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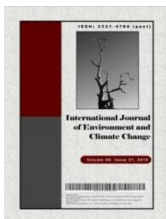
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# **Analysing the Role of Environmental Stresses on Species Richness and the Process of Hierarchical Structuring of Species Abundances in Marine Gastropods communities at Suva (Fiji Islands)**

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## **Author's contribution**

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

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## **ABSTRACT**

Anthropogenic environmental stresses, especially physio-chemical pollution, are causing steadily increasing threat to many ecosystems, among which coastal marine communities in tropical shallow waters are especially sensitive. In particular, species-rich marine gastropod assemblages are doomed to bear sharp drops in species diversity when exposed to pollutants released offshore. Yet, the details of the process of decline in species diversity remain to be addressed and analysed more deeply. By addressing a series of previously reported inventories of marine gastropod communities along a sharp gradient of pollution along southern coast at Suva (Fiji Archipelago), I first confirm the already recognised trend towards both a severe decrease in species richness and a strong increase of the unevenness in species abundance distribution, as a response to incremental pollution. Yet, the last trend – increased unevenness – reveals being essentially the purely mathematical consequence of the concomitant decline in species richness. In fact, the genuine intensity of the process of hierarchical structuring of species abundances proves remaining virtually unaffected by environmental degradation, contrary to what has been generally thought so far. Also, another unexpected aspect of the decline in species richness with growing pollution is that this decline is far from being primarily restricted to the set of rarest species; in fact, the originally abundant species are also largely implied in this decline. Moreover, considering separately the two co-occurring feeding guilds, it is shown that herbivores and carnivores are substantially involved the same in the drop in species diversity; as a result, their relative contributions in the community do not seem markedly contrasted by growing pollution. In another respect, a recently proposed paradigmatic hypothesis is supported, according to which the

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herbivore-guild has quite less numerous species with more unevenly distributed abundances, as compared to the carnivore-guild. Yet, once again, this increased unevenness is essentially the purely mathematical consequence of the concomitant decline in species richness; the genuine intensity of the process of hierarchical structuring of species abundances does remain substantially unchanged. At last, a comparatively extremely high sensitivity to pollution is highlighted for the emblematic genus *Conus*, which suffers, here, a dramatic drop in species diversity.

**Keywords:** *Coral reef; pollution; species diversity; ranked abundance distribution; incomplete inventory; evenness; unevenness; feeding guild.*

## 1. INTRODUCTION

Tropical marine ecosystems in shallow waters are of major interest, being considered as embodying remarkably high levels of diversity and biological complexity [1-4]. Also, these ecosystems are of major concerns to ecologists and conservationists, as they are considered as one of the first kind of ecosystems to suffer significantly from the on-going *climate-warming* [3,5] and also from other categories of environmental stresses of either anthropogenic or natural origins.

Marine Gastropods communities are most often important components of these tropical ecosystems, reflecting locally the major taxonomical contribution of Gastropods to marine faunas worldwide. Accordingly, marine Gastropods are among the more significant biota to consider, when addressing the fundamental question of how various environmental stresses can more or less affect the species richness and the degree of internal structuration of tropical marine communities, at the *local* scale.

Now, the usually high diversity of marine gastropod communities – which precisely makes them especially attractive for such studies – inevitably leads to the need to address a methodological issue which cannot be ruled out: the difficulty and often the virtual impossibility to complete samplings so as to reach (or at least to closely approach) exhaustive inventories. And this, in turn, can result in severely unreliable inferences, since sampling incompleteness not only delivers undetermined underestimates of the true species richness but also hampers any comprehensive and unbiased approach to the hierarchical structuration of species abundances within communities [6-9]. Hence, the necessity to implement a reliable procedure of *numerical extrapolation* of partial sampling [10] able to provide estimates with minimised bias of (i) the number of the still unrecorded species and (ii) the distribution of abundance of these

unrecorded species. This is all the more important that rare species that often escape recording in practice may yet disproportionately contribute to the functional structuring of communities in the wild [11-16].

A recently developed procedure of numerical extrapolation takes into account these needs, aiming to provide *relevant* and *comprehensive* inferences regarding both the true (total) species richness and the full range of species abundance distribution, in spite of having to rely only on *incomplete* inventories.

In particular, this invites to revisit the already available reported data based upon non-extrapolated partial inventories and to critically reconsider the as-derived interpretations. The purpose being to tentatively establish more relevant interpretations, based on *numerically extrapolated* – and thus numerically completed – samplings. More specifically, once properly numerically completed (and *only* when it is so: [8]), the distribution of species abundances can provide synthetic data, in both qualitative and quantitative terms, about the underlying process that drives the hierarchical structuring of species abundances within community [17-21].

Hereafter, I address the true level of species richness and the internal structuration of three marine gastropod communities exposed to various levels of environmental stresses along the southern coast of Suva Island (Fiji Archipelago). In particular, I examine how the consequences of growing environmental stresses – especially increasing levels of pollution – are shared among gastropod species according to (i) their original respective abundance and (ii) their feeding mode (primary or secondary consumers). These analysis are based on the partial inventories of three communities, each of these partial inventories being first submitted to the procedure of *least-biased* numerical extrapolation.

## 2. MATERIALS AND METHODS

### 2.1 The Reported Field Data

The three communities of shell-bearing gastropods on which is based this study, were partially sampled from three selected habitats along Nassese shore, south east of Suva (Fiji Archipelago) with the collected field data reported by Suratissa and Rathnayake [22]. According to these authors, these habitats differ sharply by their degree of exposition to anthropogenic sources of pollution with habitat H4, H1 and H2 respectively exposed to “low”, “medium” and “strong” pollution levels. Besides, the underwater substrata itself also differ between habitats, with H4 having rocky and coral substrate, H1 having mixed rocky, sandy and muddy substrate and H2 having sandy and muddy substrate. According to Suratissa and Rathnayake, the strong gradient of pollution between the three habitats, however, plays the major role on the recorded differences between them. Additional details on localisation and sampling procedure are given in [22].

The number  $N_0$  of collected individuals and the number  $R_0$  of recorded species in each community are recalled in Table 1. The subsistence of numerous singletons (species recorded only once), especially in the samplings of habitats H4 and H1, predicts substantial levels of sampling incompleteness – indeed a rather common situation in practice, as already underlined. Yet, as the species lists reported by the authors also include the respective abundances of the recorded species, the corresponding data was appropriate to implement the procedure of numerical extrapolation.

### 2.2 The Numerical Extrapolation Procedure and Its Exploitation

#### 2.2.1 Implementation of the procedure of numerical extrapolation

\* *Total species richness*: the least-biased estimation of the number of still undetected species during partial sampling and the resulting estimation of the total species richness of the partially sampled community are derived according to the procedure defined in [23-24] and briefly summarised in Appendix 1, on the basis of the numbers  $f_x$  of species observed  $x$ -times during partial sampling. The same procedure

allows to derive the least-biased extrapolation of the “Species Accumulation Curve”, which predicts the expected increase of the number of newly recorded species,  $R(N)$ , as a function of growing sampling size  $N$  (Appendix 1). In practice, this extrapolation allows to forecast the likely additional sampling efforts that would be required to obtain any desirable increment in sampling completeness.

\* *Species Abundance Distribution*: as mentioned above, the Species Abundance Distribution (“S.A.D.”) is intended to provide the basic data necessary (i) to describe the *pattern* of structuration of species abundances within community and (ii) to qualify and quantify the underlying *process* that drives this structuration. Yet, to accurately exploit its full potential [25-26], the “S.A.D.” requires:

- first, to be *corrected* for bias resulting from drawing stochasticity, liable to the finite size of samplings,
- 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, as is the case here.

The appropriate procedure of correction and, subsequently, of least-biased numerical extrapolation of the as-recorded partial “S.A.D.” is described in details in [26] and briefly summarised in Appendix 2. Also, a concrete example of implementation of the procedure is commented in details in [27].

Classically, the “S.A.D.” is graphically presented according to the so-called “Ranked Abundance Distribution” (also known as “Whittaker plot”), according to which the (log-transformed) abundances  $a_i$  are plotted against the rank  $i$  of species ordered by decreasing values of abundance (with, thus,  $a_1$  and  $a_{St}$  respectively standing for the highest and the lowest abundances in a community of  $S_i$  species).

#### 2.2.2 Description of the pattern of species abundance structuration

The “S.A.D.” (exhaustive or, else, completed by numerical extrapolation) conveys all the relevant quantitative data required to address the internal organisation among species within a local community, especially the hierarchical structuration of abundances (i.e. the differential allocation of relative abundances among all the member-species of the community). In particular,

it is always advisable to use such species-abundance plots to study evenness or unevenness [28]. Optionally, the “S.A.D.” may be synthetically reduced to its two major descriptors: the *total species richness*  $S_t$  and the *degree of unevenness*,  $U$ , of the abundance distribution (note that, following [29], the degree of *unevenness* – rather than evenness itself – should be the preferred way to address the hierarchical structuring of species abundances in communities).

According to the aforementioned, classical mode of representation of “S.A.D.”, it goes natural to quantify the degree of abundance unevenness,  $U$ , as the average slope of the abundance decrease along the whole range of the abundance distribution, as already proposed by [30], that is:

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

### 2.2.3 Qualification of the underlying structuring process: Type and intensity

Beyond the mere description of the pattern of hierarchical structuration, quantified by the degree of unevenness  $U$ , the complete “S.A.D.” can help addressing several important questions regarding the genuine *intensity* and the *type of underlying mechanism* driving the process that rules the hierarchical structuration of abundances within community.

As regards the *type* of structuring process involved, it is appropriate to distinguish between two major alternative hypotheses: schematically, the hierarchical structuration of abundances may result either (i) from the major contribution of one dominant factor or (ii) from the combined contributions of many mutually independent factors acting 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 [17,31-34].

Now, as regards the *intensity* of the structuring process, it is first necessary to remind that the degree of unevenness  $U$  is inadequate in this particular respect, due to its additional mathematical dependence upon the species richness  $S_t$  [35-36]; see also Appendix 3. This mathematical dependence ultimately results in masking the *genuine* – i.e. biologically significant – intensity of the structuring process itself [19,20,37]. To get rid of this dependence, it has

been shown appropriate to cancel its influence by comparing the actual “S.A.D.” to the corresponding “broken-stick” distribution [38], computed for the same species richness  $S_t$  [26,27,39,40]. Accordingly, the genuine intensity, “ $I_{str}$ ”, of the hierarchical structuring process is relevantly defined by standardising the degree of unevenness  $U$  of the “S.A.D.” to the degree of unevenness  $U'$  of the corresponding “broken-stick” distribution, computed for the same species richness  $S_t$ , that is:

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

that is:

$$I_{str} = \log(a_1/a_{S_t}) / \log(a'_1/a'_{S_t}) \quad (2)$$

with  $a_1$  and  $a_{S_t}$  standing for the highest and the lowest abundances in the studied community and  $a'_1$  and  $a'_{S_t}$  standing for the highest and the lowest abundances in the corresponding “broken-stick” distribution (the abundances being classically log-transformed).

Thus defined, freed from the purely mathematical influence of species richness, the index  $I_{str}$  accounts for those biological factors only that contribute to the hierarchical structuring of species abundances within community.

Note, at last, that the methodological approach above may be applied, as well, to any subsets of interest, for example to each of the feeding guilds that may co-occur in the community.

