of species abundances within communities. Thus, it is in this sense that should be understood the following warning by Southwood & Henderson [36]: "*A great deal of time and expertise has been expended on the compilation of faunal lists for particular habitats, but the consequent increase in our understanding [...] is still meagre.*"

4.1 True Species Richness of Communities

While the inventories of most invertebrate communities are often doomed to remain incomplete in practice - due to their usually high species richness including numerous rare species - the exhaustive sampling of vertebrates and, here of frog communities, is usually less out of reach. Thus, among the eight frog communities sampled by Katwate, Apte & Raut [3] in northern-western Ghats of India, five may be considered as already virtually exhaustive while the other three prove being only moderately incomplete (from 80% to 85% completeness: Table 1) but nevertheless require numerical extrapolation. Total species richness levels, either recorded (communities A, C, D, E, G) or extrapolated (communities B, F, H), range from 10 to 17 species. Interestingly, it should be noted that the three incompletely sampled communities B, F, H, are precisely those ones that are the most strongly structured, i.e. having the least even distribution of species abundances, as shown later in Fig. 12. Correlatively, in each of communities B, F, H, the rarest species have, by far, the smallest relative abundance levels: see Table 1. As a result, the product No.a_{St} of the abundance a_{St} of the rarest species times the sample-size No remains far *less* than unity in the incomplete samplings of communities B, F, H, while this product largely *exceeds* unity in the exhaustive samplings of the five other communities (Table 1). This, indeed, is the reason for the sampling incompleteness of communities B, F, H (rather than a lesser sampling effort, as compared to the five exhaustively sampled communities).

4.2 The Hierarchical Structuring of Species Abundances: Only One Dominant Causal Factor or Many Independent Ones Jointly Involved?

Schematically, the structuration of species abundances within natural communities may result either from the influence of one dominant factor or from the interplay of numerous independent factors. As a result, the corresponding Species Abundance Distribution would fit more closely the "*log-series*" model or the "*log-normal*" model respectively [12–16]. Reliably testing each hypothesis requires, however, to consider the *whole range* of the Species Abundance Distribution [15,37–40]. Accordingly, if it cannot be recorded exhaustively, the Species Abundance Distribution *must be numerically extrapolated*.

When considered along their whole range, the Species Abundance Distributions of the eight

frog communities most often fit the "log-normal" model best (Figs. 2 & 3). This suggests that the hierarchical structuring of species abundances in these communities is generally driven by the combined influences of numerous, independent factors (related to ecological and/or historical constraints), rather than by the sole influence of one major, strongly determinant factor [15,39–43].

4.3 The Degree of Hierarchical Structuring of Species Abundances in Each Community

The degree of unevenness of the distribution of species abundances in a community mainly depends, of course, on the intensity of the hierarchical structuring. But, as aforementioned, the total species richness also influences "mechanically" the degree of unevenness, at the risk of providing, thus, a *biased appreciation* of the intensity of hierarchical structuring. This is because, the degree of species dominance unavoidably tends to decrease with increasing total species richness, all other things being equal: the dominance tends to be somewhat "diluted" by the increasing number of co-occurring species [1,18–20]. This trend – and its essentially *numerical rather than biological* origin – is clearly demonstrated theoretically by considering a constant process of abundance structuring (such as the random apportionment of abundances among species in the "broken-stick" model) applied to communities of varying species richness. The average steepness of the "broken-stick" distribution consistently decreases with increasing species richness: see Appendix 3.

Accordingly, a relevant appreciation of the intensity of the hierarchical structuring process requires to separate and *leave out* the purely "mechanical" influence of the level of species richness. This is appropriately achieved:

- *Graphically*, by plotting simultaneously the Species Abundance Distribution under study and the corresponding "broken-stick" model, computed for the same level of species richness (Figs. 4 to 11),
- *Quantitatively*, by standardising the average slope of the Species Abundance Distribution under study to the average slope of the corresponding "broken-stick" model, leading to the definition of a structuring index, I_{str} (equation (1)), which thereby reflects the *genuine* contribution of the hierarchical structuring process driving species abundances, leaving aside the influence of the level of species richness, devoid of biological sense (Table 2).

