



Numerical Extrapolation of the Species Abundance Distribution Unveils the True Species Richness and the Hierarchical Structuring of a Partially Sampled Marine Gastropod Community in the Andaman Islands (India)

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Author's contribution

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

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ABSTRACT

Even when it remains substantially incomplete, the partial inventory of a species assemblage can provide much more information than could be expected at first. This can be achieved by applying a rigorous numerical extrapolation procedure that fully extends the incomplete sampling in numerical terms and, thereby, provides reliable estimates regarding not only the number but also the distribution of abundances for the whole set of the undetected species. As a result, this makes available the full range of the Species Abundance Distribution of the yet partially sampled assemblage and, thus, allows to address a series of interesting issues regarding the process and pattern of the hierarchical structuring of species abundances within the studied assemblage of species. Moreover, the same kind of numerical extrapolation may be applied separately to each subset of species, within the whole assemblage, that may have relevant interest (taxonomic subgroups, feeding guilds, etc...). Thus, deconstructing the Species Abundance Distribution can provide further detailed insights into the functional organisation of the studied assemblage.

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The mathematical and algorithmic basis for this extrapolating procedure has been developed recently, to be applied to the numerical extension of both the Species Accumulation Curve and the Species Abundance Distribution.

The wide potential interest of this new methodological approach, when having to deal with substantially incomplete inventories of species (which is doomed to become inevitable with increasingly species-rich assemblages), is illustrated by a detailed case study of a marine gastropod assemblage on rocky shore under tropical climate.

Keywords: *Species richness; diversity; rank-abundance; marine snails; trophic rank; least-biased estimation; incomplete sampling.*

1. INTRODUCTION

Total species richness, taxonomic composition and hierarchical structuring of species abundances are three key features that appropriately characterise species communities. Unfortunately, partial, incomplete inventories – which are doomed to become even more frequent with the inevitable generalisation of “rapid assessments” and “quick surveys” – prevent an in-depth appreciation of each of these key aspects of species communities [1–3]. However, a properly implemented procedure of *numerical extrapolation* can provide reliable estimations relative to both the *number* and the respective *abundances* of the undetected species and, thereby, allows the derivation of reliable inferences as regard (i) the true, *total* species richness and (ii) the distribution of species abundances *completed* by including the subset of still *undetected* species. Only the taxonomic identities of the latter inevitably escape to any attempt of extrapolation. In turn, once numerically *completed* (and *only* when it is so: [4]), the distribution of species abundances can provide some synthetic pieces of information about the process at work (either deterministic or stochastic) that drive the hierarchical structuring of species abundances within the community [5–9]. Although no further mechanistic details may be extracted from this synthetic overview, it has, yet, the advantage of being straightforward, as it does not require the long and tedious analytical approaches that would be required otherwise to go deeper in the details of structuring processes. As such, this synthetic approach can serve as a convenient preliminary approach.

As *complete abundance distributions* (or, if not the case, their *completed version using numerical extrapolation*) are mandatory, a procedure for the numerical extrapolation of the Species Accumulation Curve and the Species Abundance Distribution (the former directly linked to the latter) has recently been developed,

aiming at providing reliable, *least-biased* inferences about the number and the respective abundances of undetected species, when having to deal with substantially incomplete inventories.

Tropical marine ecosystems in shallow waters are of major interest to ecologists and conservationists, as they are considered as embodying remarkably high levels of biological complexity among marine communities [10–12]. However, and precisely because of their usually high species richness and diversity (including *numerous rare* species), samplings of these communities often remain substantially incomplete [4]. For all the reasons just mentioned above, such partial inventories thus require implementing reliable numerical extrapolation procedure, so as to release as much information as possible regarding (i) the true species richness of sampled community, (ii) a synthetic overview of the hierarchical structuring of species abundances and (iii) how specific are the respective functional contributions of the different trophic levels involved in the community.

Hereafter, I report and discuss the results derived from the numerical extrapolation of a partial inventory of an intertidal gastropod community established on a rocky shore near Rangat, Andaman Islands, India [12].

2. MATERIALS AND METHODS

2.1 Materials

The rocky shore of Andaman and Nicobar Islands is home to a rich fauna of marine gastropods [13]. Yet, detailed inventories of gastropod communities at the local scale, including species abundances, remain very scarce. A recent report by JEEVA et al. [12] opportunely provides such a series of local inventories along the rocky shores of Andaman Islands. But, referring to the high proportion of singletons (species that were detected only once

during sampling), these inventories remain substantially incomplete [14–16]. Accordingly, implementing *numerical extrapolation* of such inventories is required to uncover the series of useful information that may be derived from complete (here *completed by extrapolation*) Species Abundance Distributions, as mentioned above.

Hereafter, I shall focus on the particular community that provides the highest number of recorded species; this community is located near Rangat, in the southern part of Middle Andaman. According to JEEVA et al. [12]. The sampled area is mainly covered by rocky outcrops with boulders and pebbles and the partial inventory was conducted by these authors at the intertidal level.

2.2 Numerical Extrapolation Procedures

- * *Total species richness*: the least-biased estimation of the number of still undetected species during partial sampling and the resulting least-biased estimation of the total species richness of the sampled community are derived according to the procedure defined by Béguinot [17,18] and briefly summarised in Appendix 1, on the basis of the numbers f_x of species observed x -times during partial sampling, as provided in Appendix 3).

- * *Species Abundance Distribution*: to accurately exploit their full potential, the as-recorded Species Abundance Distributions (“S.A.D.s”) require [19,20]:

- First, to be *corrected* for statistical sampling bias, resulting from the finite size of samplings and,
- Second, but 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 *least-biased* numerical extrapolation and correction of the as-recorded S.A.D.s - described in details in Béguinot [20] - is briefly recalled in Appendix 2.

After being *corrected* and *extrapolated* accordingly, the S.A.D.: (i) not only provides an overview of both the true species richness of the sampled community and the diversity of the respective abundances of member species, but also, (ii) can help addressing several important questions regarding the kind of process driving the hierarchical structuration of the community, including possible specificities according to the different trophic levels involved in the community of interest (Fig. 1).

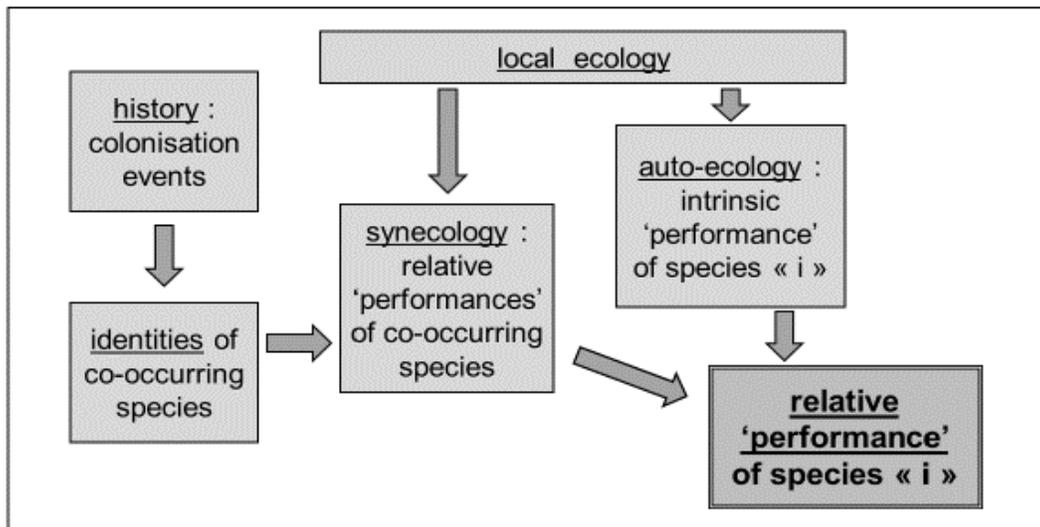


Fig. 1. Schematic sketch showing how the combination of both historical and ecological contexts peculiar to a given community of species drive the relative “performance” - *sensu latissimo* - of each member species “i”, thus generating the hierarchical structuring of species abundances in the community

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, do many independent factors are contributing together; which 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 [5,21–24];
- 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 “broken-stick” model [20]. 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. Thus standardising the degree of structuration (the slope of the S.A.D.) with respect to the “broken-stick” model is particularly relevant as this allows to leave aside the “mechanistic”, trivial influence of the number of member species and, thus, to account only for the *genuine* hierarchical structuring [7,8,25]. Thus standardised, the degree of structuration of the community becomes independent of its richness in species. This “mechanistic” influence of the level of species richness on the degree of community structuration, that is on the

slope of the abundance distribution, is demonstrated in Appendix 3.