## 3. RESULTS

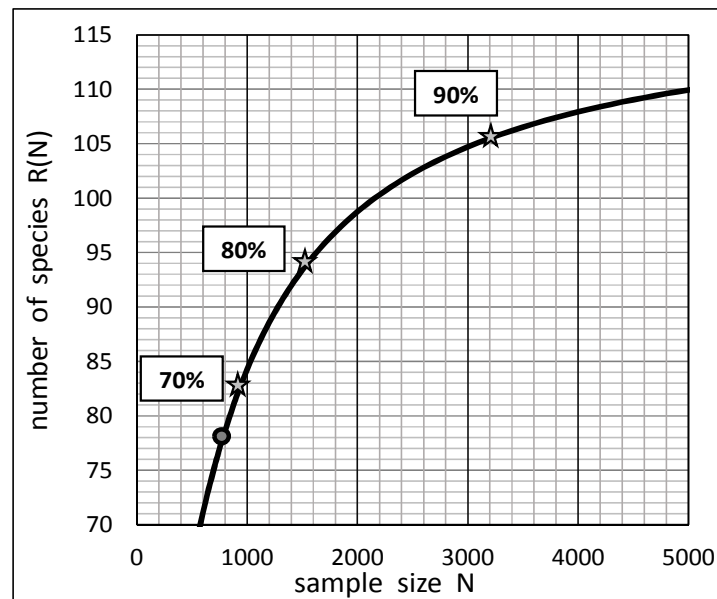
### 3.1 Estimated Total Species Richness of Each Community

The three marine gastropod communities have strikingly different true total species richness  $S_t$ , in compliance with what could be expected from the increasing environmental stresses from H4 to H1 and H2: Table 1. Note that the recorded species richness  $R_0$  underestimates the true species richness  $S_t$  not only in absolute but even in relative values, as the degree of incompleteness substantially differs between the three samplings (Table 1).

Considering the large set of unrecorded species, especially for the community H4, further sampling might be considered of interest. In this perspective, the least-biased extrapolation of the

**Table 1.** The number of collected individuals  $N_0$ , the number of recorded species  $R_0$ , the type of nonparametric estimator (Jackknife) selected as being the least-biased one, the estimated number  $\Delta$  of unrecorded species, the resulting estimate of the “true” total species richness  $S_t$  ( $= R_0 + \Delta$ ), the resulting estimated level of sampling completeness  $R_0/S_t$ . Estimations are computed according to the least-biased procedure [23], the selection key is provided in Appendix 2.

Habitat	H4	H1	H2
nb. collected individuals $N_0$	780	116	102
nb. recorded species $R_0$	78	16	13
least-biased estimator	JK-3	JK-5	JK-1
nb. unrecorded species $\Delta$	39	6	1,2
<b>total species richness <math>S_t</math></b>	<b>117</b>	<b>22</b>	<b>14,2</b>
sample completeness $R_0/S_t$	67%	72%	91%



**Fig. 1.** 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 ( $N_0 = 780$ ,  $R_0 = R(N_0) = 78$ , sampling completeness 67%). In practice, this extrapolation highlights the expected additional sampling effort required to reach higher levels of sampling completeness (for example, the sample sizes required to reach 70%, 80% and 90% completeness would be around  $N = 900$ ,  $1500$ ,  $3200$  respectively).

Species Accumulation Curve (Fig. 1) can help to forecast which additional sampling effort would be necessary to achieve any desirable increase in sampling completeness.

### 3.2 Completed Species Abundance Distribution for Each Community

Figs. 2, 3, 4, provide the graphical representations of the Species Abundance Distribution (“S.A.D.”) for each of the three communities under study. These “S.A.D.s” have been (i) bias-corrected and then (ii) numerically

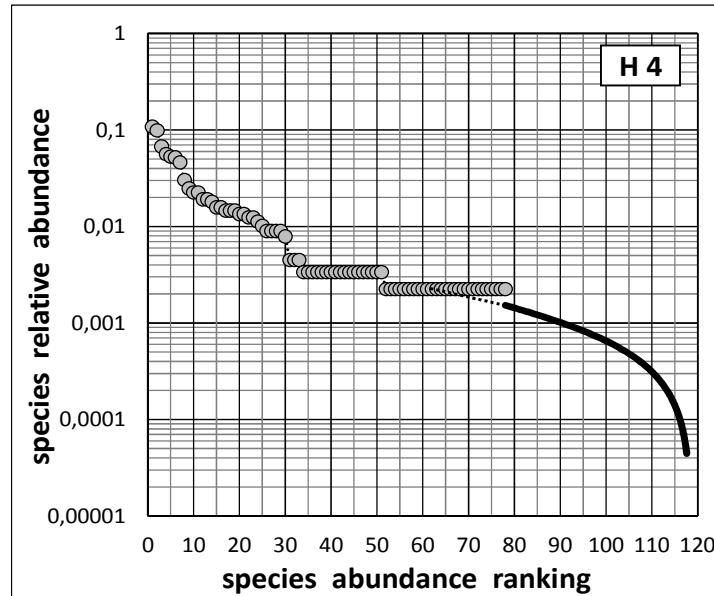
extrapolated according to the procedure reported in [26]: see Appendix 2, equations (A2.1) and (A2.2) respectively.

According to the usual convention of graphical representation for S.A.D.s:

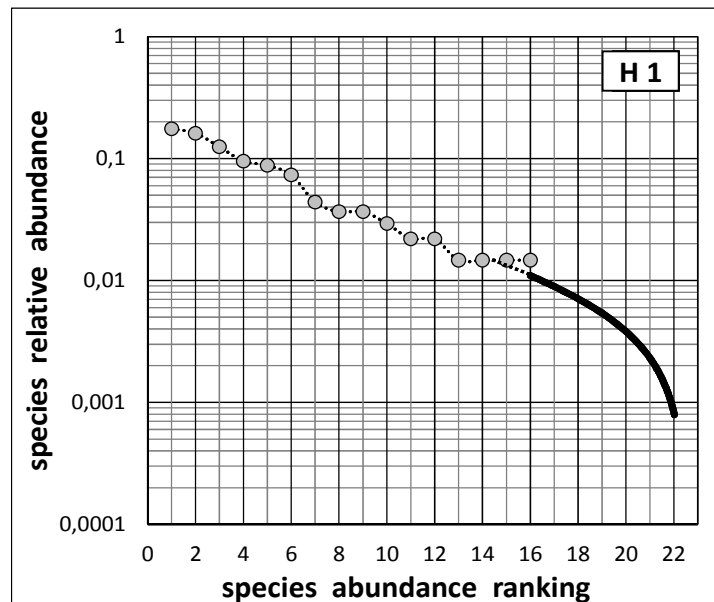
- along the abscissa, the member-species are ranked by decreasing values of their respective abundances (relative abundance ‘ $a_i$ ’ for the species of rank ‘ $i$ ’);
- along the ordinate, the relative abundances are plotted according to a logarithmic scale

( $\log_{10}$ ) (although, for specific purpose, an ordinary untransformed scale may be adopted, as suggested by [38]).

The abundances of the *recorded* species are plotted as grey circles, while the *extrapolated* part of the abundance distribution is plotted as a thick solid line.



**Fig. 2.** The bias-corrected and numerically extrapolated species abundance distribution (“S.A.D.”) for the marine gastropod community H4. *Grey circles*: recorded part of the “S.A.D.” after correction for bias. *Solid line*: least-biased extrapolation of the abundance distribution for the set of species remaining unrecorded (sampling completeness: 67%).



**Fig. 3.** The bias-corrected and numerically extrapolated species abundance distribution (“S.A.D.”) for the marine gastropod community H1. *Grey circles*: recorded part of the “S.A.D.” after correction for bias. *Solid line*: least-biased extrapolation of abundance distribution for the set of species remaining unrecorded (sampling completeness: 72%).

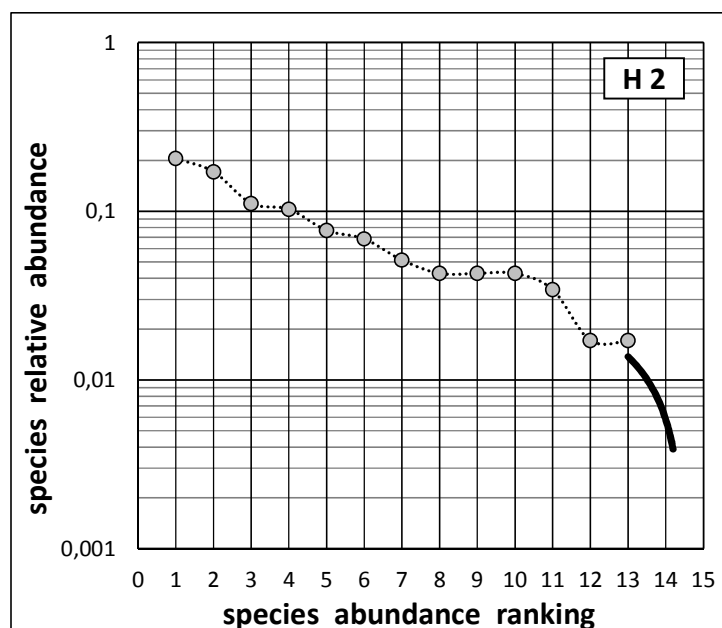


Fig. 4. The bias-corrected and numerically extrapolated species abundance distribution ("S.A.D.") for the marine gastropod community H2. Grey circles: recorded part of the "S.A.D." after correction for bias. Solid line: least-biased extrapolation of abundance distribution for the set of species remaining unrecorded (sampling completeness: 91%).



*Harpa amouretta* Röding 1798, one of rarest species at Suva © lesgrandesimprimeries.com



### 3.3 Testing for the Type of Process Involved in the Structuring of Species Abundances

In Figs. 5, 6, 7, the “S.A.D.” of each community is compared to the corresponding “log-series” and to the corresponding “log-normal” models, computed for the same species richness. As

mentioned in Methods section, these comparisons allow to infer which kind of process is more likely to be involved in the hierarchical structuration of species abundances. For all three communities, the species abundance distributions clearly fit best the “log-normal” model than the “log-series” model.

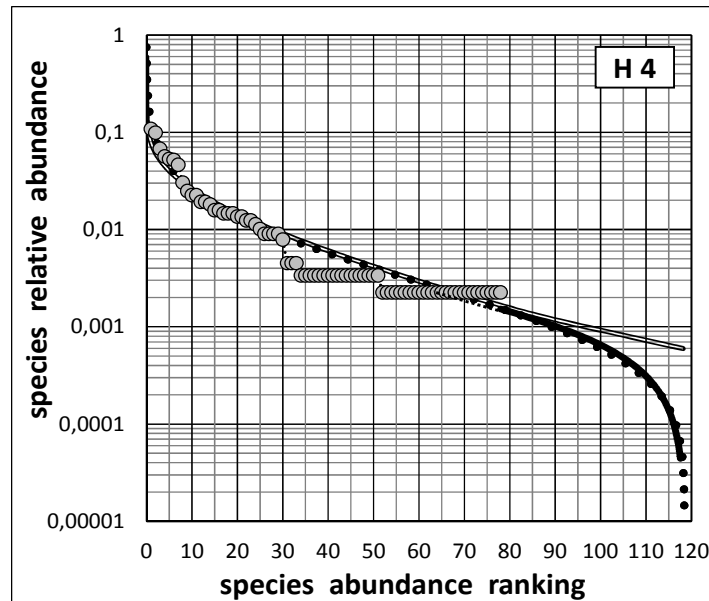


Fig. 5. Two classical models: “log-normal” (coarse dotted line) and “log-series” (double line) fitted to the Species Abundance Distribution of community H4 (corrected and extrapolated cf. Fig. 2). Best fit is with “log-normal” distribution.