Thus removing the trivial influence of species richness S_t in the definition of the structuring index, I_{str}, warrants the independence *a priori* between I_{str} and S_t. Accordingly, an empirically observed dependence or, on the contrary, independence, between I_{str} and S_t will gain *true biological significance*. Hence, the interest of plotting I_{str} against S_t, as proposed in Figs. 12 & 13. In addition, this representation has the advantage of providing a *synthetic overview* of the main results derived from this study.

The intensity of the hierarchical structuring process, relevantly quantified by I_{str}, varies to a large extent, ranging from 0.52 to 2.01, according to communities (Fig. 12 and Table 2). No correlation is empirically highlighted between I_{str} and S_t (Fig. 12), which means that, *here*, the true intensity of the hierarchical structuring process, driving the species abundance pattern, develops *independently* of species richness in the community. This is an original and important finding that was by no means obvious *a priori*.

Looking further in the detail of structuring process (Figs. 4 to 11, Fig. 12 and Table 3), it is worth noting that the hierarchical structuration may be either:

- "regular", i.e. with a gently varying rate in the abundance decrease, as observed in communities C, D, E, F, G, or
- "irregular", i.e. suddenly exhibiting a sharp acceleration of the decreasing rate of species abundances and, thus, a brutal and statistically significant recess of the abundance level for the few rarest species, as in communities A, B, H (Figs. 4, 9, 11).

Being limited to three communities out of eight, the "irregular" pattern invites to seek for some *species-specific* rather than *generic* causes.

In this respect, the species list provided in Table 3 of the paper by Katwate, Apte & Raut [3] leads to the following remarks:

- *Fejervarya caperata* Kuramoto *et al*. (in community A), *Fejervarya* cf. *keralensis* Dubois (in community B), *Ramanella marmorata* Jerdon (in comm. A & B), *Uperodon globulosus* Gunther (in community A), *Sphaerotheca dobsonii*

Boulenger (in communities A & H) are *strongly affected* by the recess of abundances, sharply disconnecting from the "broken-stick" model; while, on the contrary,

- *Raorchestes bombayensis* Annandale (in community C), *Polypedates maculatus* Gray (in community F), *Indirana leithii* Boulenger (in community F), *Pseudophilautus* cf. *amboli* Biju & Bossuyt (in community F), *Indirana beddomii* Gunther (in community F), *Hylarana malabarica* Tschudi (in community F) are *by no means* affected the same, although these species occur at similar or even lower levels of relative abundance.

Now, what makes *Fejervarya caperata, Fejervarya* cf. *keralensis, Ramanella marmorata, Uperodon globulosus, Sphaerotheca dobsonii* specifically affected (as compared to the other six species cited above) remains conjectural.

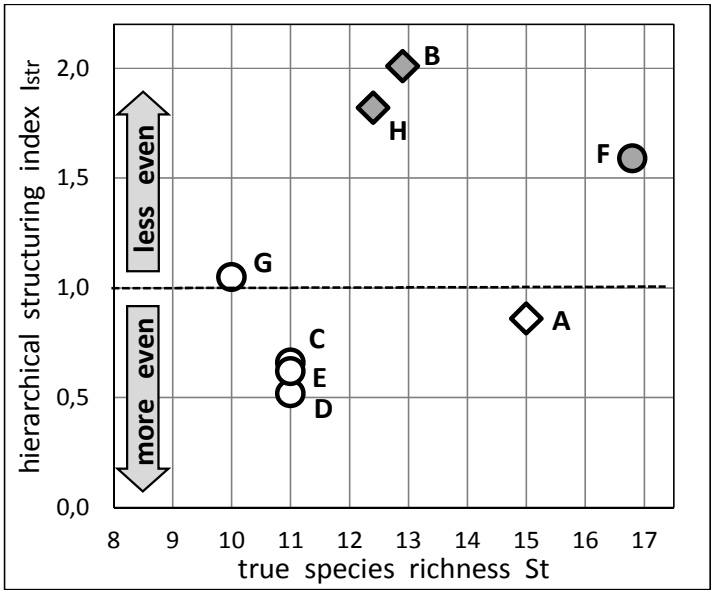


Fig. 12. A synthetic presentation of the situation of the eight frog communities with respect to two major quantitative features describing species communities: (i) the true (total) species richness S_t and (ii) the genuine intensity of the hierarchical structuring of species abundances, quantified by the structuring index I_{str}. *White* figures: exhaustively sampled communities; *grey* figures: communities requiring numerical extrapolations. The hierarchical structuring may be "regular" (i.e. roughly constant among species: *discs*) or "irregular" (i.e. with the sharp recess of abundance for the 3 or 4 rarest species: *diamonds*)