3. RESULTS

3.1 Estimation of the Total Species Richness of the Community as a Whole and Separately by Kind of Feeding Guild

Accounting for the values of the numbers f_x of species observed x -times during partial sampling (Fig. A1 in Appendix 1), the *least-biased* nonparametric estimator of the number of undetected species during the partial sampling proves to be Jackknife-5 (see the selective key in Appendix 1). The corresponding least-biased estimations of (i) the number Δ of undetected species, (ii) the resulting level S_t of the total species richness of the sampled community and (iii) the level of completeness, Ro/St of the incomplete sampling are provided in Table 1. With a 54% level of completeness only, the partial sampling confirms remaining very far from exhaustivity.

The separate estimations of Δ and S_t , according to feeding guilds – primary and secondary consumers respectively – are subsequently derived. Similar levels of sampling completeness are inferred for both guilds (56% and 53% respectively).

Due to the relatively low level of achieved sampling completeness, further sampling could be considered of interest. In this perspective, the least-biased extrapolation of the Species Accumulation Curve highlights the expected increase in the number of detected species, $R(N)$, as a function of growing sampling size N , beyond the actually achieved inventory. And, thereby, the additional sampling efforts that would be required to obtain any desirable increase in sampling completeness can be forecasted, as shown in Fig. 2.

Table 1. Numerical characteristics of a marine Gastropod community at the intertidal level of a rocky shore at Rangat (Andaman Islands), including: the sampling-size No , the number of detected species Ro (= $R(No)$), the estimated number of undetected species Δ , the resulting evaluation of total species richness St and the level of sampling completeness Ro/St

	No	Ro	Δ	St	Ro/St
Whole community	157	42	35.7	77.7	54%
Primary consumers	96	17	13.3	30.3	56%
Secondary consumers	61	25	22.4	47.4	53%
Primary / secondary	/	0.68	0.59	0.64	1.06

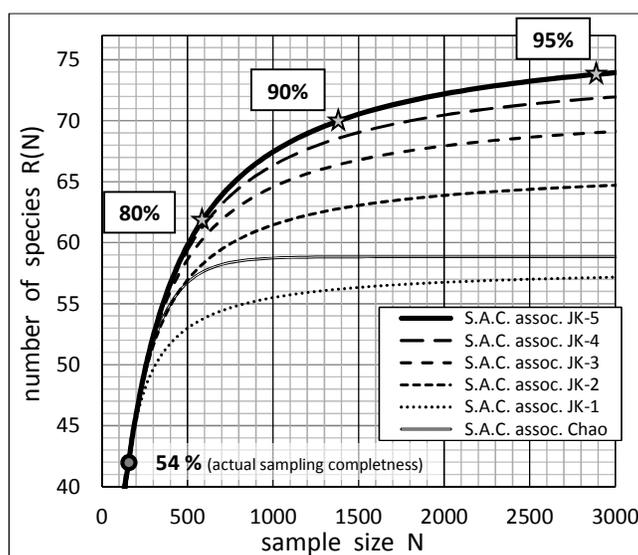


Fig. 2. Extrapolated part of the Species Accumulation Curve accounting for the increase of the number of detected species $R(N)$ as a function of growing sample size N beyond the actually achieved sampling ($N_0 = 157$, $R(N_0) = 42$). Here, the selected, least-biased, nonparametric estimator of the number of undetected species is Jackknife-5, leading to a total species richness $St = 78$, with the associated least-biased extrapolation plotted as the coarse solid line. Also plotted for comparison are the extrapolations of the S.A.C. associated to the other, more biased estimators. In practice, the least-biased extrapolation (coarse solid line) highlights the expected additional sampling effort required to reach improved levels of sampling completeness (for example, the sample sizes required to reach 80%, 90% and 95% completeness would be around $N = 600$, 1400 , 2900 respectively)

3.2 Correction and Extrapolation of the Species Abundance Distribution

The as-recorded part of the Species Abundance Distribution (i.e. the part restricted to the set of actually detected species only) needs being corrected, as shown in Fig. 3. Corrections, made according to equation (A2.1) in Appendix 2, involve both: (i) a *positive* correction due to the multiplicative factor $(1+1/n_i)$ being >1 and (ii) a *negative* correction due to the multiplicative factor $(1-f_i/N_0)/(1+R_0/N_0)$ being <1 . The positive correction, decreasing progressively with increasing species abundances, outweighs the negative correction only for the lower species abundances, that is along the second part of the recorded Species Abundance Distribution (here for species ranks $i = 19$ to $i = 42$, as highlighted in Fig. 3).

The least-biased extrapolation of the Species Abundance Distribution, from rank 43 to rank 78, is computed according to equation (A2.3) in Appendix 2 and is plotted as the solid line in Fig. 4. This figures thus unveils the *entire development* of the Species Abundance

Distribution, duly corrected for its recorded part and extrapolated with minimized bias for the whole set of the still undetected species. Note that, although most undetected species are expected to be among the less abundant in the community, their ecological importance is no less and, thus, deserve as much attention, as already emphasised by several authors [26–28].

The same procedure of correction and extrapolation is, then, conducted separately for *primary* and for *secondary* consumers, as shown in Figs. 5 and 6. The superposition of the Species Abundance Distributions for each guild in Fig. 7 allows an easy, direct comparison of the degrees of structuration of species abundances in each guild. An alternative comparative approach is provided in Figs. 8 and 9, in the form of a common histogram of species abundances for the two guilds together. In these Figs, the abundances are plotted on an arithmetic scale, rather than the usual log-transformed scale, in order to offer a direct visual appreciation of the respective contributions of the member species of each guild. As shown in Figs. 7 and 8, the dominant species in term of number of

individuals, are predominantly *primary* consumers: the four numerically dominant species all belong to the herbivorous family Neritidae: *Nerita albicilla* Linnaeus 1758, *Nerita*

polita Linnaeus 1758, *Nerita insculpta* Récluz 1841, *Nerita costata* Gmelin 1791 (with corrected relative abundances: $a_1 = 0.122$, $a_2 = 0.077$, $a_3 = 0.049$, $a_4 = 0.045$, respectively).

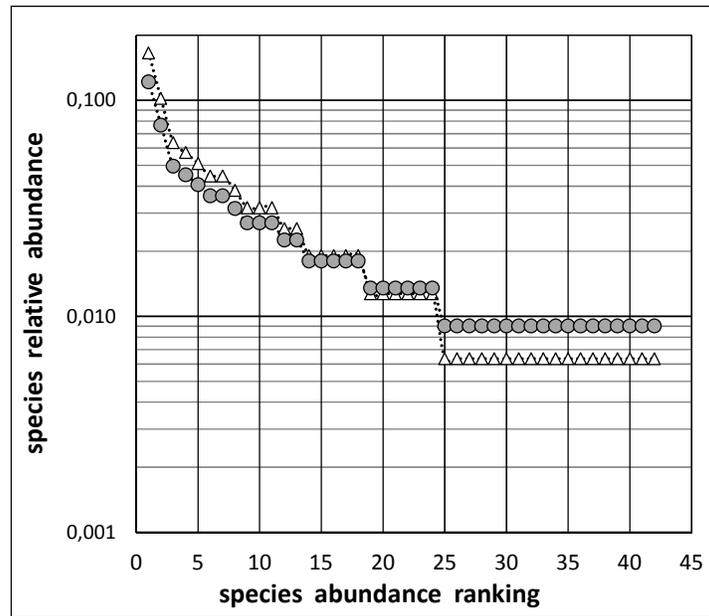


Fig. 3. The as-recorded part of the Species Abundance Distribution (white triangles) and the same after correction (grey discs): see text for further explanation