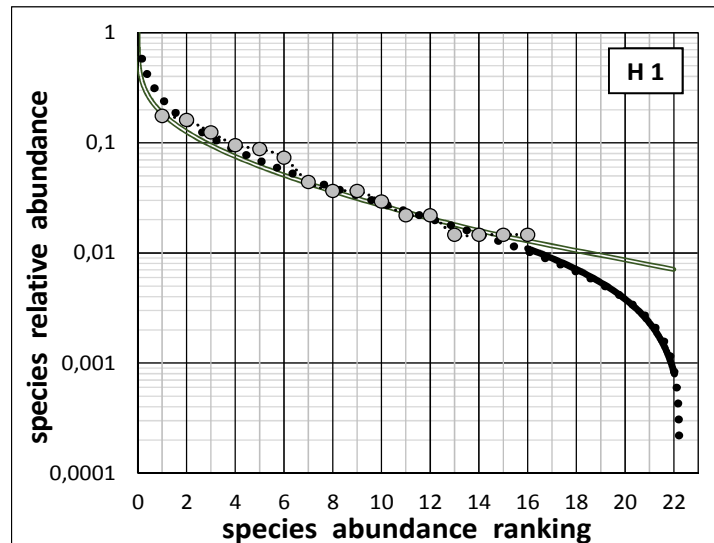


Fig. 6. Two classical models: “log-normal” (coarse dotted line) and “log-series” (double line) fitted to the Species Abundance Distribution of community H1 (corrected and extrapolated cf. Fig. 3). Best fit is with “log-normal” distribution.

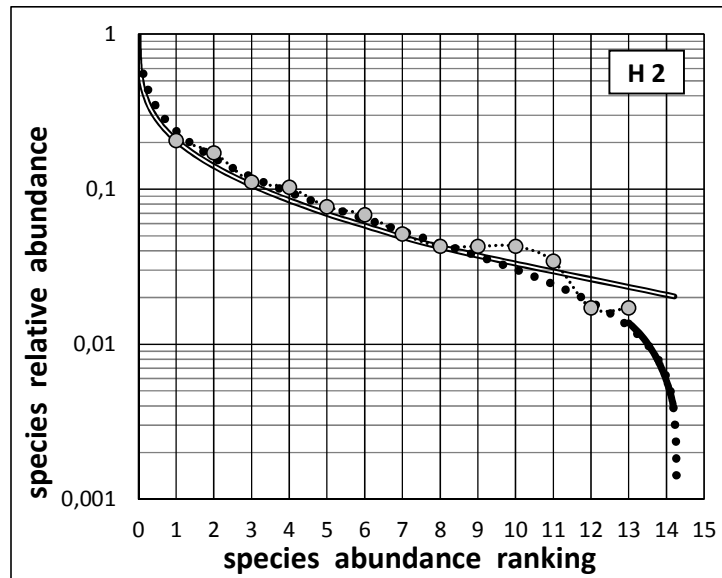
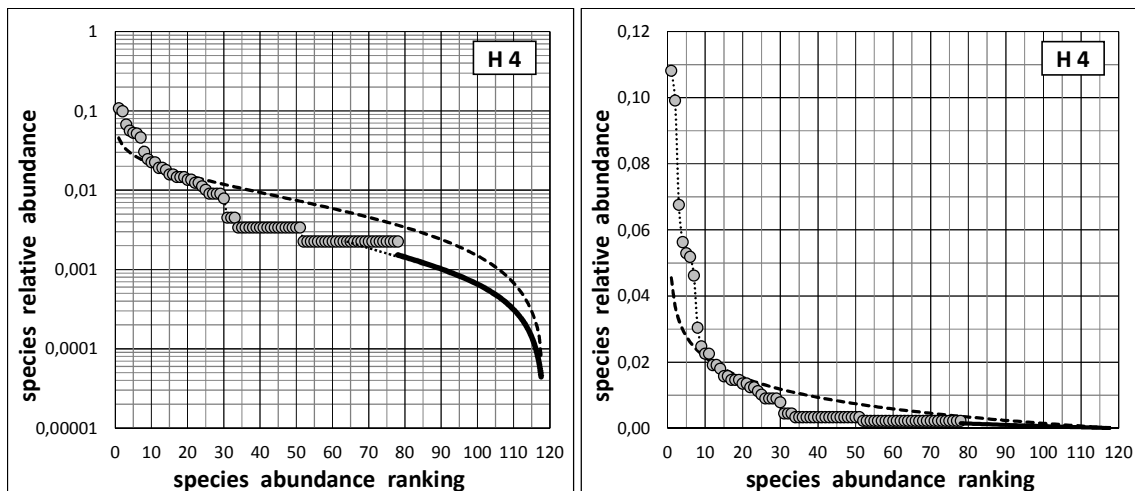


Fig. 7. Two classical models: “log-normal” (coarse dotted line) and “log-series” (double line) fitted to the Species Abundance Distribution of community H2 (corrected and extrapolated cf. Fig. 4). Best fit is with “log-normal” distribution.

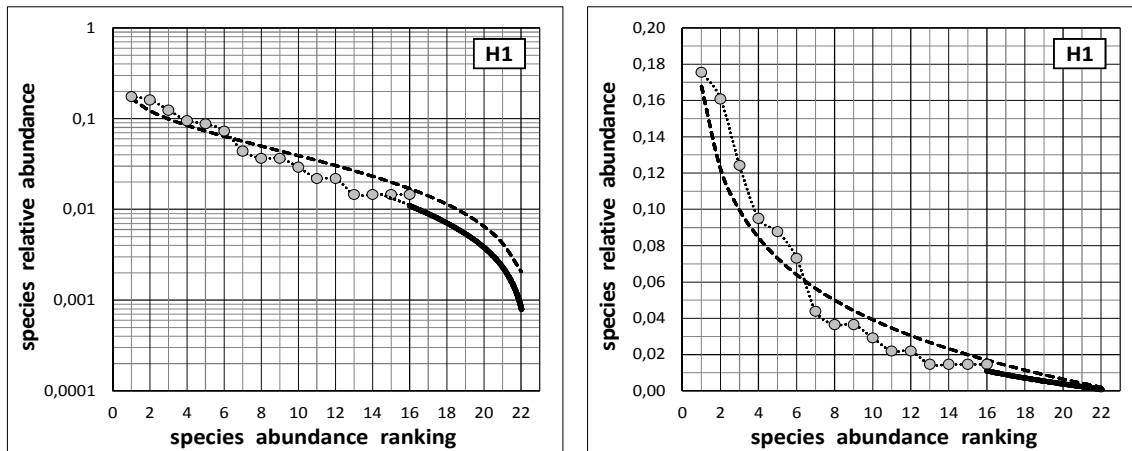
### 3.4 Beyond the Apparent Unevenness of Species Abundances: The Genuine Intensity of the Hierarchical Structuring Process

As emphasised in Methods section, the genuine intensity of the process driving the hierarchical

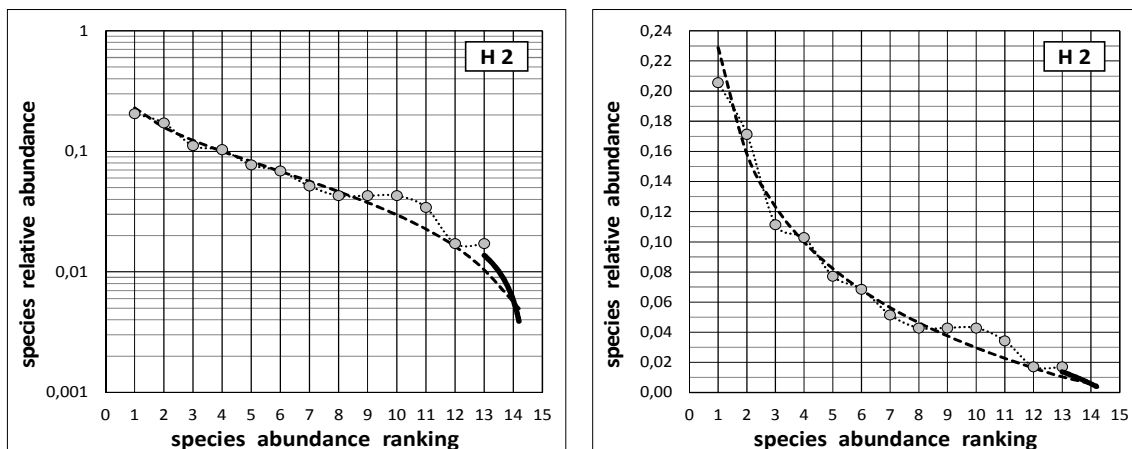
structuration of abundances is relevantly appreciated by comparing the “S.A.D.” of the studied community to the corresponding “broken-stick” model computed for the same species richness. Figs. 8 to 13 provide such comparisons.



Figs. 8 & 9– Comparison between the bias-corrected and numerically extrapolated “S.A.D.” for the community at habitat H4 (grey circles and solid line) and the corresponding “broken-stick” model (dashed line) – ordinate with *logarithmic* scale: Fig. 8; ordinate with *arithmetic* scale : Fig. 9.



**Figs. 10 & 11– Comparison between the bias-corrected and numerically extrapolated “S.A.D.” for the community at habitat H1 (grey circles and solid line) and the corresponding “broken-stick” model (dashed line) – ordinate with *logarithmic* scale: Fig. 10; ordinate with *arithmetic* scale : Fig. 11.**



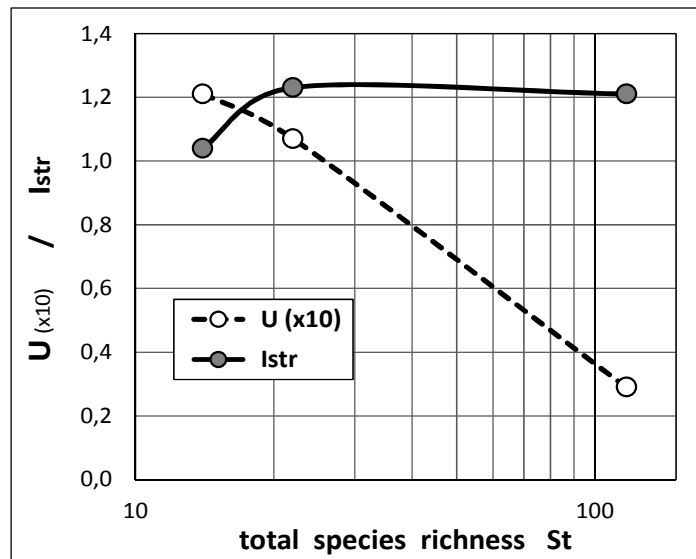
**Figs. 12 & 13– Comparison between the bias-corrected and numerically extrapolated “S.A.D.” for the community at habitat H2 (grey circles and solid line) and the corresponding “broken-stick” model (dashed line) – ordinate with *logarithmic* scale: Fig. 12; ordinate with *arithmetic* scale: Fig. 13.**

These results are summarised more synthetically in Table 2 which highlights the variations of (i) the true total species richness  $S_t$ , (ii) the ratio  $a_1/a_{St}$  between the abundances of the commonest and the rarest species, (iii) the degree of unevenness of species abundances  $U$  (defined by equation (1)) and, finally, (iv) the genuine intensity  $I_{str}$  of the process driving the hierarchical structuration of species abundances (defined by equation (2)). The parameters  $U$  and  $I_{str}$  respectively quantify (i) the apparent *pattern* of species abundance structuration and (ii) the genuine intensity of the underlying *process* driving this structuration.