Table 3. Contrasting features of the Species Abundance Distributions between communities B, H, (and to a lesser extent A) and the other five communities: under a threshold abundance value ≈ 0.04, the decreasing rate of species abundances communities abruptly accelerates for communities A, B and H : see Figs. 4, 9, 11. The resulting sudden recess of species abundances below the "broken-stick" distribution, as a consequence of this sharp acceleration, is statistically significant (statistical test based on Bayesian inference: $p < 0.05$)

	What	When
B	Sharp acceleration of decreasing rate	For $a_i < 0.030$ (i.e. $a_i < a_9$)
H	Sharp acceleration of decreasing rate	For $a_i < 0.030$ (i.e. $a_i < a_9$)
A	Less sharp acceleration of decreasing rate	For $a_i < 0.023$ (i.e. $a_i < a_{11}$)
D	No such acceleration	Even down to $a_i = a_{St} = 0.038$
C	No such acceleration	Even down to $a_i = a_{St} = 0.027$
E	No such acceleration	Even down to $a_i = a_{St} = 0.015$
F	No such acceleration	Even down to $a_i = a_{St} = 0.008$
G	No such acceleration	Even down to $a_i = a_{St} = 0.006$

Yet, *species-specific* reasons for the brutal acceleration of the decreasing rate under a given threshold of relative abundance may be speculated and attributed to:

(i) an *intrinsic* rarity of species being very rare *all across* their respective ranges of repartition ;
(ii) a *local* rarity of species, approaching, here, *the limits* of their respective ranges of repartition ;
(iii) an *occasional* rarity of "vagrant" species, *poorly adapted to the local ecological conditions* prevailing in communities B, H, (A) and, accordingly, only present by more or less *brief incursions*;
(iv) a rarity resulting from some *negatively density-dependent* detrimental factor, applying to those species specifically (such as the increasing difficulty of finding mates to reproduce, below some threshold level of abundance);
(v) a rarity related to the *stochastic character of colonisation events along time* with, for example, exceptionally recent establishments assumed for those species in communities B, H, (A).

Here, numerical extrapolations reach the limits of their explanatory capacities and going on any further would require specific biological knowledge regarding each of these species.

4.4 The Role of Forest Degradation on the Total Species Richness and the Intensity of the Hierarchical Structuring of Species Abundances

No consistent trend emerges in this respect that could yet have been expected (Fig. 13). Thus, pristine forests are by no means host to the most species-rich frog communities. And the hierarchical structuring of abundances fails, as well, to clearly correlate with the level of forest degradation. This suggests, among other possibilities, that historical aspects (such as the more or less stochastic succession of species colonisation events at a given site) may partially obliterate the more deterministic influence of environmental parameters, including the level of forest degradation. Alternatively, this may also signify that expectations on the subject (such as the compelling decrease of species richness with increasing disturbance) are simply irrelevant, here.

4.5 Tentatively Speculating About the Effect of Climatic Change on the Features of the Species Abundance Distribution

Let consider a pejoration of environmental conditions assumed to occur around a given frog community – say community G, actually having 10 species with its Species Abundance Distribution shown in Figs. 2 and 8. This pejoration may be due, for example, to a steadily increasing climate change. It is assumed, here, that pejoration affects species abundances all the more than these abundances are already low, thus making the slope of the species abundances distribution becoming steadily steeper, as pejoration progressively increases. In addition, there inevitably exists some threshold level of absolute abundance below which the survival of a species becomes no longer possible, for example because of too low probability of finding mates for reproduction. Let this minimum survival threshold be fixed, for example, as half the *absolute* abundance of the rarest species (rank 10) as presently recorded, i.e. before pejoration goes on increasing.

Fig. 14 highlights graphically what is expected to happen with such increasing pejoration, in terms of (i) species richness St and (ii) hierarchical structuring intensity, I_{str}.

In a first step (0 → 1), the hierarchical structuring intensity, I_{str}, will increase (see equation (1)) since a_1/a_{St} steadily increases while a'_1/a'_{St} remains of course unchanged, as long as St remains equal to 10.