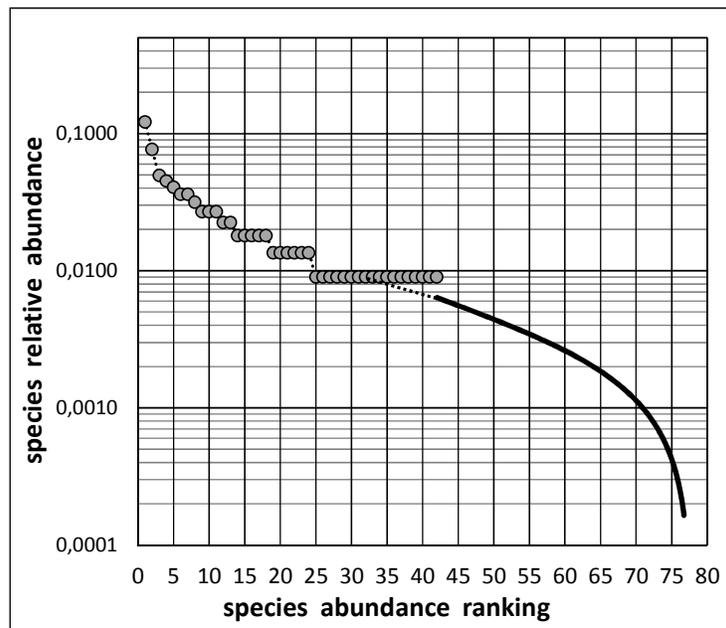


Fig. 4. The completed Species Abundance Distribution, including both (i) The correction of the recorded part (involving the 42 detected species: grey discs) and (ii) The least-biased extrapolation of the unrecorded part (i.e. the 36 undetected species: ranks $i = 43$ to 78: solid line)

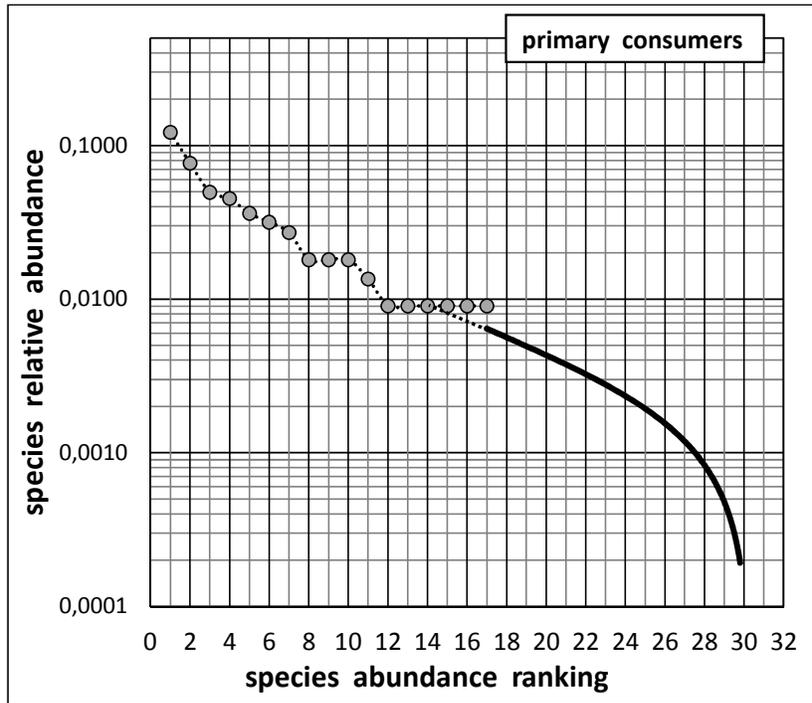


Fig. 5. The completed Species Abundance Distribution (corrected: grey discs ; extrapolated: solid line) considering the guild of primary consumers (“herbivores”)

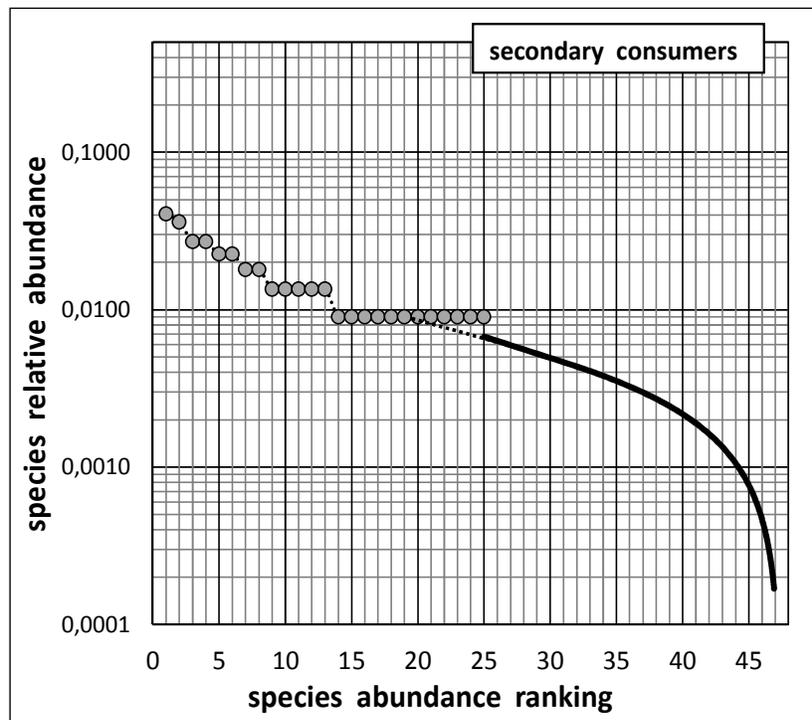


Fig. 6. The completed Species Abundance Distribution (corrected: grey discs; extrapolated: solid line) considering the guild of secondary consumers (“carnivores, scavengers,...”)

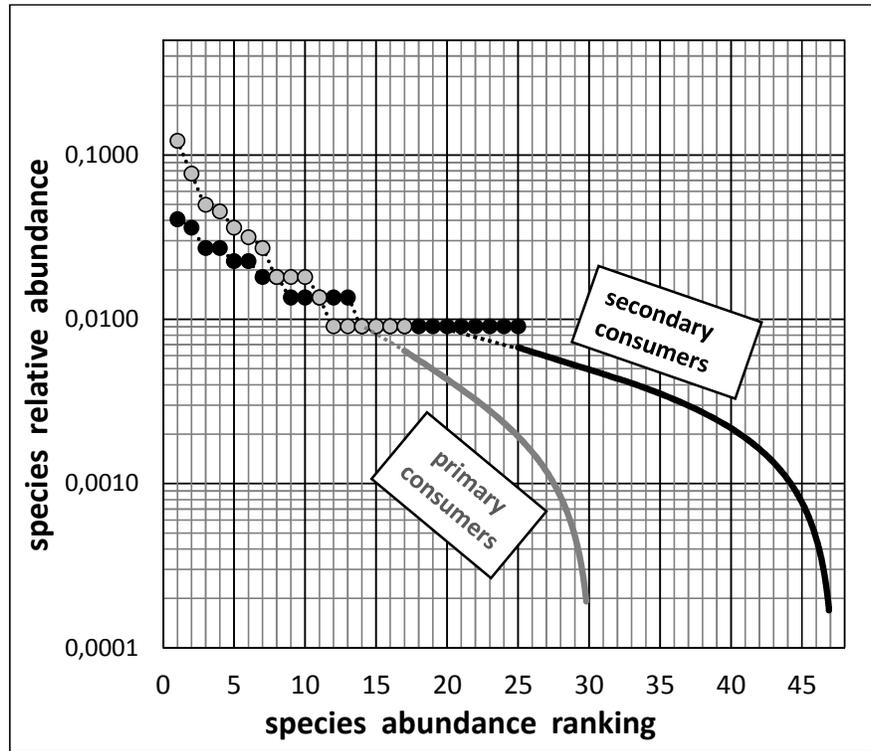


Fig. 7. Superposition of the completed Species Abundance Distributions for primary and secondary consumers (plotted in Figs. 5 and 6), thus allowing direct comparison between both feeding guilds