The main trends derived from these results are graphically highlighted in Fig. 14, where both the apparent unevenness  $U$  and the genuine intensity of the structuring process  $I_{str}$  are plotted together against the species richness  $S_t$ , for each three communities. While the intensity of the structuring process remains approximately unchanged along the range of variation of species richness  $S_t$ , the degree of unevenness  $U$ , on the contrary, consistently decreases with  $S_t$ . This striking discrepancy between the *process* (its genuine intensity  $I_{str}$ ) and the corresponding *pattern* (apparent unevenness  $U$ ) is entirely due to the already underlined negative mathematical dependence of  $U$  upon  $S_t$ .

**Table 2. A synthetic summary of the main quantitative features of the hierarchical organisation of species abundances within community, as derived from each numerically completed “S.A.D.” : (i) the total species richness  $S_t$  of the community ; (ii) the relative abundances  $a_1$  and  $a_{St}$  of the most and least abundant species (species rank 1 and  $S_t$ ) ; (iii) the unevenness of abundances of the community:  $U = \log(a_1/a_{St})/(S_t-1)$ ; (iv) the unevenness of abundances of the corresponding “broken-stick” distribution:  $U' = \log(a'_1/a'_{St})/(S_t-1)$  and, at last, (v) the genuine intensity of the structuring process  $I_{str} = U/U'$**

	$S_t$	$a_1$	$a_{St}$	$a_1/a_{St}$	$U$	$U'$	$I_{str}$
H4	117	0.10817	0.000044	2458	0.0288	0.0238	1.21
H1	22	0.17555	0.00079	222	0.107	0.087	1.23
H2	14	0.20563	0.00389	53	0.121	0.117	1.03



**Fig. 14. The degree  $U$  of unevenness of species abundances (*dashed line*) and the intensity  $I_{str}$  of the underlying structuring process (*solid line*) plotted against the total species richness  $S_t$ , for the three studied communities. Unevenness  $U$  decreases with increasing species richness while the genuine intensity of the structuring process  $I_{str}$  remains approximately unchanged: comments in text. *Note that for commodity of graphical comparison between  $U$  and  $I_{str}$ , the values of  $U$  are uniformly multiplied by a same factor 10.***

### 3.5 Species Richness and the Hierarchical structuring of species Abundances in Each Feeding Guild Considered Separately

Two feeding guilds usually coexist among marine gastropods: *primary* consumers (“herbivores”) and *secondary* consumers (“carnivores”). The numerical extrapolation procedure, applied above to each community as a whole (both feeding guilds together) may be implemented as well for each feeding guild *separately*.

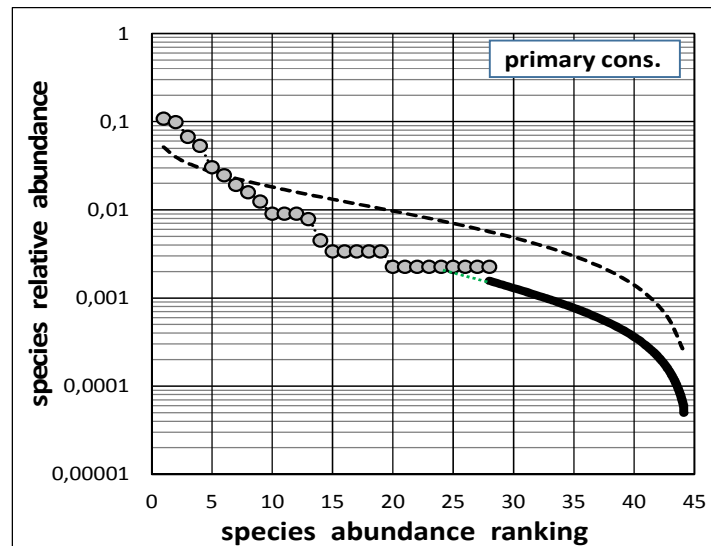
The respective contributions of each feeding guild – in terms of both the total species richness

and the cumulated number of individuals per guild – are derived accordingly for the community of habitat H4 (by far the richest community): Table 3. The guild of *secondary* consumers is almost twice more species-rich than is the guild of *primary* consumers. Yet, the cumulated number of individuals does not substantially differ between the primary and the secondary consumers.

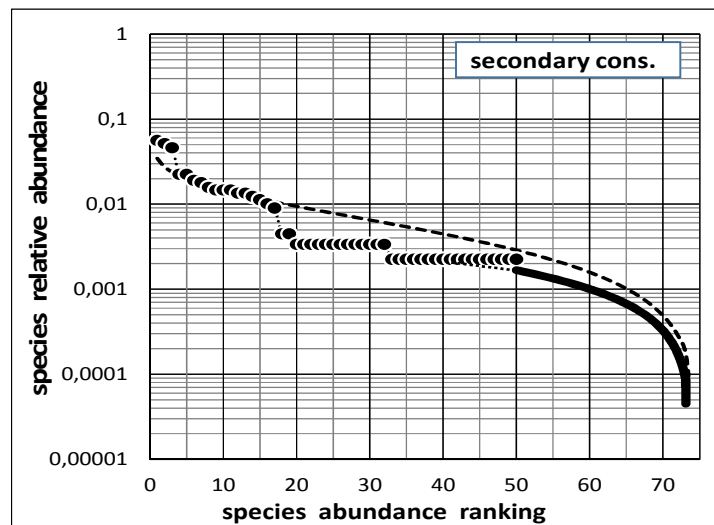
In more details, the Species Abundance Distributions of each feeding guild in the community of habitat H4 are jointly provided in Figs. 15, 16, 17.

**Table 3. Respective contributions of each feeding guild (primary and secondary consumers): (i) to the recorded and the total species richness and (ii) to the cumulated numbers of individuals in community H4**

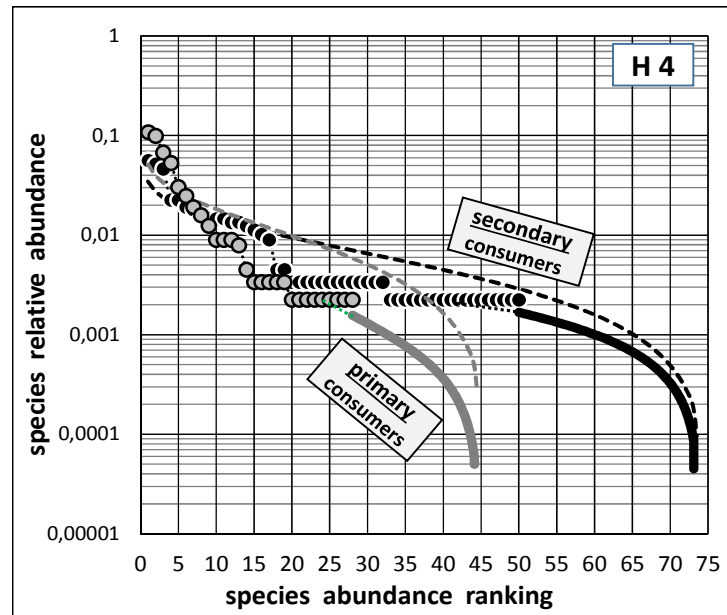
Community H4	Primary	Secondary
nb. recorded indiv. $N_0$	358	422
nb. recorded species $R_0$	28	50
nb. unrecorded species $\Delta$	16	23
<b>total species richness <math>S_t</math></b>	<b>44</b>	<b>73</b>
<b>contrib. to sp. richness %</b>	<b>38 %</b>	<b>62 %</b>
<b>contrib. to nb. individ. %</b>	<b>54 %</b>	<b>46 %</b>



**Fig. 15. The bias-corrected and extrapolated “S.A.D.” for the guild of *primary* consumers (“herbivores”) in the marine gastropod community established in habitat H4; dashed line: the corresponding “broken stick” model.**



**Fig. 16. The bias-corrected and extrapolated “S.A.D.” for the guild of *secondary* consumers (“carnivores”) in the marine gastropod community established in habitat H4; dashed line: the corresponding “broken stick” model.**



**Fig. 17. Superposition of Figures 15 & 16, for easy comparison. The distribution of species abundances is markedly more uneven (steeper slope of abundance decrease) among *primary* consumers than it is among *secondary* consumers. Also, the intensity of the structuring process  $I_{str}$  (mirrored by the difference of steepness between the S.A.D. and the corresponding “broken stick” model) is greater for *primary* consumers than for *secondary* consumers.**

These abundance distributions are strikingly different, with a strongly steeper slope of the “S.A.D.” for *primary* consumers than for *secondary* consumers. The distribution of species abundances among *primary* consumers appears thus far more uneven than it is among *secondary* consumers. This striking difference between the two feeding guilds still remains obvious when the slope of each species abundance distribution is compared to the slope of the corresponding “broken-stick” model (computed for the same species richness : dashed lines in Figs. 15, 16, 17). This means that not only the apparent unevenness  $U$  (as a *descriptive* parameter), but also the intensity  $I_{str}$  of the underlying process driving the hierarchical structuration of abundances (as a *functional* parameter) are stronger for *primary* consumers, as compared to *secondary* consumers.  $U = 0.078$  and  $I_{str} = 1.46$  for *primary* consumers against  $U = 0.043$  and  $I_{str} = 1.21$  only for *secondary* consumers. The difference between the two feeding guilds is less pronounced, however, for  $I_{str}$  than for  $U$  because the apparent unevenness  $U$  accounts not only for the intensity  $I_{str}$  of the structuring process but also mathematically depends negatively upon species richness, as aforementioned.

Fig. 18 provides a complementary focus on the compared distributions of species abundances between primary and secondary consumers in community H4. The three dominant species in the community as a whole are all *primary* consumers: *Cerithium coralium* Kiener 1841, *Strombus urceus* Linnaeus 1758, *Ophicardelus ornatus* Ferrusac 1841, while the most abundant secondary consumer, *Natica colliciei* Récluz 1844 is hardly half as abundant as *Cerithium coralium* and immediately followed by the fourth primary consumer, *Rhinoclavis aspera* Linnaeus 1758.

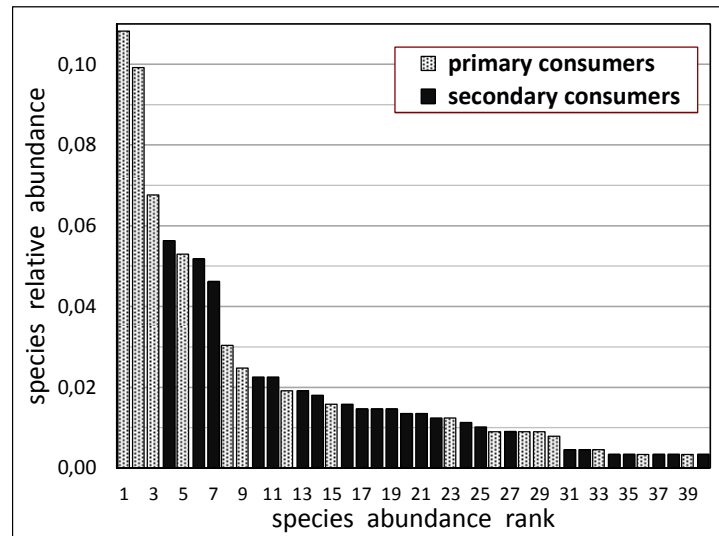
At last, Figs. 19 and 20 summarise graphically the preceding results, highlighting the trend for *primary* consumers to have lower species richness  $S_t$ , higher abundance unevenness  $U$  and stronger intensity of structuring process  $I_{str}$  than *secondary* consumers. A trend already reported for two other marine gastropods communities located in Bengal Sea (Andaman and Mannar Gulf), although these communities are very distant from the Fiji's, both geographically and taxonomically [27,40].