Then, when the absolute abundance of the rarest species (rank 10) finally falls below the survival threshold, it disappears (step 1 → 2) and, consequently, the hierarchical structuring intensity, I_{str}, abruptly decreases because species ranked 9 – now becoming the rarest species – is appreciably more abundant than was species ranked 10 at the moment of its disappearance. Thus, at stage 2, $I_{str} = \log(a_1/a_9)/\log(a'_1/a'_9)$ is lower than $\log(a_1/a_{10})/\log(a'_1/a'_{10})$ at stage 1 (namely: $I_{str} = 0.82$ and $I_{str} = 1.30$, respectively).

Then, with now $S_t = 9$, the same happen as for the first step at $S_t = 10$: the hierarchical structuring intensity I_{str} increases, as long as St remains equal to 9: (step 2 → 3).

And so on, in a saw-tooth pattern, as shown in Fig. 14.

Let consider now the overall trend, behind the detail of the sequential, saw-tooth variations. As might have been expected, this overall trend mainly consist in:

(i) The steadily *decrease of species richness* S_t, consequence of the thinning effect due to the minimum abundance threshold for survival and

(ii) A global *increase of the genuine intensity of hierarchical structuring*, I_{str} (note, yet,

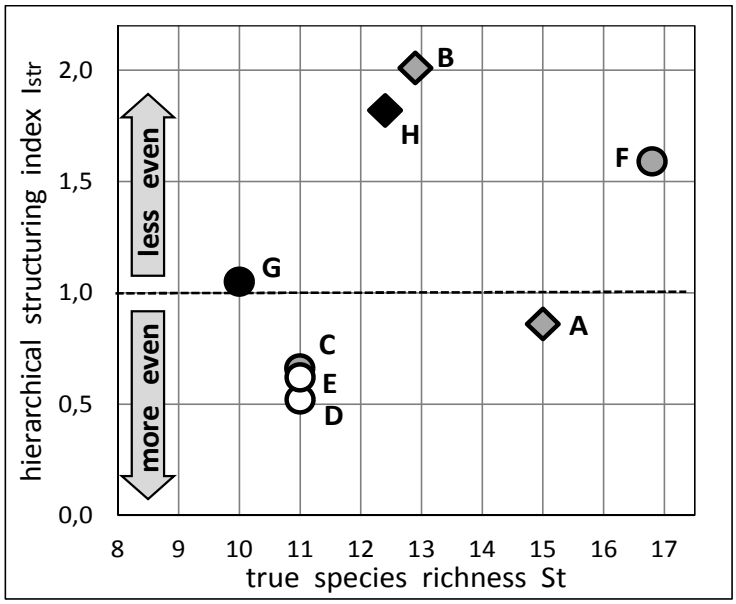


Fig. 13. Seeking for the possible influence of the degree of forest degradation on (i) the true species richness S_t and (ii) the intensity of the hierarchical structuring of species abundances I_{str}. *Pristine* forest (E, D): *white* figures ; *intermediate* degree of forest degradation (A, B, C, F): *grey* figures ; strong degrees of forest degradation (G, H): *black* figures

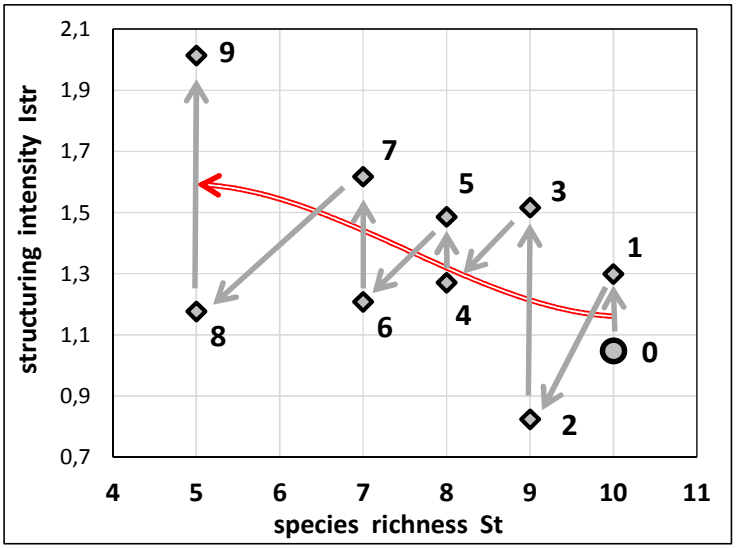


Fig. 14. Simulation of the consequences of an increasing environmental pejoration (for example related to climate change,) on (i) the total species richness "St" and (ii) the *genuine* intensity of the hierarchical structuring "Istr" of species abundances for the frog community "G". See text for the influence of this pejoration on the respective abundances of species