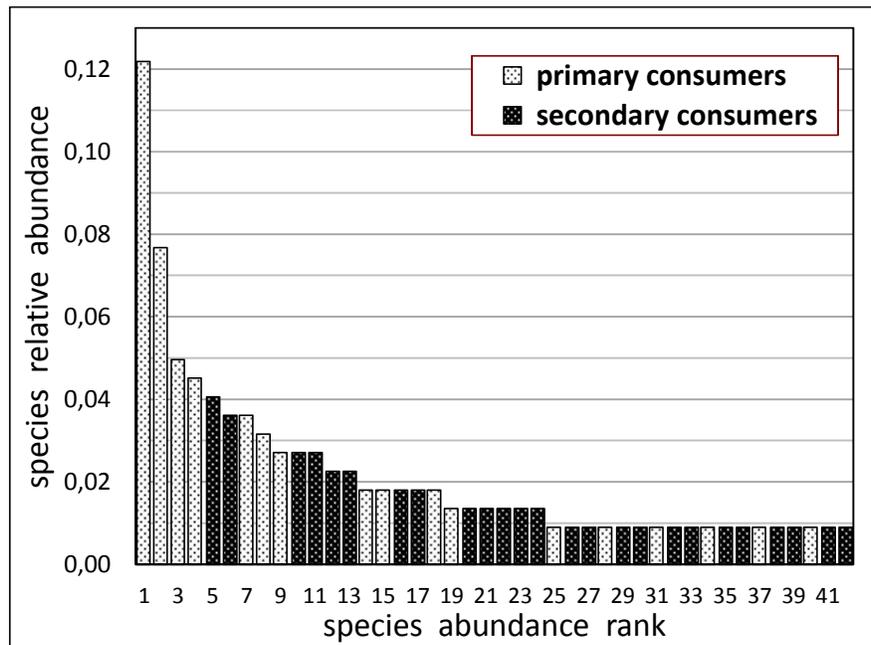


Fig. 8. The Species Abundance Distribution for the 42 already detected species, highlighting the feeding mode of each species. Note the arithmetic (instead of log-transformed) scale for abundances. Directly derived from Figs. 5 & 6

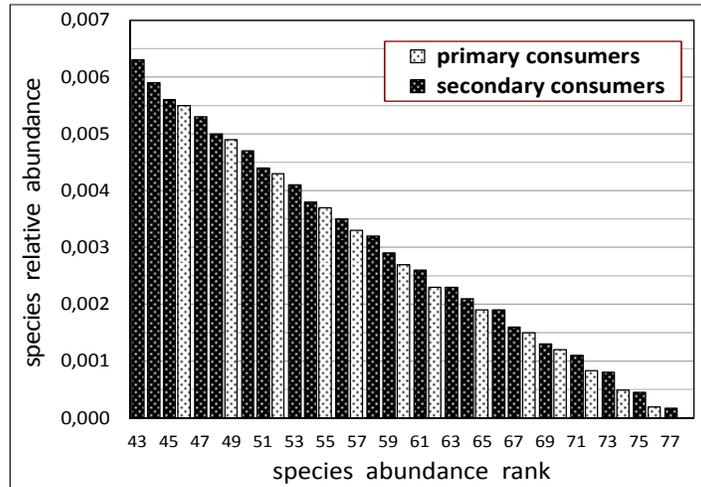


Fig. 9. The Species Abundance Distribution extrapolated for the 35 still undetected species, highlighting the feeding mode of each species. Note the arithmetic (instead of log-transformed) scale for abundances. Directly derived from Figs. 5 & 6

3.3 Quantitative Characterisation of the Hierarchical Structuring of Species Abundances in the Studied Community

3.3.1 The type of structuring process

In order to investigate which kind of structuring process is at work in the studied community, two models of abundance distribution – the “log-

normal” distribution and the “log-series” distribution – were tentatively fitted to the completed Species Abundance Distribution provided at Fig. 4. As shown in Figs. 10 and 11, a fairly good fit is obtained with the *log-normal* model, while the accordance with *log-series* is comparatively less satisfactory. The same holds true for both feeding guilds, primary and secondary consumers, considered separately: Figs. 12, 13, 14, 15.

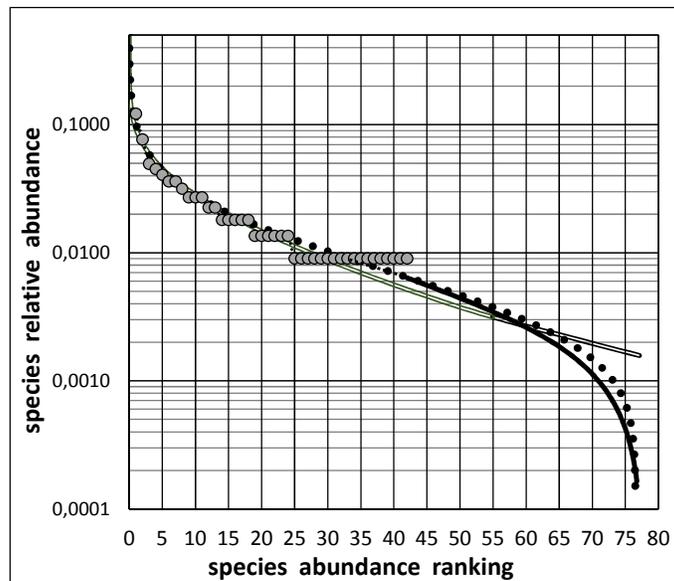


Fig. 10. Two classical models: “log-normal” (coarse dotted line) and “log-series” (double line) fitted to the Species Abundance Distribution of the whole community (corrected and extrapolated cf. Fig. 4). The best fit is clearly with the “log-normal” distribution

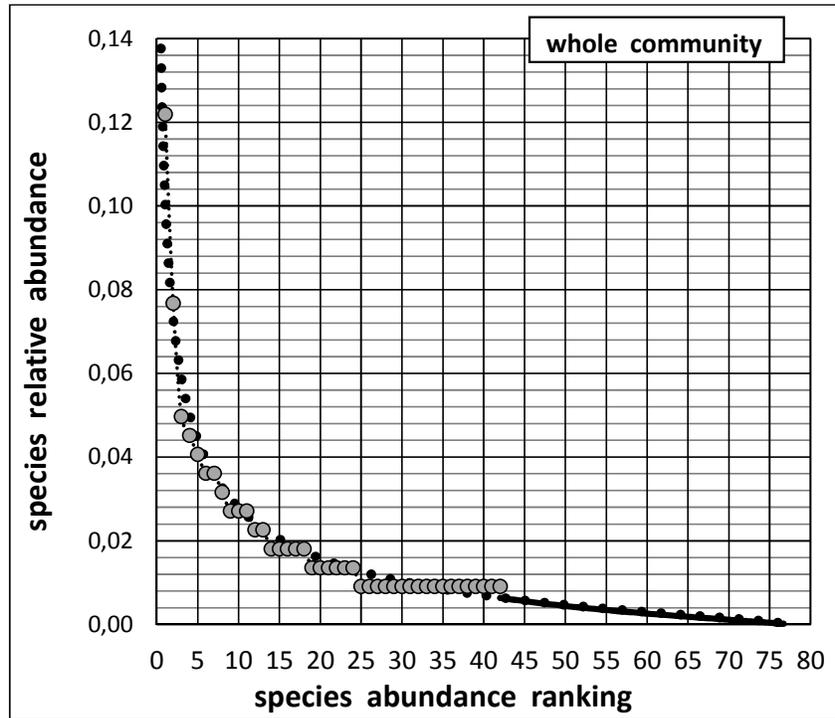


Fig. 11. The “log-normal” model (coarse dotted line) fitted to the Species Abundance Distribution (as in Fig. 10). Note the arithmetic scale for abundances (instead of log-transformed scale), which allows a more direct visual appreciation of relative abundances, as suggested by MacArthur [29]

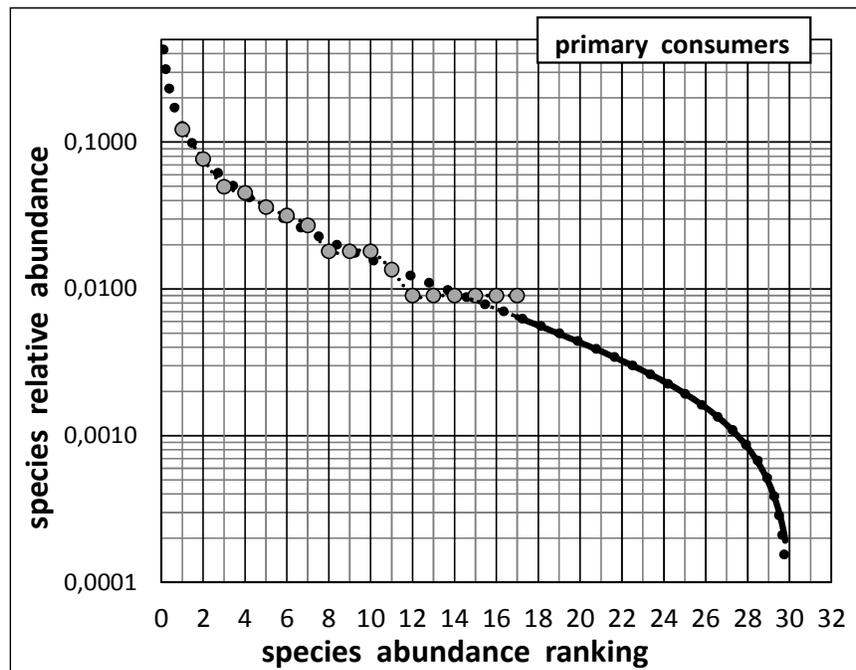


Fig. 12. The “log-normal” model (coarse dotted line) fitted to the Species Abundance Distribution for the guild of *primary consumers*