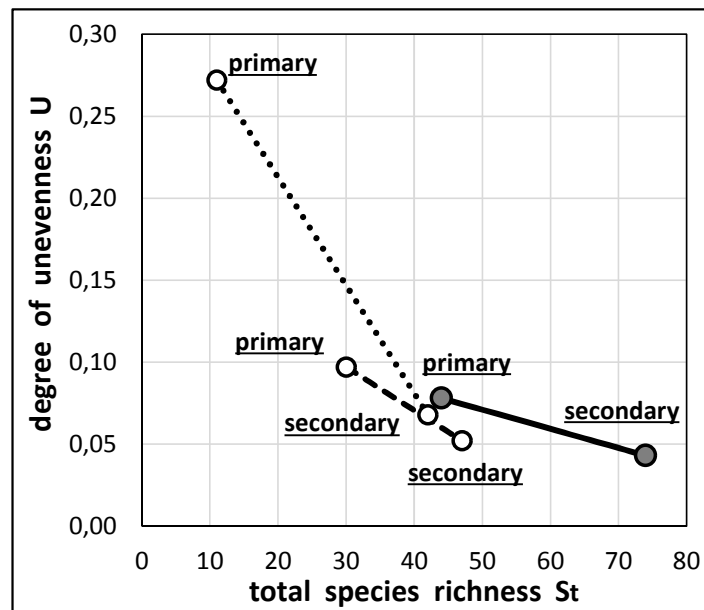
*Cerithium coralium* Kiener 1841 (typical shell length  $\approx$  30 mm) © H. Zell



*Strombus urceus* Linnaeus 1758 (typical shell length  $\approx$  50 mm) © H. Zell



**Fig. 18.** The Species Abundance Distribution for the 42 already detected species in community H4, highlighting the feeding mode of each species. Note the arithmetic (instead of log-transformed) scale for abundances. Directly derived from Figures 15 & 16. The pattern here is remarkably similar to what has been already reported for a marine Gastropod community at Andaman Islands (see [27]), although the two communities have almost no species in common, as expected from the large distance that separates the Andaman's and the Fiji's.



**Fig. 19.** The degree of unevenness  $U$  of species abundances plotted against the total species richness  $S_t$ , for (i) the marine snail community H4 at Fiji (*solid line*) and (ii) two distant marine snail communities at Mannar Gulf (*dotted line*, [40]) and Andaman Islands (*dashed line*, [27]). The trend for primary consumers to have lower species richness  $S_t$  and stronger unevenness  $U$  as compared to secondary consumers is common to all three communities although they share almost no species in common.



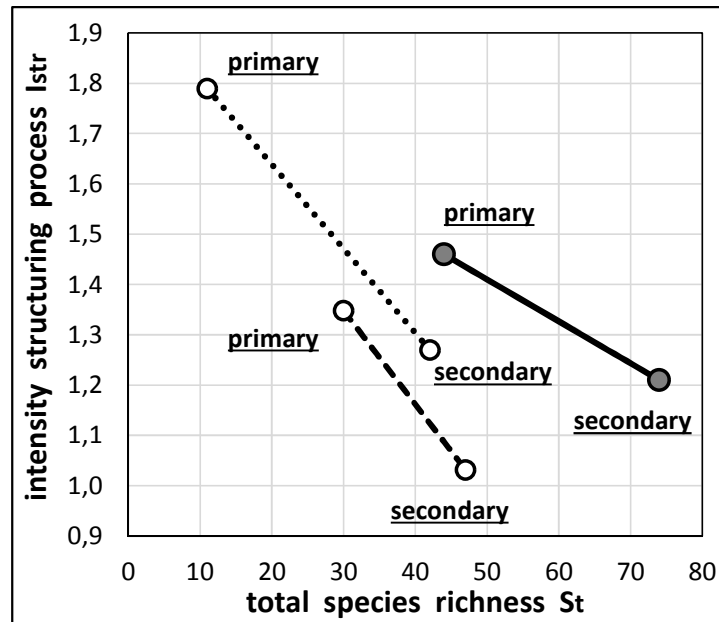


Fig. 20. The intensity  $I_{str}$  of the structuring process plotted against the total species richness  $S_t$ , for (i) the marine snail community H4 at Fiji (solid line) and (ii) two distant marine snail communities at Mannar Gulf (dotted line, [40]) and Andaman Islands (dashed line, [27]). The trend for primary consumers to have lower species richness and stronger intensity of the structuring process as compared to secondary consumers is common to all three communities although they share almost no species in common.

### 3.6 The Genus *Conus* Selected as Emblematic among Secondary Consumers

As advocated below in the Discussion section, the genus *Conus* deserves specific focus as being a major component of the set of *secondary* feeders considered above.

The distribution of species abundances among *Conus* species also requires numerical extrapolation because one third of the recorded species remain as singletons and, indeed,

numerical extrapolation reveals an estimated sampling completeness equal to 79% only. Fig. 21 provides the bias-corrected and extrapolated "S.A.D." for the assemblage of *Conus* species (estimated species richness  $S_t = 20.3$ ) within the community H4, together with the corresponding "broken-stick" model serving as a reference to quantify the intensity  $I_{str}$  of the structuring process. Fig. 23 positions the "S.A.D." for the subset of *Conus* species in the context of the entire guild of secondary consumers, from which it is extracted. Table 4 summarises the quantitative data issued from Figs. 21 & 23.

Table 4. The position of the assemblage of *Conus* species within the *whole* guild of secondary consumers in community H4: the number  $N_0$  of recorded individuals, the number  $R_0$  of recorded species, the true species richness  $S_t$ , the corresponding sampling completeness  $C\%$ , the apparent degree of unevenness  $U$  of species abundances and the genuine intensity of the underlying structuring process  $I_{str}$ . Note that the apparent unevenness and the genuine structuring intensity are varying in opposite direction: a pseudo-paradox once again due to the negative mathematical dependence of unevenness  $U$  on species richness  $S_t$ .

Community H4	$N_0$	$R_0$	$S_t$	$C\%$	$U$ (x100)	$I_{str}$
the <i>Conus</i> subset	49	16	20.3	79%	9.2	0.95
the <i>whole</i> second. guild	780	50	73	68%	4.3	1.21

The assemblage of *Conus* comprises an estimated 20 species out of the 73 secondary consumers – that is about a quarter of the species richness of the whole guild of secondary consumers in H4. This is, yet, a little less than the figure of near one third (16 out of 50) obtained from the recorded data. This difference stems from the fact that the *Conus* subset had been slightly better sampled than the entire guild of secondary consumers (completeness 79% against 68%). This, in turn, results from the rarest *Conus* species being six times less rare than is the rarest secondary consumer (relative abundances 0.0003 against 0.00005 respectively: see Fig. 23). In fact, the *Conus* subset occupies the middle of the range of species abundances for all secondary consumers, as highlighted from Fig. 23 and contrary to what would be deduced from the crude recorded data only: Fig. 24.

The apparent unevenness  $U$  of species abundances is more than twice higher in the *Conus* subset than in the whole guild of secondary consumers (Table 4), so that the abundance distribution of *Conus* species seems far more uneven than is the abundance distribution of the other secondary consumers. But, once again, relying upon crude evenness is misleading, due to the “parasitic” mathematical influence of species richness on apparent unevenness. In fact, on the contrary, the intensity  $I_{str}$  of the structuring process is slightly lower in the *Conus* subset. At last, comparing the “S.A.D.”

for the subset of *Conus* species to the corresponding “log-series” and “log-normal” models shows that the latter fits best: see Fig. 22.

Now, how sensitive is the genus *Conus* to environmental stresses, here mainly the anthropogenic increase in pollution level? Out of the 16 *Conus* species recorded in community H4, only one subsists among recorded species in community H1. Interestingly, this surviving species in community H1 is one the rarest in community H4 – *Conus nussatella* Linnaeus 1758 – while all other species, including the dominant ones, have been wiped out! Moreover, the number of recorded individuals in the genus *Conus* suffers a still stronger decrease, from 49 recorded individuals in community H4 down to one unique recorded individual in community H1. As a comparison, considering now the communities as a whole, the decrease in the number of recorded individuals is from 780 to 116 and, considering the subset of secondary consumers, from 422 to 63. That is, the reduction in the number of individuals is more than seven times still more drastic in the genus *Conus* than it is in the gastropod communities as a whole and, as well, in the subset of secondary consumers ( $\chi^2$  test with Yates correction for the difference between *Conus* and (i) communities as a whole or (ii) secondary consumers subsets:  $\chi^2 = 4.27$  and  $\chi^2 = 4.21$  respectively,  $p < 0.05$  in both cases).



*Conus ebraeus* Linnaeus 1758, most abundant species in H4 © Ph. Bourjon



*Conus nussatella* Linnaeus 1758, unique *Conus* sp. in H1 © H. Zell

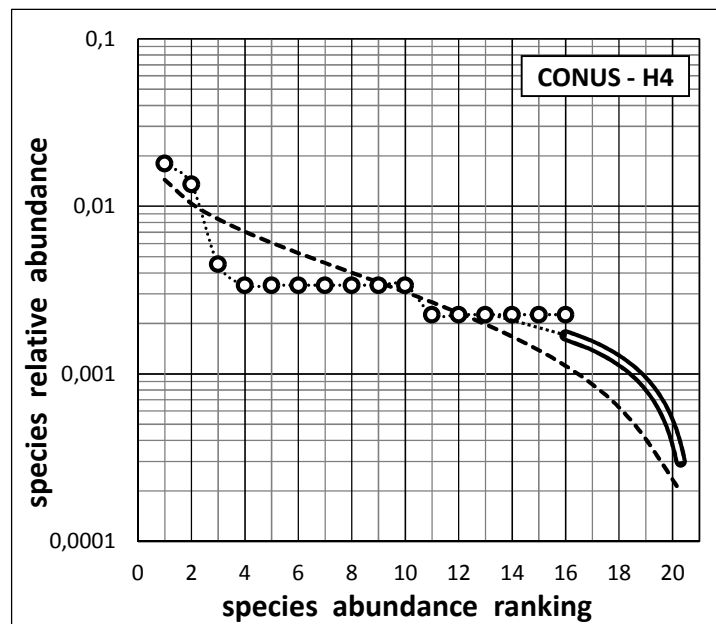


Fig. 21. The bias-corrected and numerically extrapolated “S.A.D.” for the assemblage of *Conus* species within the community in habitat H4 and the corresponding “broken-stick” model (dashed line). Estimated total species richness  $S_t = 20.3$  out of which  $R_0 = 16$  species were recorded.