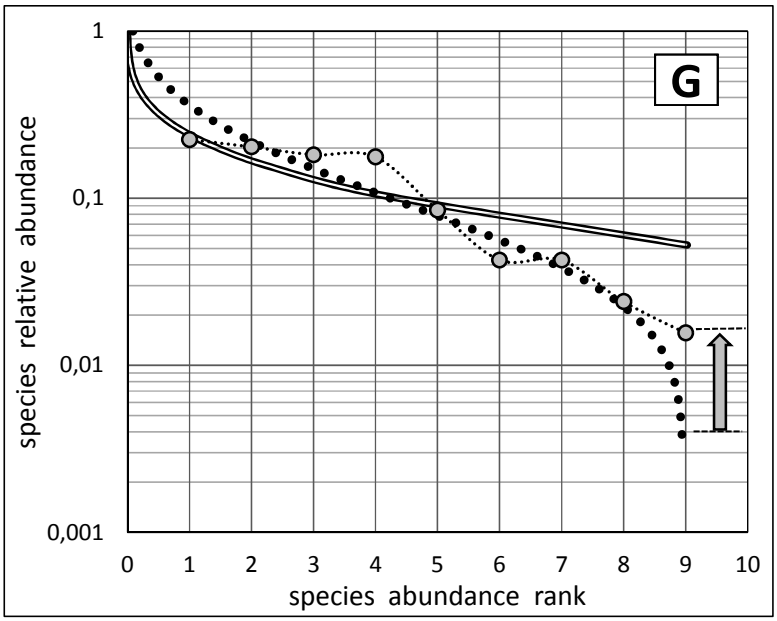


Fig. 15. The new Species Abundance Distribution when community "G" has reached *stage 2* (S_t = 9 ; I_{str} = 0.83) as a consequence of the environmental pejoration (see Fig. 14). The arrow highlights the beginning separation from the log-normal model (dotted line) towards the "log-series" model (double line). Initial situation (step 0) of community "G" is provided at Fig. 2

that, *without standardisation* to the "broken-stick", the *apparent* unevenness level would, on the contrary, seem to decrease, instead of increase; see [35]).

After having considered the consequences of environmental pejoration on species richness and the intensity of hierarchical structuring, let move now to the expected effect on the *shape* of the Species Abundance Distribution and its related functional significance. One might expect that, as the pejoration goes on increasing, the role of this detrimental factor would progressively become more and more predominant on the other ecological factors that drive the distribution of species abundances. Accordingly, it is expected that the Species Abundance Distribution progressively shifts from its original compliance with the "log-normal" model (see Figs. 2 and 3) towards a progressively better compliance with the "log-series" model [12–16]. This, indeed, is what is demonstrated by the simulation. Thus, as soon as stage 2 is reached (Fig. 15), the Species Abundance Distribution already clearly disconnects from the "log-normal" model, and is already halfway towards the "log-series" model.

However, it should be noted also that, in this schematically simplified scenario, the focused community is implicitly considered as isolated from the metapopulation context; that is implicitly out of reach from external inputs of new species that would possibly be better adapted to the currently evolving local environment. Such colonisation by "appropriate" new species would likely more or less compensate for both the reduction of abundances and the ultimate disappearance of the successively rarest species and, thus, would tend to more or less buffer the consequences of environmental pejoration on the shape of the Species Abundance Distribution.

To now conclude this speculative section, I would like to draw attention on the practical interest of considering Species Abundance Distributions in the context of evolving environmental conditions. Devoting attention at each of the three main aspects that shape Species Abundance Distributions (i.e. species richness, hierarchical structuring intensity and selective fitting to either reference models), will offer a corresponding set of typically diagnostic features, able to reliably highlight the consequences of an increasing degree of environmental pejoration. As already emphasised, this may have major practical interest in the perspective of monitoring the consequences of environmental pejoration in general and, in particular, for the monitoring of this major cause of pejoration represented by the *ongoing climatic change* worldwide.