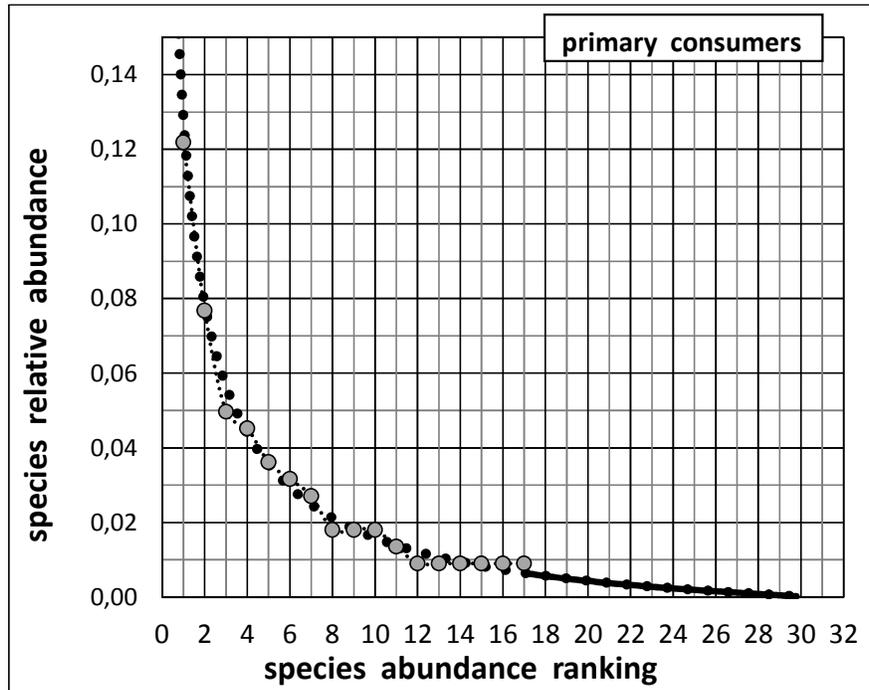


Fig. 13. Same as Fig. 12 but with arithmetic scale for abundances (instead of log-transformed scale), which allows a more direct visual appreciation of relative abundances, as suggested by MacArthur [29]

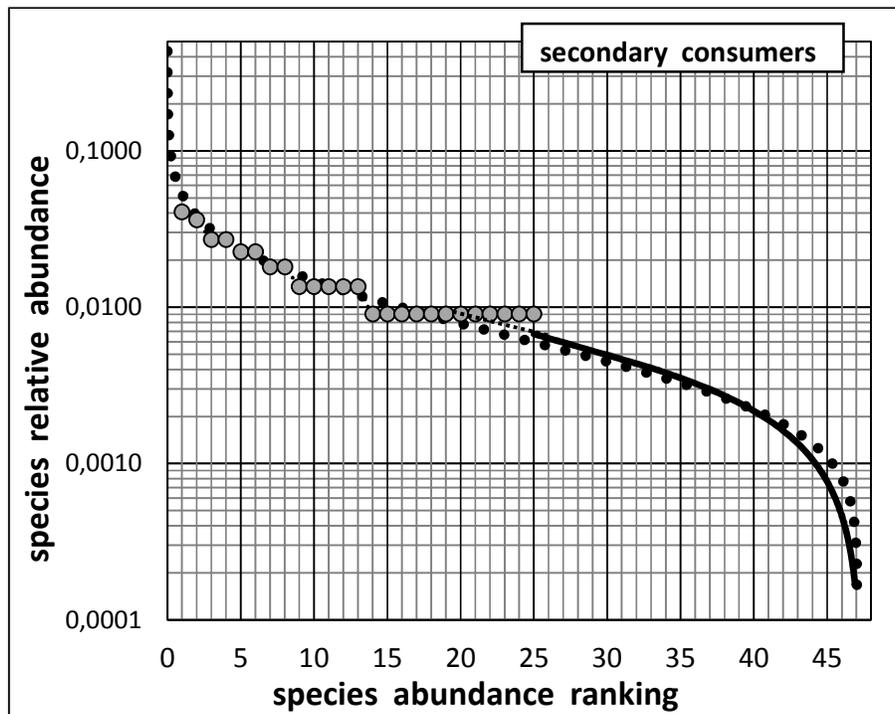


Fig. 14. The “log-normal” model (coarse dotted line) fitted to the Species Abundance Distribution for the guild of *secondary consumers*

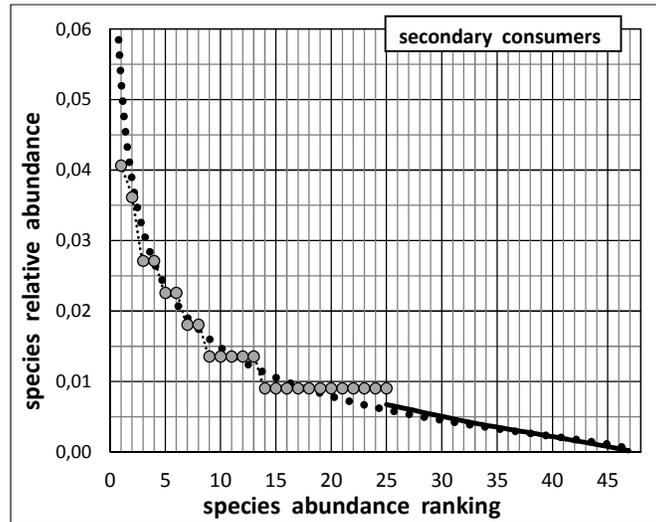


Fig. 15. Same as Fig. 14 but with arithmetic scale for abundances (instead of log-transformed scale), which allows a more direct visual appreciation of relative abundances, as suggested by MacArthur [29]

3.3.2 The intensity of the structuring process

The shape of the Species Abundance Distribution characterises in details the intensity of the hierarchical structuring of species abundances in the community.

As emphasised in the Methods section, in order to unveil the *genuine* intensity of the structuring process (leaving aside the trivial contribution of the level of species richness), the slope of the Species Abundance Distribution should

preferably be standardised to the slope of the corresponding "broken-stick" distribution (corresponding meaning that the "broken-stick" is computed for the same species richness). Accordingly, in Figs. 16, 17, 18, the completed (corrected and extrapolated) Species Abundance Distribution is plotted together with the corresponding "broken-stick" distribution. Comparing the slopes on the same graph thus provides a reliable appreciation of the degree of hierarchical structuring of species abundances.

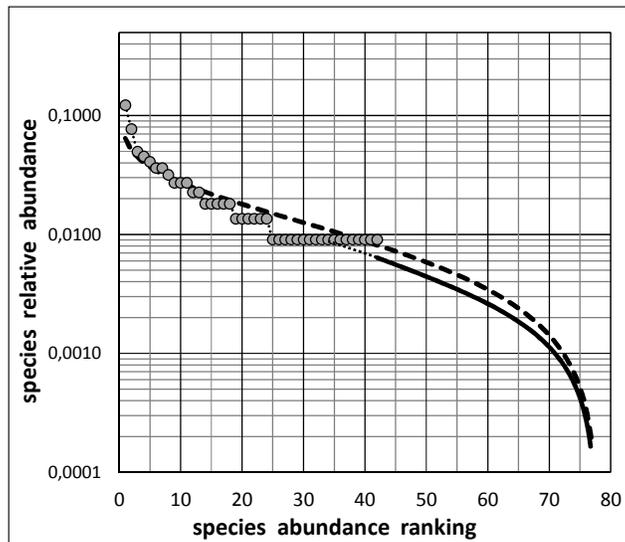


Fig. 16. The Species Abundance Distribution of the *whole community* plotted together with the corresponding "broken-stick" distribution (dashed line)