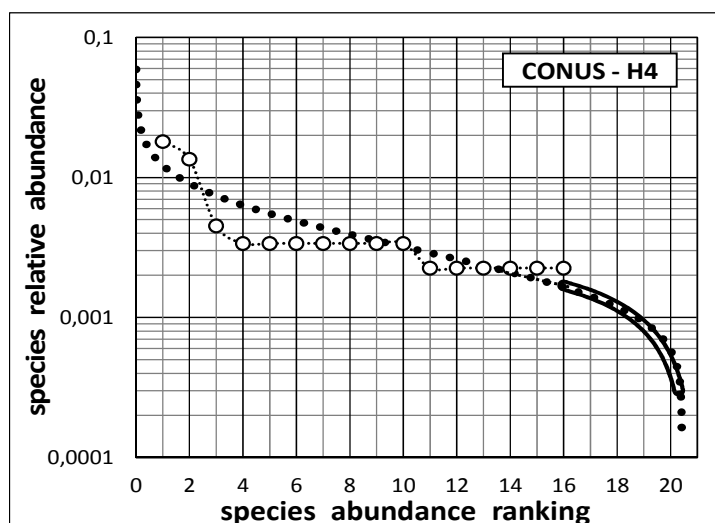


Fig. 22. The “log-normal” model (coarse dotted line) is best fitting the Species Abundance Distribution for the subset of *Conus* species, suggesting the combined influences of many independent factors in the process of hierarchical structuring of species abundances.

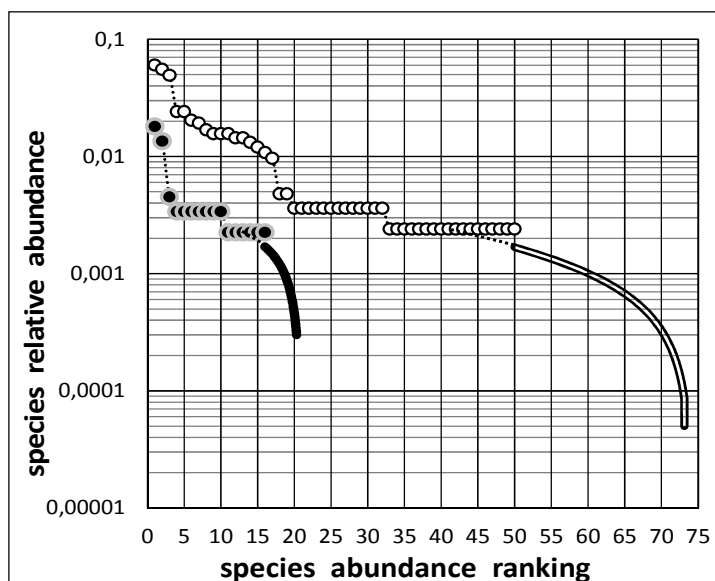


Fig. 23. The bias-corrected and numerically extrapolated “S.A.D.” for the assemblage of 20 *Conus* species within the community in habitat H4 (black figures) compared to the whole assemblage of 73 secondary consumers (white figures).

### 3.7 Deciphering the Consequences of Increasing Environmental Stresses on the Richness and the Degree of Structuring of Marine Gastropod Communities

Habitats H4 and H1 strikingly differ by the species richness of their respective gastropods

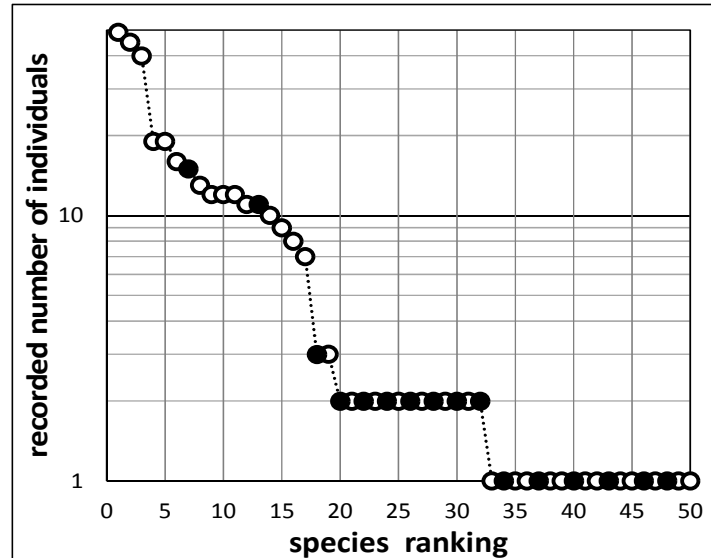
communities, the likely consequence of the substantial pejoration of environmental conditions in H1 as compared to H4, especially regarding anthropogenic pollution [22].

#### 3.7.1 General scope

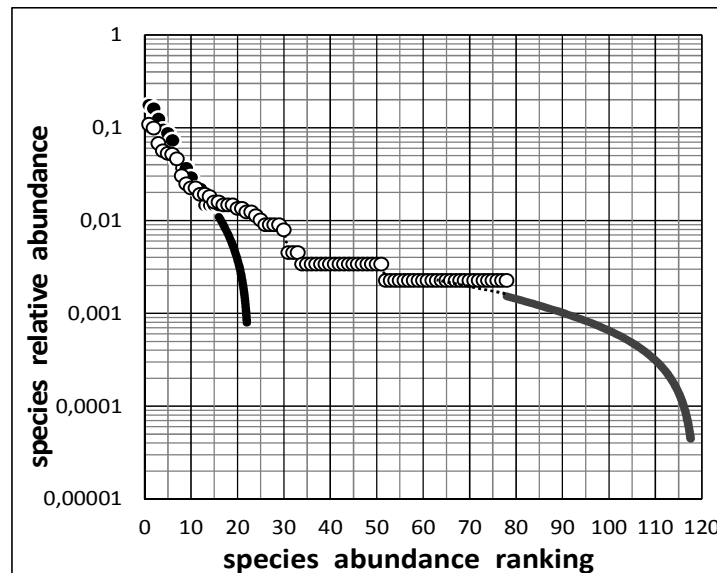
The species richness has dropped from 117 species in H4 down to 22 species in H1 (Tables

1 & 2). Compared to H4, the species richness in H1 is thus reduced by a factor of more than 5. Besides, the apparent unevenness  $U$  of species abundance distribution increases, by a factor 2.7

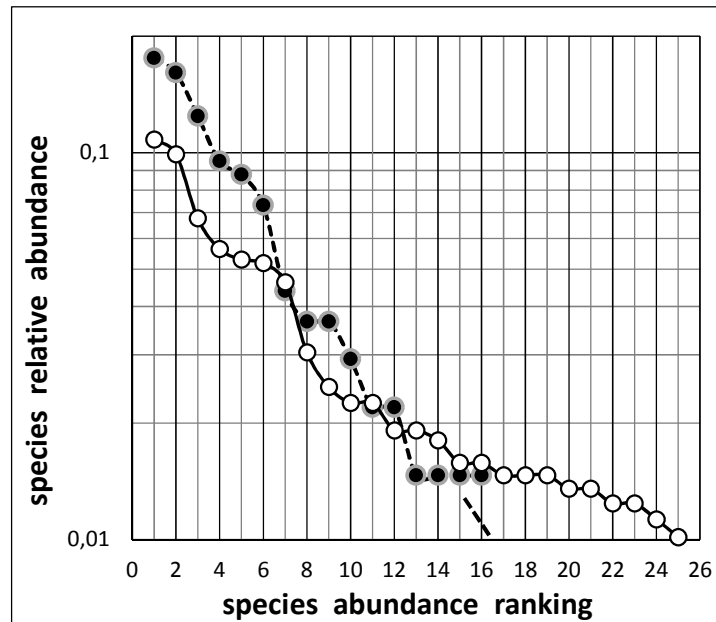
(0.107/0.0288, see Table 2 and Figs. 25 & 26). Yet the genuine intensity  $I_{str}$  of the hierarchical structuring process remains practically unchanged (1.21 against 1.23, see Table 2).



**Fig. 24.** The recorded numbers of individuals per species for the 50 secondary consumers recorded in the partial sampling of the community H4. *Black discs*: the 16 species belonging to the genus *Conus*. *White discs*: the 34 other secondary consumers. Based only on this recorded data, issued from the partial sampling of community H4, the subset of *Conus* species would erroneously be considered as mainly concentrated in the lower part of the range of abundances; which, yet, is not the case when the *whole range* of abundance distribution is considered, as shown in Figure 23.



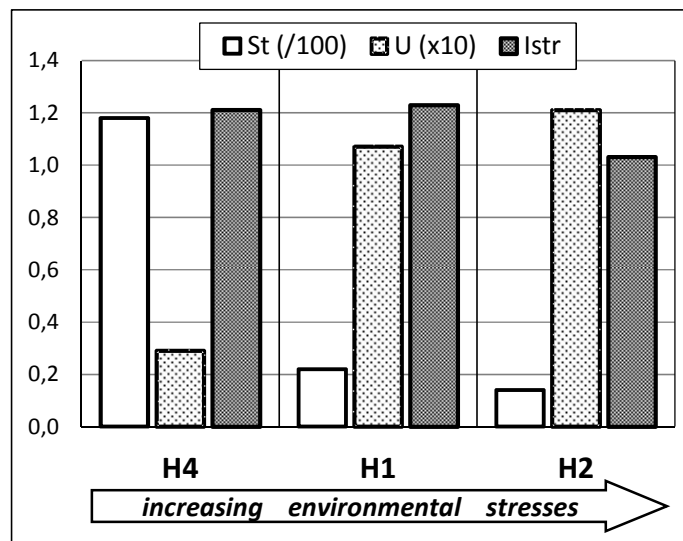
**Fig. 25.** Comparison between the bias-corrected and numerically extrapolated “S.A.D.s” for the marine gastropod communities established in habitat H4, with 117 co-occurring species (*white discs*) and habitat H1, with only 22 co-occurring species (*black discs*). Note the strikingly steeper slope of the “S.A.D.” of abundance distribution for H1, as compared to H4.



**Fig. 26. A zoom of Figure 25, with an enlarged focus on the beginning of “S.A.D.s”. Habitat H4: white discs; habitat H1: black discs.**

Fig. 27 summarises the preceding results obtained for communities H4 and H1 and furthermore includes the community H2 which undergoes still stronger environmental stresses, especially regarding anthropogenic pollution [22]. In summary, with steadily increasing levels of environmental stresses, especially pollution, the

*species richness*  $S_t$  dramatically decreases, the *apparent unevenness*  $U$  of species abundance distribution sharply increases, while the *intensity*  $I_{str}$  of the underlying structuring process remains almost unchanged, only starting a slight decrease for the highest level of stresses in H2.



**Fig. 27. The consequences of increasing environmental stresses, especially anthropogenic pollution: variations of (i) the true total species richness  $S_t$ , (ii) the unevenness pattern  $U$  of species abundances and (iii) the genuine intensity  $I_{str}$  of the structuring process.**

### 3.7.2 Analysing the species turn-over

The sharp drop in species richness with the peioration of environmental conditions (especially anthropogenic pollution) raises, at first, the question of the corresponding turn over in species composition. That is, how many species have disappeared and how many new species have occurred in habitat H1 as compared to H4? Among the 22 species occurring in the community of habitat H1, 16 were actually recorded during sampling of H1 and 6 were remaining unrecorded (Table 2):

- among the 16 species actually recorded during the partial sampling of H1, 13 of them were already recorded in H4 while the 3 other species were not, namely: *Busycon contrarium* (Conrad 1840), *Strombus gracilior* Sowerby I 1825 and *Tonna marginata* (Philippi 1845). Of course, these three species, unrecorded in H4, may - or may not - be present among the 39 unrecorded (and thus unidentified) species present in H4.
- among the 6 species still remaining unrecorded (and thus unidentified) after the partial sampling of H1, either none of them, part of them or all of them were already present among the 117 species of the community H4 (i.e. among the 78 recorded and identified species and/or among the 39 unrecorded and unidentified species in H4).