5. CONCLUSION

Estimating the level of *total species richness* in animal communities, as well as getting insights on the genuine *causes and intensity of the hierarchical structuring* of species abundances, are major topics that likely contribute to a more comprehensive understanding of these communities. Acquiring such knowledge also provides a basic reference for the future monitoring of the consequences of the on-going climatic change on living communities. However, this program imperatively requires performing exhaustive species inventories or, if impractical, impose to *extrapolate numerically the incomplete samplings with minimum bias*. An appropriate methodological approach in this respect is provided above and its implementation is exemplified by the treatment of a series of communities of tropical frogs, a particularly exposed and endangered group of animals, potentially under threat of excessive heat and drought.

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COMPETING INTERESTS

Author has declared that no competing interests exist.

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APPENDIX 1

Bias-reduced extrapolation of the Species Accumulation Curve and associated bias-reduced estimation of the number of still unrecorded species, based on the recorded numbers of species occurring 1 to 5 times

Consider the survey of an assemblage of species of size N_0 (with sampling effort N_0 typically identified either to the number of recorded individuals or to the number of sampled sites, according to the inventory being in terms of either species abundances or species incidences), including $R(N_0)$ species among which f_1, f_2, f_3, f_4, f_5, of them are recorded 1, 2, 3, 4, 5 times respectively. The following procedure, designed to select the less-biased solution, results from a general mathematical relationship that constrains the theoretical expression of *any* theoretical Species Accumulation Curves R(N) (see [9,44,45]):

$$\partial^x R_{(N)}/\partial N^x \;=\; (-1)^{(x-1)}\, f_{x(N)}/C_{N,\,x} \;\approx\; (-1)^{(x-1)}\,(x!/N^x)\, f_{x(N)} \quad (\approx \text{as } N >> x) \qquad \text{(A1.1)}$$

Compliance with the mathematical constraint (equation (A.1)) warrants *reduced-bias* expression for the extrapolation of the Species Accumulation Curves R(N) (i.e. for $N > N_0$). Below are provided, accordingly, the polynomial solutions $R_{\mathbf{x}}(N)$ that respectively satisfy the mathematical constraint [1], considering increasing orders x of derivation $\partial^x R_{(N)}/\partial N^x$. Each solution $R_{\mathbf{x}}(N)$ is appropriate for a given range of values of f_1 compared to the other numbers f_x (according to [9]):

* *for* f_1 *up to* f_2 → $R_{\mathbf{1}}(N) = (R(N_0) + f_1) - f_1.N_0/N$

* *for larger* f_1 *up to* $2f_2 - f_3$ → $R_{\mathbf{2}}(N) = (R(N_0) + 2f_1 - f_2) - (3f_1 - 2f_2).N_0/N - (f_2 - f_1).N_0^2/N^2$

* *for larger* f_1 *up to* $3f_2 - 3f_3 + f_4$ → $R_{\mathbf{3}}(N) = (R(N_0) + 3f_1 - 3f_2 + f_3) - (6f_1 - 8f_2 + 3f_3).N_0/N - (-4f_1 + 7f_2 - 3f_3).N_0^2/N^2 - (f_1 - 2f_2 + f_3).N_0^3/N^3$

* *for larger* f_1 *up to* $4f_2 - 6f_3 + 4f_4 - f_5$ → $R_{\mathbf{4}}(N) = (R(N_0) + 4f_1 - 6f_2 + 4f_3 - f_4) - (10f_1 - 20f_2 + 15f_3 - 4f_4).N_0/N - (-10f_1 + 25f_2 - 21f_3 + 6f_4).N_0^2/N^2 - (5f_1 - 14f_2 + 13f_3 - 4f_4).N_0^3/N^3 - (-f_1 + 3f_2 - 3f_3 + f_4).N_0^4/N^4$

* *for* f_1 *larger than* $4f_2 - 6f_3 + 4f_4 - f_5$ → $R_{\mathbf{5}}(N) = (R(N_0) + 5f_1 - 10f_2 + 10f_3 - 5f_4 + f_5) - (15f_1 - 40f_2 + 45f_3 - 24f_4 + 5f_5).N_0/N - (-20f_1 + 65f_2 - 81f_3 + 46f_4 - 10f_5).N_0^2/N^2 - (15f_1 - 54f_2 + 73f_3 - 44f_4 + 10f_5).N_0^3/N^3 - (-6f_1 + 23f_2 - 33f_3 + 21f_4 - 5f_5).N_0^4/N^4 - (f_1 - 4f_2 + 6f_3 - 4f_4 + f_5).N_0^5/N^5$