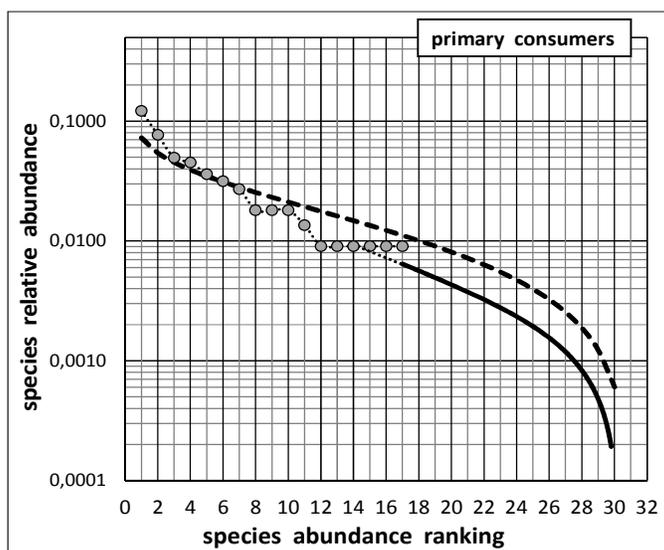


Fig. 17. The Species Abundance Distribution for the guild of *primary consumers* plotted together with the corresponding “broken-stick” distribution (dashed line)

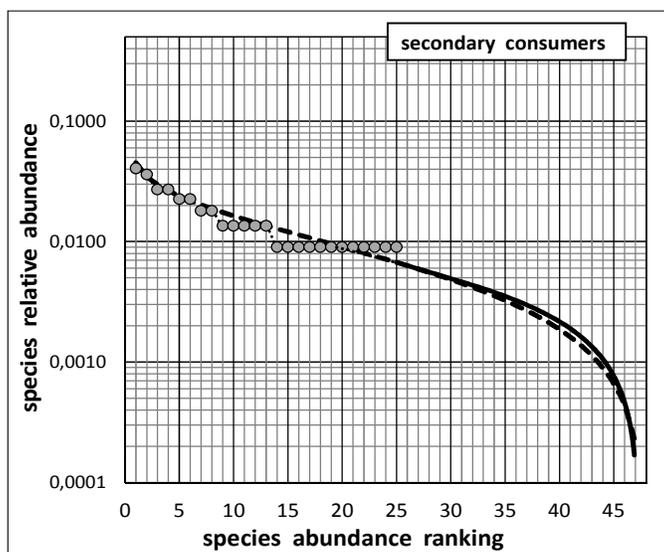


Fig. 18. The Species Abundance Distribution for the guild of *secondary consumers* plotted together with the corresponding “broken-stick” distribution (dashed line)

In a more concise, but reductionist approach, the *average* slope of the Species Abundance Distribution provides a convenient appreciation of the degree of hierarchical structuring. Accordingly, a “structuring index” (i) highlighting the degree of structuring and (ii) standardised to the corresponding “broken-stick” distribution (for the aforementioned reason), can be defined as the ratio between the average slope of the actual abundance distribution and the average slope of the corresponding “broken-stick” model, with

abundances being classically log-transformed. Thus defined, the structuring index is equal to:

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

where a_1 and a_{St} stand for the highest and the lowest abundances in the studied assemblage and a'_1 and a'_{St} stand for the highest and the lowest abundances in the corresponding “broken-stick” distribution having the same species richness S_t . Results are given in Table 2.

Table 2. The degree of hierarchical structuration (unevenness) of species abundances, quantified as the average slope of the Species Abundance Distribution standardised to the average slope of the corresponding “broken-stick” distribution (see Figs. 16, 17, 18)

	Sp. Abund. Distr.		“broken-stick”		structuring index $\frac{\log[a_1/a_{st}]}{\log[a'_1/a'_{st}]}$
	a_1	a_{st}	a'_1	a'_{st}	
Whole community	0.122	0.00016	0.0640	0.00017	1.12
Primary consumers	0.122	0.00019	0.0725	0.00060	1.35
Secondary consumers	0.085	0.00035	0.0451	0.00022	1.03

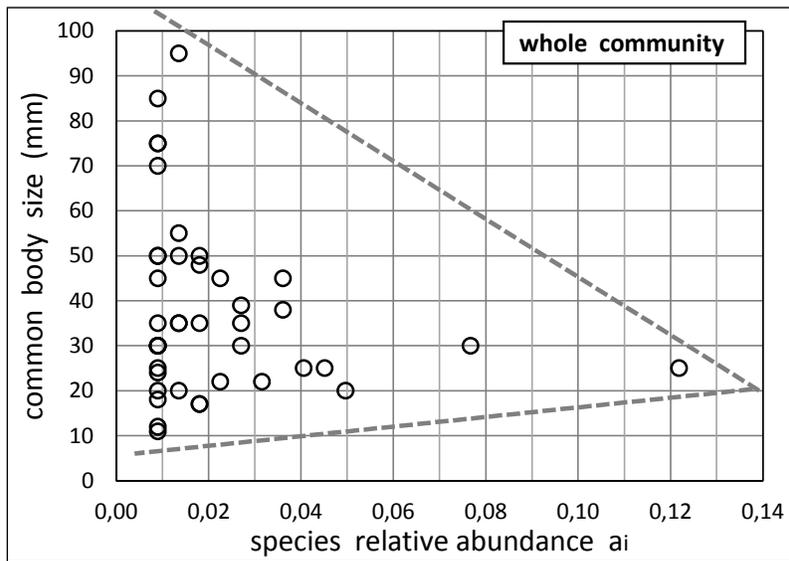


Fig. 19. Body-size versus relative abundance relationship for the 42 sampled species in the whole community. Relative abundances corrected according to equation (A2.1)

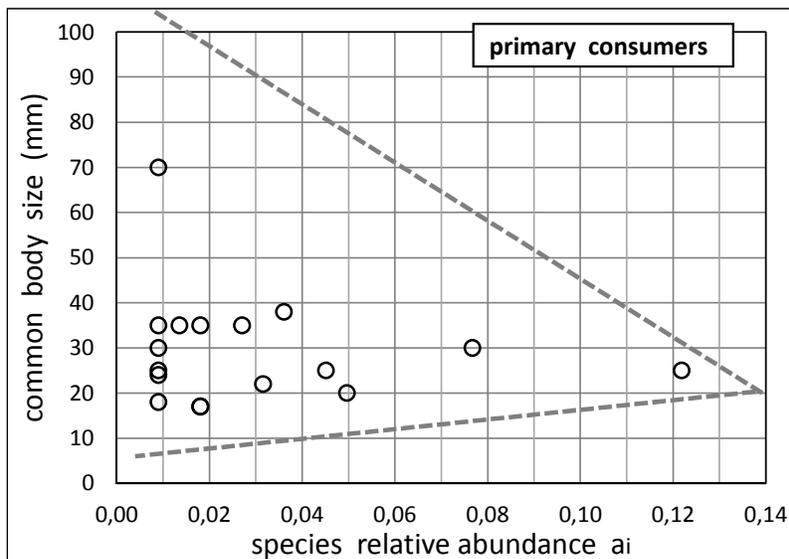


Fig. 20. Body-size versus relative abundance relationship for the 17 sampled species of the guild of primary consumers. Relative abundances corrected according to equation (A2.1)

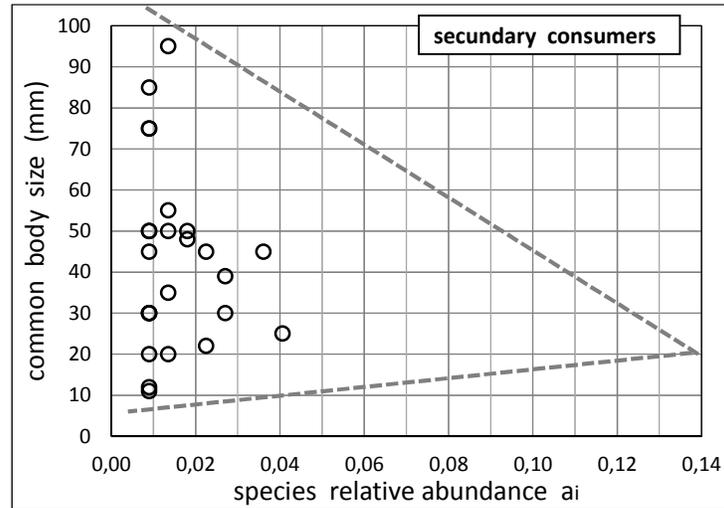


Fig. 21. Body-size versus relative abundance relationship for the 25 sampled species of the guild of secondary consumers. Relative abundances corrected according to equation (A2.1)

3.3.3 Body-size versus relative abundance relationships

Figs. 19, 20, 21 highlight the relationships between the shell-size – as a surrogate to body-size – and the corresponding relative abundance of each actually sampled species (of course, numerical extrapolation provides no information on body-size of undetected species).