In total, between 0 and 9 (= 3 + 6) species are newly occurring in H1 as compared to H4. And,

accordingly, among the 117 species present in H4, between 95 species (=  $117 - 22 + 0$ ) and 104 species (=  $117 - 22 + 9$ ) are absent in H1. The turn over from H4 to H1 thus involves (i) from 0 to 9 occurrences of new species and, correspondingly, (ii) from 95 to 104 species being lost. With of course, in any case, a deficit of 95 (=  $117 - 22$ ) species in H1 as compared to H4.

### 3.7.3 Analysing the sensitivity to species loss according to the original level of abundance

Investigating still further, one can wonder whether this sharp environment-induced drop in species richness involves more particularly those species already rare in H4? Or, on the contrary, does this species thinning is more or less equally distributed among all species-members in H4, independently of their respective abundances?

Among the 117 species of the community H4, 78 species have been recorded. As such, most of these 78 species are – statistically – expected to be among the two-thirds more abundant species in habitat H4. Now, of these 78 species, only 13 are still present among the 16 recorded species in community H1. Also, an additional contribution of 0 to 6 species among these 78 might be present among the 6 unrecorded species of H1. That is, in total, between 13 and  $13 + 6 = 19$  species are subsisting in H1, out of the two-thirds more abundant species of H4. Accordingly, from  $(78 - 19)/78 = 76\%$  to  $(78 - 13)/78 = 83\%$  of the *more abundant* species in H4 are expected to have disappeared in H1.



*Strombus gracilior* Sowerby I 1825 (typical shell length  $\approx 75$  mm) © Udo Schmidt





*Tonna marginata* (Philippi 1845) (typical shell length  $\approx$  100 mm) © Guy Guerrero

Now, let consider the 39 unrecorded species of H4, thus – statistically – expected to account for the one-third less abundant species in habitat H4. The number of them that may possibly subsist in H1 is necessarily comprised between 0 and  $22 - 13 = 9$ . Accordingly, from  $(22 - 9)/22 = 59\%$  to  $(22 - 0)/22 = 100\%$  of the *less abundant* species in H4 are expected to have disappeared in H1. Thus, finally, from 76% to 83% of the two-thirds *more abundant* species in H4 have disappeared in H1 and from 59% to 100% of the *less abundant* species in H4 have disappeared in H1. That is a sensitivity to species loss, between the originally abundant and the originally rare species in H4, which is less different than might have been hypothesised at first.

#### 3.7.4Analysing the sensitivity to species loss according to gastropod feeding modes

Here, relying upon the recorded data only is sufficient to aptly conduct the analysis. Table 5 provides the recorded numbers and proportions of *species* respectively belonging to the two co-occurring feeding guilds (*primary* and *secondary*

consumers) in the sampled communities in habitat H4 and H1. The proportions remain substantially similar for both habitats ( $\chi^2 = 0.01$ ,  $p > 0.05$ ).

Table 6 provides the recorded numbers and proportions of *individuals* (all species together) respectively belonging to the two co-occurring feeding guilds (*primary* and *secondary* consumers) in the sampled communities in habitat H4 and H1. The proportions still remain rather similar for both habitats ( $\chi^2 = 2.9$ ,  $p > 0.05$ ).

**Table 5. The recorded number (and corresponding proportion %) of those species respectively belonging to each of the two feeding guilds (*primary* versus *secondary* consumers) for the marine gastropod communities in habitat H4 and H1**

	Primary cons.	Secondary cons.
habitat H4	28 (36%)	50 (64%)
habitat H1	6 (38%)	10 (62%)

**Table 6. The recorded number (and corresponding proportion %) of those individuals respectively belonging to each of the two feeding guilds (*primary* versus *secondary* consumers) for the marine gastropod communities in habitat H4 and H1**

	Primary cons.	Secondary cons.
habitat H4	422 (54%)	358 (46%)
habitat H1	53 (46%)	63 (54%)



## 4. DISCUSSION

Marine gastropods communities in tropical shallow waters are among the most threatened ecosystems, as a consequence of anthropic activities, in particular the on-going climate change [3,5]. Also, increasing levels of offshore *water pollution* and the degradation of the coral substratum are responsible for steadily increasing environmental stresses which may more or less drastically affect the species richness and the hierarchical structuring of species abundances within invertebrates benthic communities.

Yet, assessing the main quantitative descriptors of these benthic communities at the local scale (in particular, the true total species richness, the apparent level of unevenness of species abundances and the genuine intensity of the structuring process within community) faces several methodological issues.

*First*, the urgency to report on the current state of these threatened communities reduces the time available which can be devoted to the sampling of each of these communities, thereby seriously limiting the degree of completeness and the representativeness of these samplings. Hence, the usual constraint of having to cope with substantially incomplete inventories and, accordingly, the necessity to apply numerical extrapolations to such partial samplings. Indeed, least-biased *numerical extrapolations* allows to infer major quantitative information relative to the set of *unrecorded* species: (i) estimating their *number* and (ii) inferring their *abundance distribution*. Thereby, both the total species richness and the full-range Species Abundance Distribution ("S.A.D."), *including the undetected species*, may be derived, thus providing essential information that, otherwise, would have remain out of reach. Practical procedures to carry out these numerical extrapolations with *minimum bias* have been recently reported [23,24,26], so that now, nothing prevents from making the most of "rapid samplings" or "quick assessments".

*Second*, it reveals important to make clear distinction between the genuine intensity of the structuring process driving the allocation of species abundances and the resulting pattern of species abundance unevenness, since the latter does not mirror reliably the former, due to the mathematical dependence of unevenness upon the level of species richness. Thus, unveiling the

genuine intensity of the underlying structuring process is necessary to more thoroughly understand the internal organisation of species communities. Here also we now dispose of a routine procedure to reach this goal [39].

Implementing these newly derived procedures has made it possible to more thoroughly address the effects of local environmental pejouration on the marine gastropod communities of Fiji Islands, along Nasese shore, Suva, based on *available partial samplings* reported by [22]. Three communities were retained for further analysis, established in three neighboring habitats (labelled H4, H1, H2, according to authors' designations) which respectively undergo increasing environmental pejouration. Also, as deconstructing ecological assemblages into various subsets can reveal additional patterns of interest when each subset is analysed separately [41], the consequences of local environmental pejouration have been examined in more details, by separating at first the two co-occurring feeding guilds – primary and secondary consumers – and, then, still further, by focusing on the genus *Conus*, as an emblematic part of the secondary consumers.

### 4.1 Consequences of Environmental Pejouration on Community Structure

#### 4.1.1 Consequence on true total species richness

The best preserved habitat H4 remains home to a relatively rich assemblage of marine gastropods with an estimated richness  $S_t = 117$  species, including in particular 20 species belonging to the genus *Conus* (Tables 1 & 4). Yet, as expected, the species richness of gastropod communities in less preserved habitats responds very negatively to environmental pejouration (Table 1) with a striking decrease from  $S_t = 117$  species in community H4 down to  $S_t = 22$  species in community H1 and, finally,  $S_t = 14$  species in community H2 which suffers by the highest pollution level. This is a still more drastic reduction (by a factor 8.4 between H4 and H2) than would have been assumed on the basis of the recorded numbers (a factor 6 only, due to community H2 being less partially sampled than community H4: see Table 1). Once again, this is a reminder to caution when conclusions are tentatively drawn from incomplete samplings only...

This negative effect of environmental degradation, especially growing water pollution [22], is commonly reported indeed [41-47].

Incidentally, the relatively low level of estimated sampling completeness of the preserved community H4 (67% completeness) may arguably invite to plan further investigation, on proviso that the expected gain in newly detected and identified species actually balance the required additional sampling efforts to be consented. In this respect, the extrapolated Species Accumulation Curve, beyond the actually reported sampling size (Fig. 1), provides useful forecast as to the balance between the expected gain in completeness and the corresponding additional effort required and, thus, helps making an argued decision as to the opportunity to go on further sampling.

#### 4.1.2 Consequences on abundance unevenness and the intensity of the structuring process

The bias-corrected and numerically extrapolated Species Abundances Distributions ("S.A.D.") of each three communities (Figs. 2, 3, 4) and the comparisons made, for each of them, with the classical models ("broken-stick": Figs. 5, 6, 7; "log-normal" and "log-series": Figs. 8 to 13) finally lead to the following main conclusions:

i) the *degree U of unevenness* of species abundance within each community is steadily increasing with environmental stresses, in a manner which seems directly opposite to that of species richness: a strong increase from H4 to H1, then a much moderate increase from H1 to H2 (Table 2, Figure 14). This trend for growing unevenness of abundances with environmental peioration is commonly reported as well as the corresponding species impoverishment [42-46];

ii) yet, the *intensity  $I_{str}$  of the underlying structuring process*, driving the distribution of species abundances, is far from following the same trend as the "apparent" degree of unevenness U: on the contrary,  $I_{str}$  remains *almost unchanged*, even slightly decreasing for community H2 (Table 2, Fig. 14). In fact, this inconsistency between the hierarchical structuring process and the resulting unevenness *pattern* simply proceeds from the (negative) mathematical dependence of unevenness U upon species richness [35-36], thus making the "apparent" unevenness a somewhat misleading descriptor, as already cautioned by several authors [19,20,37]. A warning, yet, remaining too frequently ignored.

This rather weak, even negligible influence of environmental degradation on the genuine intensity of the hierarchical structuring process is an *important disclosure* highlighted by this study and to be emphasised as it goes directly *opposite* to the common opinion, erroneously based on the implicit (but false) idea that apparent unevenness reliably mirrors the intensity of the underlying structuring process.

iii) the kind of *mechanism* involved in the structuring process driving the allocation of species abundances remains also substantially unchanged along the gradient of environmental stress. All three "S.A.D.s" remain best fitted by the "log-normal" model (Figs. 5, 6, 7), thus implying that the hierarchical structuration of abundances remains dependent upon the multiplicative influences of many independent factors even at the higher pollution levels considered here. Note that the persistence of this fairly good fit of the three "S.A.D.s" to the "log-normal" model differs from previously reported observations [41,47], according to which strongly polluted environments would favor a better conformity to the "log-series" model. Perhaps, this divergence may be due to the fact that "S.A.D.s" remaining more or less incomplete (as is often the case when extrapolation is not implemented) are prone to spuriously fit the "log-series" model instead of the "log-normal" model [8,33].

Fig. 27 summarises graphically the consequences of the degradation of environmental conditions on the three main descriptors of the structure of gastropod communities along sea shore at Siva: (i) a strong negative influence on total species richness  $S_t$ , (ii) a negligible influence on the genuine intensity  $I_{str}$  of the process structuring species abundances and (iii) a strong increase of apparent unevenness U, yet deprived of intrinsic significance, being the quasi exclusive consequence of the decrease in species richness.