The associated non-parametric estimators of the number Δ_J of missing species in the sample [with $\Delta_J = R(N=\infty) - R(N_0)$] are derived immediately:

* $\mathbf{f_1} \le f_2$ → $\Delta_{J1} = f_1$; $R_{\mathbf{1}}(N)$

* $f_2 < \mathbf{f_1} \le 2f_2 - f_3$ → $\Delta_{J2} = 2f_1 - f_2$; $R_{\mathbf{2}}(N)$

* $2f_2 - f_3 < \mathbf{f_1} \le 3f_2 - 3f_3 + f_4$ → $\Delta_{J3} = 3f_1 - 3f_2 + f_3$; $R_{\mathbf{3}}(N)$

* $3f_2 - 3f_3 + f_4 < \mathbf{f_1} \le 4f_2 - 6f_3 + 4f_4 - f_5$ → $\Delta_{J4} = 4f_1 - 6f_2 + 4f_3 - f_4$; $R_{\mathbf{4}}(N)$

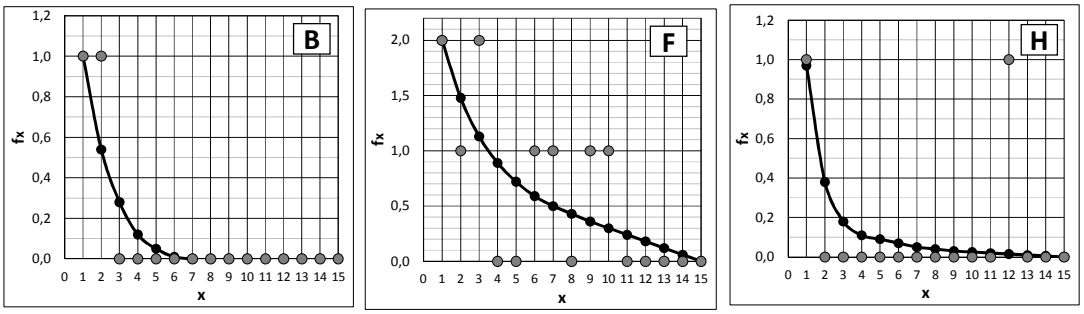
* $\mathbf{f_1} > 4f_2 - 6f_3 + 4f_4 - f_5$ → $\Delta_{J5} = 5f_1 - 10f_2 + 10f_3 - 5f_4 + f_5$; $R_{\mathbf{5}}(N)$

N.B. 1: As indicated above (and demonstrated in details in [9]), this series of inequalities define the ranges that are best appropriate, respectively, to the use of each of the five estimators, JK-1 to JK-5. That is the respective ranges within which each estimator will benefit of minimal bias for the predicted number of missing species.

Besides, it is easy to verify that another consequence of these preferred ranges is that the selected estimator will *always* provide the highest estimate, as compared to the other estimators. Interestingly, this mathematical consequence, of general relevance, is in line with the already admitted opinion that all non-parametric estimators provide *under*-estimates of the true number of missing species [7,8,46–48]. Also, this shows that the approach initially proposed by Brose et al. [49] – which has regrettably suffered from its somewhat difficult implementation in practice – might be advantageously reconsidered, now, in light of the very simple selection key above, of *far much easier practical use*.

N.B. 2: In order to reduce the influence of drawing stochasticity on the values of the f_x, the as-recorded distribution of the f_x should preferably be smoothened: this may be obtained either by rarefaction processing or by regression of the as-recorded distribution of the f_x versus x.

N.B. 3: For f_1 falling beneath 0.6 x f_2 (that is when sampling completeness closely approaches exhaustivity), then Chao estimator may alternatively be selected: see reference [10].



Figs. A1.1, A1.2, A1.3 – The recorded values of the numbers f_x of species recorded x-times (grey discs) and the regressed values of f_x (black discs) derived to reduce the consequence of stochastic dispersion for the three incomplete samplings of frog communities labelled B, F, H

APPENDIX 2

Correction and extrapolation of the as-recorded Species Abundance Distribution (S.A.D.)