Primary and secondary consumers differ regarding their respective ranges of shell-size (Figs. 20 and 21). Considering an arbitrarily fixed threshold-size of 40 mm:

- Only one species (out of 17) has a common-size in excess of 40 mm among primary consumers;
- Eleven species (out of 25) have a common-size in excess of 40 mm among secondary consumers.

The difference in proportions (6% against 44%) is statistically significant: χ^2 with Yates correction = 6.8, $p < 0.01$. The largest species among secondary consumers are: *Harpa major* Röding 1798 (≈ 95 mm), *Vasum turbinellus* (Linnaeus 1758) (≈ 85 mm), *Chicoreus brunneus* (Link 1807) (≈ 75 mm), *Semicassis bisulcata* (Schubert & Wagner 1829) (≈ 55 mm), *Bufo naria echinata* (Link 1807) (≈ 50 mm), *Latirolagena smaragdulus* (Linnaeus 1758) (≈ 50 mm), *Gemmula vagata* (E.A. Smith 1895) (≈ 50 mm), *Bursa granularis* (Röding 1798) (≈ 48 mm), *Tylothais virgata* (Dillwyn 1817) (≈ 45 mm), *Pollia undosa* (Linnaeus 1758) (≈ 45 mm),

Polinices mammilla (Linnaeus 1758) (≈ 45 mm). The largest species among primary consumers is: *Scutellastra flexuosa* (Quoy & Gaimard 1834) (≈ 70 mm).

4. DISCUSSION

A thorough approach to the species diversity and the hierarchical structuring of abundances in species assemblages would arguably require (quasi-) exhaustive samplings. Yet, incomplete samplings usually become unavoidable practice as soon as species-rich assemblages are addressed, especially when dealing with invertebrate's communities. Hopefully, the implementation of appropriate extrapolating methods can "force" incomplete samplings and partial inventories to reveal much more information than one might think *a priori*. Thus, proper numerical extrapolations of both the Species Accumulation Curve and the Species Abundance Distribution provide an unexpected set of additional information relative to all those species that remained undetected after partial samplings. This, in turn, allows to tackle the main issues relative to (i) the evaluation of species richness and (ii) the highlighting of internal organisation within partially sampled communities – all subjects that would normally require an exhaustive species inventory.

A thorough analysis of the intertidal gastropod community on the rocky shore at Rangat location (Andaman Islands) was conducted accordingly, in compliance with this methodological approach.

4.1 Total Species Richness Estimates and the Forecasted Additional Sampling Efforts Required to Improve Sampling Completeness

At first, the estimator *Jackknife at order 5* reveals being the *least-biased* one among the series of classical nonparametric estimators of the number of undetected species (according to the selective key in Appendix 1). This selection of *Jackknife-5* proves satisfying, here, not only for the community as a whole but also for each of the two feeding guilds considered separately. The estimated true species richness reaches 77 species for the whole community, among which 30 primary-consumers and 47 secondary-consumers (Table 1), which substantially exceeds the corresponding recorded numbers (42, 17, 25 species respectively). Thus, the sampling-completeness levels reached for the whole community as well as for the sub-inventories of the two feeding guilds all hardly exceed 50%. This justifies, *a posteriori*, the need of implementing an accurate numerical extrapolation of the partial inventory of this marine gastropod community.

As a comparison, the total species richness of marine gastropods assemblages on coral reefs around each of three small islands in Mannar Gulf (India) was estimated from 49 to 53 species only [30].

Although these extrapolations will provide a lot of additional interesting information regarding the set of still unrecorded species (as described below), further field investigation effort, aiming at increasing the completeness of inventory, might nevertheless be considered. If so, a reliable forecast of the additional sampling effort required to meet a given target gain in sampling-completeness would be useful for the optimal planning of required resources and efforts. The least-biased extrapolation of the Species Accumulation Curve associated to the least-biased estimator (here *Jackknife-5*) answers appropriately this demand, as shown in Fig. 2. Clearly, any further improvement of sampling completeness rapidly requires strong additional investment of sampling effort. Thus, increasing completeness from the actual 54% level to 80% or 90% would require multiplying the actual sample-size by *four* or by *ten* respectively.

Being able to reliably estimate the level of such additional efforts is of obvious prime interest to rationally decide whether to continue sampling

operation any further or to rely only on the actual inventory as such but adequately extended by numerical extrapolation.

4.2 Correction and Extrapolation of the Species Abundance Distribution

The *as-recorded* distribution needs correction and extrapolation because it is both (i) slightly *biased*, due in particular to sampling stochasticity and, most importantly, (ii) *incomplete* to the extent of the proportion of those species of the sampled community that remained undetected during sampling.

The *corrections*, computed according to equation (A2.1), involve (i) a negative contribution (multiplying factor $(1-f_i/N_0)/(1+R_0/N_0)$ which is < 1) related to the degree of sampling incompleteness and (ii) a positive contribution (multiplying factor $(1+1/n_i)$ which is > 1) that compensates for statistical bias during sampling [20]. These combined corrections result in a slight reduction of higher abundances and a slight increase of lower abundances, as shown in Fig. 3.

In turn, the numerical, *least-biased extrapolation* of the distribution of abundances provides the complete development of the Species Abundance Distribution, as would be obtained by an exhaustive inventory of all member species in the community: see Fig. 4 for the whole community and Figs. 5, 6, 7, 8, 9 for each feeding guild. Indeed, dealing with a *full range* Species Abundance Distribution (by using extrapolation as far as necessary) is essential, not only to deliver a full description of the *pattern* of abundances but, also, to question the kind of *process* actually involved in the hierarchical structuring of abundance distribution. This is achieved, in particular, by comparing the studied Species Abundance Distribution to different theoretical models, each of them being considered representative of a particular kind of process at work in the structuring of species abundances in the community [5]. However, it turns out that such comparisons, when conducted with incomplete – non extrapolated – distributions often leads to erroneous diagnostics, as in shown in the present work (Fig. 10) and already emphasised by several authors [4,6,23,31,32]. Hence the requirement to conduct reliable comparisons based on *full range* Species Abundance Distribution only (duly *extrapolated* if necessary).

Beyond considering globally the Species Abundance Distribution of the whole community, it looks worth considering also, separately, the distributions peculiar to each feeding guild, here *primary consumers* and *secondary consumers*. Indeed, deconstructing the global abundance distribution according to the member subsets of the whole community can lead to more focused and detailed analysis, as indicated by [22,32].

4.3 Inferring the Type of Process Driving the Hierarchical Structuring of Species Abundances

Considered in its full range, the Species Abundance Distribution of the whole community clearly fits best the “log-normal” distribution than the “log-series” distribution (Figs. 10 & 11). This suggests, accordingly, that the *process of structuration* of the whole community is likely driven by the combined contributions of many independent factors, rather than by only one (or very few) dominant factors, as already frequently reported [5,21,22–24]. Moreover, the same holds true as well for the structuring process at work in each feeding guild: both *primary consumers* (Figs. 12 & 13) and *secondary consumers* (Figs. 14 & 15) are likely structured by the combined influences of multiple independent factors (probably rather different in each guild).

4.4 Quantifying the Degree of Hierarchical Structuration of Species Abundances

Here also, considering the full range of the Species Abundance Distribution is necessary not only to duly include the set of still undetected species but, also, to allow the relevant comparison with the corresponding “broken-stick” reference: Figs. 16, 17, 18. The degree of hierarchical structuring of species abundances in the whole community, quantified by the “structuring index” (Table 2), is slightly higher than for the “broken-stick” reference ($I_{str} = 1.12$). Besides, the two feeding guilds differ from each other in this respect, with *secondary consumers* being close to the reference ($I_{str} = 1.03$) while *primary consumers* are more strongly structured ($I_{str} = 1.35$).

4.5 Dependence between Body-size and Relative Abundance

Globally, shell-size (taken as a surrogate to body-size) and relative abundance are fairly independent among the 42 recorded species and the same hold true for each feeding guild

considered separately (Figs. 19, 20, 21). Yet, the maximum shell-size reached at a given level of species abundance is clearly decreasing with increasing abundance, for the whole community as for each feeding guild. This last pattern is not surprising and may possibly have wide validity [33]; in particular, the same trend was observed in land snail communities as well (Béguinot, *unpublished results*).