#### 4.1.3 The pruning of species richness, following environmental peioration, is far from being restricted to rare species

Going further in details, it appears clearly from reasoning on species turn-over (section 3.7.2) that the progressive disappearance of species following steadily increasing environmental peioration is far from being restricted to those originally less abundant species: in fact, the

“species pruning” is not so far from being almost as severe for the originally most abundant species as it is for the rarest ones. As a result, the average steepness of the slope of ranked abundances is strongly reinforced *all along* the “S.A.D”, as highlighted in Figs. 25 and 26.

Also, it turns out that *both feeding guilds* are roughly *equally* submitted to this pruning of species richness, with primary and secondary consumers bearing similar ratios of reduction of their number of species and of their number of individuals (Tables 5 and 6).

As regards now the genus *Conus*, it has been demonstrated that this group of highly predacious gastropods – emblematic among all other secondary consumers – reveals much more sensitive to environmental pejoration (seven times more!) than are the other co-occurring gastropods or the subset of secondary consumers to which belong *Conus*.

#### 4.2 Specificities of Feeding Guilds in Terms of Species Richness and Hierarchical Structuring of Species Abundances

Attention has been called recently, in reference [48], to what may seem to be a rather general trend opposing the *primary* and the *secondary* feeding guilds. Namely, for marine as well as terrestrial animal communities, the subset of *primary* consumers would tend to have significantly lower species diversity than the subset of *secondary* consumers, at least when diversity is quantified by the “Hill number”. This remarkable trend, although already largely supported by numerous case studies (review in [48]) still calls for supplementary testing, since several issues are remaining raised and unresolved in the background of this interesting hypothesis:

i) “Hill number”, as other species-diversity indices, intermingles species richness and evenness so that the respective contributions of each of these two parameters cannot be disentangled from each other, which precludes meaningful comparisons between guilds in terms of species richness and (un)evenness considered *separately*;

ii) besides, would the contribution of (un)evenness be correctly separated from that of species richness, the mathematical dependence of the former upon the latter would still limit the

relevance of the result, hence the need to consider also the genuine intensity  $I_{str}$  of the hierarchical structuring process;

iii) at last, even being conducted separately, the respective assessments of the species richness on the one hand and of the abundance (un)evenness on the other hand both require dealing with exhaustive samplings or, else, duly numerically extrapolated partial samplings.

Accordingly, the hypothesis suggested by [48] was rechecked, in the course of this study, by taking full account of the three preceding remarks. For this purpose, the species-rich community H4 was considered. The bias-corrected and extrapolated “S.A.D.s” of *primary* consumers and of *secondary* consumers in community H4 (Figs. 15, 16, 17) reveal that:

(i) the guild of *primary* consumers indeed has far fewer species ( $S_t = 44$ ) than has the guild of *secondary* consumers ( $S_t = 73$ ), that is, respectively, 38% and 62% of the total species richness of the community H4 (Table 3),

(ii) the apparent unevenness  $U$  is almost twice as high for *primary* consumers ( $U = 0.078$ ) than it is for *secondary* consumers ( $U = 0.043$ ).

(iii) as regards the *genuine intensity*  $I_{str}$  of the hierarchical structuring process, the trend for higher value for *primary* consumers still holds true, but is quite less pronounced than for the apparent unevenness  $U$ , with intensity  $I_{str}$  being only 20% higher for *primary* consumers ( $I_{str} = 1.46$ ) than for *secondary* consumers ( $I_{str} = 1.21$ ).

Note that remarkably similar results have already been reported for another marine gastropod community in tropical shallow waters in Andaman Islands (India) [27]: in this community, *primary* consumers and *secondary* consumers contribute respectively to 39% and 61% of the species richness of the whole community; the apparent unevenness  $U$  is almost twice as high for *primary* consumers ( $U = 0.097$ ) than for *secondary* consumers ( $U = 0.052$ ) and the genuine intensity  $I_{str}$  of the structuring process being 30% higher for *primary* consumers ( $I_{str} = 1.35$ ) than for *secondary* consumers ( $I_{str} = 1.03$ ). The structural similitude between the communities at Fiji H4 and at Andaman goes even further, considering the details of the repartition of primary and secondary species along the ranked distribution of abundances (Fig. 18): this repartition is remarkably similar between community H4 of Fiji and the community of Andaman (compare Fig. 18 to the corresponding Fig. 8 in reference [27]).

The similitude is all the more impressive that both communities are distant from each other by almost a quarter of the Earth circumference and share almost no species in common (Jaccard similarity index = 0.04 only!). This may be considered a good example of “*functional equivalence*” despite high taxonomic differences [49-52].

Another test, conducted with coral reef-associated gastropod community in Mannar Gulf [40], highlights still larger difference in species richness (*primary* and *secondary* consumers contributing respectively to 21% and 79% of the species richness of the whole community; the apparent unevenness  $U$  of *primary* consumers ( $U = 0.272$ ) reaches now four-times that of *secondary* consumers ( $U = 0.068$ ); the genuine intensity  $I_{str}$  of the structuring process being 40 % higher for *primary* consumers ( $I_{str} = 1.79$ ) than for *secondary* consumers ( $I_{str} = 1.27$ ).

Thus, the hypothesis put forward by [48] for species-diversity as a *whole* (i.e. as summarised in a unique parameter the Hill number) seems further supported by these three case studies (Figs. 19, 20). And the trend has gained enhanced reliability, being based on completed “S.A.D.s”. Moreover, the hypothesis appears now remaining still valid when extended to the genuine intensity of the structuring process itself (and not only for the resulting apparent unevenness).

#### 4.3 Peculiarities of the Genus *Conus* among Secondary Consumers

Among the 50 recorded species of secondary consumers in community H4, the genus *Conus* ranks first, with 16 species, and also stands out by its very specific and highly derived behavior to master and kill preys. As such, it deserves special interest as a subset of the whole assemblage of secondary consumers in community H4. The bias-corrected and extrapolated S.A.D. for *Conus*, shown in Fig. 21, is compared to the S.A.D. of the whole set of secondary consumers at Fig. 23. The *Conus* subset occupies the middle of the range of species abundances among secondary consumers rather than the lower half, as would *erroneously* be suggested by relying only on the crude recorded data: see Fig. 24.

The unevenness  $U$  of species abundances is twice higher in the *Conus* subset than it is in the

whole guild of secondary consumers (Table 4, Fig. 23). This would apparently suggest that the hierarchical structuring of abundances is stronger among *Conus* species than it is among other secondary consumers. But, once again, relying upon crude evenness is *misleading*, due to the “parasitic” mathematical influence of species richness on the apparent unevenness. In fact, the genuine structuring intensity  $I_{str}$  is, on the contrary, slightly lower in the *Conus* subset (Table 4), thus revealing a *slightly less intense structuring process* among *Conus* species than among the other secondary consumers.

As concerns the nature of the mechanism of hierarchical structuring of abundances among *Conus* species, the involvement of many independent factors is suggested by the better fit of the corresponding S.A.D. with the “log-normal” model (Fig. 22).

## 5. CONCLUSIONS

Considering in details the data implicitly conveyed by Species Abundance Distributions can provide an astonishing diversity of information, having both theoretical and practical interest. Yet, taking such full advantage from the treatment of Species Abundance Distributions requires dealing with the *exhaustive range* of species abundances, which, in practice, is rarely possible especially when having to cope with species-rich communities, such as, for example, most of invertebrate assemblages. Hence the necessity of implementing a reliable procedure of *numerical extrapolation* to extend the still incomplete Species Abundance Distribution, as was proceeded here.

This is all the more important that rare species, that often escape recording in practice, may yet disproportionately contribute to the functional structure of communities in the wild. Accordingly, numerical extrapolation is therefore the *only way to account for their existence and role*. Moreover, as frustrating as it may seem, the lack of taxonomic identification of these rare species – remained undetected but highlighted by numerical extrapolation – has more limited consequences that could have been thought at first. Indeed, the specific taxonomic identification turns out to be of less importance, as soon as one is aware of the generally great variability of taxonomic compositions that can equally well answer a same type of functionality (“functional equivalence”).

Implementing this procedure of *numerical extrapolation* to three marine Gastropod communities in Fiji Islands has revealed a large amount of new information and derived interpretations that, otherwise, would have remained *inaccessible* (or *severely biased* by the truncated available data issued from *incomplete* samplings). In particular, it has been highlighted that the species “pruning” that follows strong environmental pejoration is almost as severe regarding the originally most abundant species as it is for the rarest ones.

In another respect, the general hypothesis suggested by Garcia-Callejas, according to which *primary* consumers tend to have significantly lower species richness and stronger species abundance unevenness than *secondary* consumers within the same community, has been demonstrated once again with marine gastropods. Moreover, the hypothesis has been extended still further to the genuine intensity of the process of hierarchical structuring of abundances itself, which also proves being stronger among *primary* consumers as compared to *secondary* consumers.

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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 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 references [23, 53, 54]:

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

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 [23]):

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

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

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

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

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

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

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

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

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

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

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

**N.B. 1:** As indicated above (and demonstrated in details in [23]), 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, 9, 55-57]. Also, this shows that the approach initially proposed in [58] – 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 alternatively be selected: see reference [24].

## APPENDIX 2

### ***Correction and extrapolation (when required) of the as-recorded S.A.D.***

N.B.: details regarding the derivation of the following expressions are provided in reference [26].

#### ***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:

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

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  $i > R_0$ ):

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

which, in practice, comes down to:  $a_i \approx (2/N_i) / (1 + R(N_i)/N_i)$ , as  $f_1(N)$  already becomes quite negligible as compared to  $N$  for the extrapolated part.

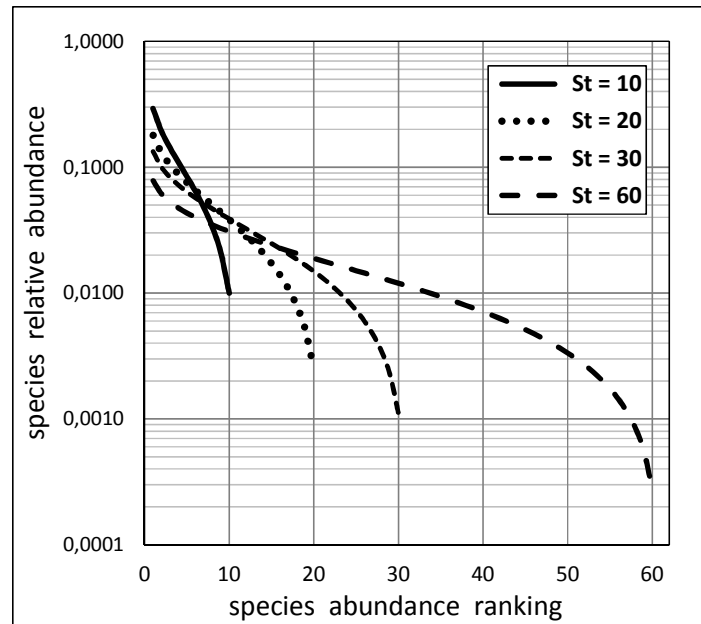
This equation provides the extrapolated distribution of the species abundances  $a_i$  (for  $i > R(N_0)$ ) as a function of the least-biased expression for the extrapolation of the species accumulation curve  $R(N)$  (for  $N > N_0$ ), 'i' being equal to  $R(N_i)$ . The key to select the least-biased 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. A1.** 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  $S_t$