N.B.: details regarding the derivation of the following expressions are provided in [1].

1) Correction for bias of the recorded part of the S.A.D.

The bias-corrected expression of the true abundance, $\tilde{a}_i$, of species of rank 'i' in the S.A.D. is given by:

$$\tilde{a}_i = p_i.(1+1/n_i).(1-f_1/N_0)/(1+R_0/N_0) \quad \text{(A2.1)}$$

where N_0 is the actually achieved sample size, R_0 (=$R(N_0)$) the number of recorded species, among which a number f_1 are singletons (species recorded only once), n_i is the number of recorded individuals of species 'i', so that $p_i = n_i/N_0$ is the recorded frequency of occurrence of species 'i', in the sample. The crude recorded part of the "S.A.D." – expressed in terms of the series of as-recorded frequencies $p_i = n_i/N_0$ – should then be replaced by the corresponding series of expected true abundances, $\tilde{a}_i$, according to equation (A2.1).

2) Extrapolation of the recorded part of the S.A.D. accounting for the complementary abundance distribution of the set of unrecorded species

The following expression stands for the estimated abundance, a_i, of the unrecorded species of rank i (thus for $i > R_0$):

$$a_i = (2/N_i).(1-[\partial R(N)/\partial N]_{Ni})/(1+ R(N_i)/N_i) \quad \text{(A2.2)}$$

which, in practice, comes down to:

$$a_i \approx (2/N_i)/(1+ R(N_i)/N_i) \quad \text{(A2.3)}$$

as $f_1(N)$ already becomes quite negligible as compared to N for the extrapolated part.

This equation provides the extrapolated distribution of the species abundances a_i (for $i > R(N_0)$) as a function of the least-biased expression for the extrapolation of the species accumulation curve R(N) (for $N > N_0$), 'i' being equal to $R(N_i)$. The key to select the least-biased expression of R(N) is provided at Appendix 1.

APPENDIX 3

The trivial ("mechanistic") contribution of the level of species richness to the degree of structuring of species abundances

All things equal otherwise, the larger the species richness, the weaker is the slope of the Species Abundance Distribution.

This can be easily exemplified and quantified, on a theoretical basis, by considering a theoretically constant structuring process - such as the random distribution of the relative abundances that characterises the "broken-stick" distribution model. By applying this model successively to a series of communities with increasing species richness, a steadily decrease of the slope of abundance distributions is highlighted: Fig. A3.

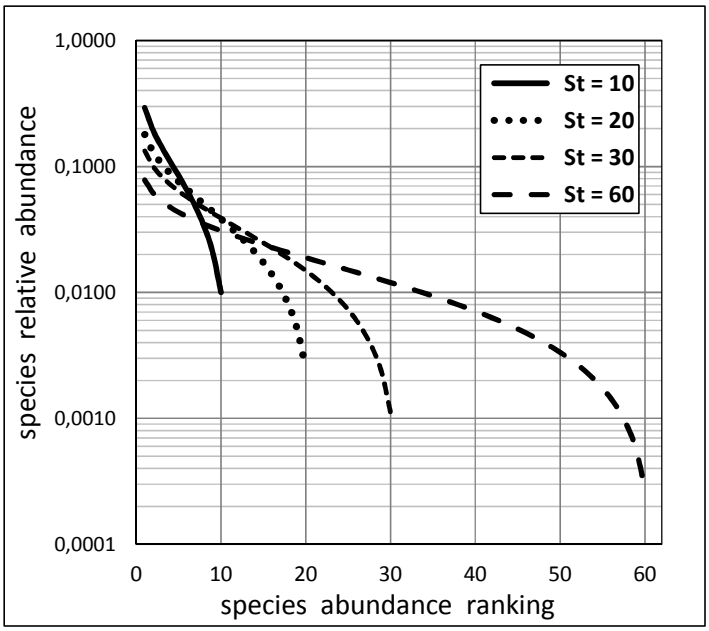


Fig. A3. The "broken-stick" distribution model applied to species communities with increasing species richness S_t = 10, 20, 30, 60. Although the theoretical structuring process involved in the "broken-stick" model remains unchanged (random apportionment of relative abundances among member species), the slope of the species abundance distribution strongly depends upon (and monotonously decreases with) the level of species richness S_t

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