Primary and secondary consumers differ however regarding the range of shell-size (Figs. 20 and 21), with a significantly larger proportion of species having shell-size above 40 mm among secondary consumers: 44% against 5% (χ^2 with Yates correction = 6.8, $p < 0.01$).

5. CONCLUSION

When dealing with substantially incomplete species inventories, the *numerical extrapolation* of both the *Species Accumulation Curve* and the *Species Abundance Distribution* offers remarkable opportunities to unveil an unexpectedly rich sum of information relative to the set of undetected species. In turn, thanks to the resulting access to the full range of the Species Abundance Distribution, interesting additional information may be derived, regarding the process and pattern of the hierarchical organisation within the partially sampled community. Still, further investigations may be conducted by deconstructing the Species Abundance Distribution in its main constitutive subsets, such as feeding guilds, which co-exist and interact within the whole community. This is made possible by the additive properties of least-biased numerical extrapolation [17,18]. The numerical extrapolations applied to the partial inventory of a marine gastropod community in Andaman Islands concretely demonstrate the wide range of ecological questions that may be addressed and successfully answered, even though no more than half of the true species richness of the community had been actually recorded only. In short, this clearly highlights the potential interest of *numerical extrapolation* when having to deal with only *incomplete* inventories, which becomes increasingly frequent, due to the generalised practice of quick assessments of biodiversity, especially for invertebrate faunas under tropical climates.

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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 missing 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 [17,34,35]:

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

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 $R_x(N)$ that respectively satisfy the mathematical constraint [1], considering increasing orders x of derivation $\partial^x R_{(N)}/\partial N^x$. Each solution $R_x(N)$ is appropriate for a given range of values of f_1 compared to the other numbers f_x , according to [17]:

* for f_1 up to $f_2 \rightarrow R_1(N) = (R(N_0) + f_1) - f_1 \cdot N_0/N$

* for f_1 up to $2f_2 - f_3 \rightarrow R_2(N) = (R(N_0) + 2f_1 - f_2) - (3f_1 - 2f_2) \cdot N_0/N - (f_2 - f_1) \cdot N_0^2/N^2$

* for f_1 up to $3f_2 - 3f_3 + f_4 \rightarrow R_3(N) = (R(N_0) + 3f_1 - 3f_2 + f_3) - (6f_1 - 8f_2 + 3f_3) \cdot N_0/N - (-4f_1 + 7f_2 - 3f_3) \cdot N_0^2/N^2 - (f_1 - 2f_2 + f_3) \cdot N_0^3/N^3$

* for f_1 up to $4f_2 - 6f_3 + 4f_4 - f_5 \rightarrow R_4(N) = (R(N_0) + 4f_1 - 6f_2 + 4f_3 - f_4) - (10f_1 - 20f_2 + 15f_3 - 4f_4) \cdot N_0/N - (-10f_1 + 25f_2 - 21f_3 + 6f_4) \cdot N_0^2/N^2 - (5f_1 - 14f_2 + 13f_3 - 4f_4) \cdot N_0^3/N^3 - (-f_1 + 3f_2 - 3f_3 + f_4) \cdot N_0^4/N^4$

* for f_1 larger than $4f_2 - 6f_3 + 4f_4 - f_5 \rightarrow R_5(N) = (R(N_0) + 5f_1 - 10f_2 + 10f_3 - 5f_4 + f_5) - (15f_1 - 40f_2 + 45f_3 - 24f_4 + 5f_5) \cdot N_0/N - (-20f_1 + 65f_2 - 81f_3 + 46f_4 - 10f_5) \cdot N_0^2/N^2 - (15f_1 - 54f_2 + 73f_3 - 44f_4 + 10f_5) \cdot N_0^3/N^3 - (-6f_1 + 23f_2 - 33f_3 + 21f_4 - 5f_5) \cdot N_0^4/N^4 - (f_1 - 4f_2 + 6f_3 - 4f_4 + f_5) \cdot N_0^5/N^5$

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:

* $0.6 f_2 < f_1 \leq f_2 \rightarrow \Delta_{J1} = f_1 ; R_1(N)$

* $f_2 < f_1 \leq 2f_2 - f_3 \rightarrow \Delta_{J2} = 2f_1 - f_2 ; R_2(N)$

* $2f_2 - f_3 < f_1 \leq 3f_2 - 3f_3 + f_4 \rightarrow \Delta_{J3} = 3f_1 - 3f_2 + f_3 ; R_3(N)$

* $3f_2 - 3f_3 + f_4 < f_1 \leq 4f_2 - 6f_3 + 4f_4 - f_5 \rightarrow \Delta_{J4} = 4f_1 - 6f_2 + 4f_3 - f_4 ; R_4(N)$

* $f_1 > 4f_2 - 6f_3 + 4f_4 - f_5 \rightarrow \Delta_{J5} = 5f_1 - 10f_2 + 10f_3 - 5f_4 + f_5 ; R_5(N)$

N.B. 1: As indicated above (and demonstrated in details in Béguinot [17], 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 from 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 [2,3,15, 16,36]. Also, this shows that the approach initially proposed by Brose et al. [37] – 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 $0.6 \times f_2$ (that is when sampling completeness closely approaches exhaustivity), then Chao estimator may be selected: see reference [18].

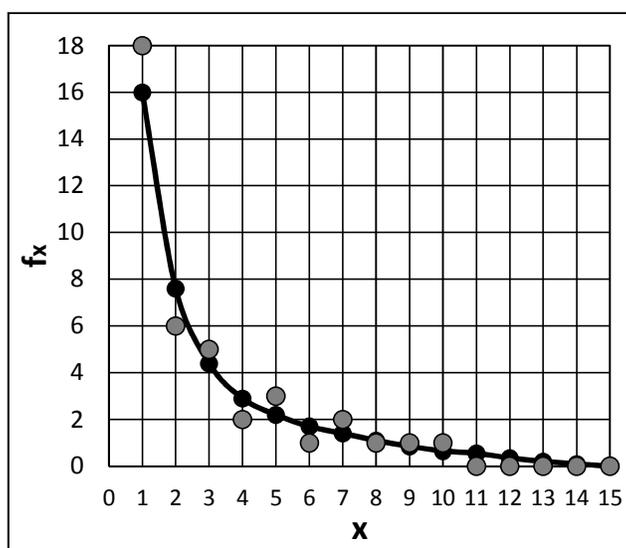


Fig. A1. The recorded values of the numbers f_x of species recorded x -times (grey discs) and the regressed values of f_x (black discs) derived to reduce the consequence of stochastic dispersion

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 Béguinot (2018).

1) Correction for a 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:

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

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 $i > R_0$):

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

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 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.

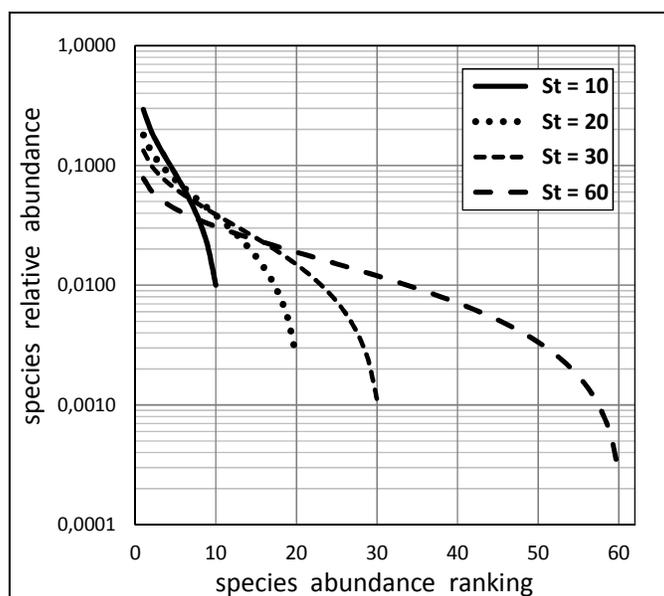


Fig. A3. The “broken-stick” distribution model applied to species communities with increasing species richness $S_t = 10, 20, 30, 60$. Although the theoretical structuring process involved in the “broken-stick” model remains unchanged (random apportionment of relative abundances among member species), 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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