Inferring totalspecies richness and the exhaustive hierarchical structuring of species abundancesintropical Sea-Stars communities (Asteroidea),using numerical extrapolation ofpartial inventories

Original Research article

Abstract

Even when remaining substantially incomplete, the partial inventory of a species assemblage can provide much more information than could be expected first. Indeed, retrieving this information is made possible by applying arigorousprocedure of numerical extrapolation to the partial inventory. This numerical extrapolationwill deliver reliable estimates ofthe number of the still unrecorded species and,furthermore, ofthe distribution of abundancesof these unrecorded species. As a result, the full range of the Species Abundance Distributionis finally made available, despitedealing with data from partial sampling only.In turn, this allows to address a series of descriptive and functional aspects of the internal organization of species assemblages, which otherwise would have required disposing of exhaustive samplings. The latter being, however, often impossible to achieve in practice. Fortunately, mathematic and algorithmic basis for a reliable numerical extrapolationof incomplete samplings have been developed recently, so that partial inventories no longer remain an obstacle to gain access to the true (total) species richness and the full-range pattern of hierarchical structuring of species abundances.

This approach is applied hereto the previously reported partial samplings of two communities of tropical sea-stars associated to coral-reefs in the Central South China Sea. Among the main newresultsderived from the numerical extrapolations of these partial samplings, the following are highlighted:

-the extrapolated true (total) species richness of each of the two studied communities largely exceed the recorded figures, thereby confirming the limited completeness of these partial samplings: 53% and 67% completeness only;

-once properly completed by numerical extrapolation, theSpecies Abundance Distributions of both communitiesprovebest fitting the “log-normal” than the “log-series” model, thereby suggesting that many independent factors (rather than only one dominant factor) contribute together to the hierarchical structuring of species abundances within thesesea-stars communities;

-the intensity of theprocess of hierarchical structurationof species abundances proves being close to what would be obtained for the corresponding “broken-stick” model, which means a rather moderate level of structuration intensity, as compared to the range of values typically obtained for other kinds of marine invertebrates.

Key-words : Echinodermata, starfish, coral reef, species richness, diversity, rank abundance distribution, evenness, incomplete inventory, Malaysia

1. INTRODUCTION

Total species richness, taxonomic composition and the hierarchical structuring of species abundances are three key features that appropriately characterize species communities in the wild. Addressing properly these key features obviously requires disposing of exhaustive inventories. Yet, inventories remaining substantially *incomplete*are common in practice and even doomed to become still more frequent with the inevitable generalization of "rapid assessments" and "quick surveys". This is especially true when having to deal with species-rich communities of invertebrates which often include a lot of rare, hard-to-detect species. Such incomplete inventories prevent deriving reliable inferences and, thus, may often lead to erroneous interpretations regarding the key aspects of species communities evoked above [1 – 3].

Fortunately, a reliable procedure of *numerical extrapolation*of partial inventories has been developed recently, which can overcome these difficulties and is able to provide least-biased estimationsof:

(i)the number of those species remained undetected and, still further,

(ii) the respective abundances of each of these undetected species.

Thereby, reliable inferencescan finally be derived regarding (i) the*true*(total) species richness and (ii) the *completed*distribution of species abundances, i.e. including the set of the still unrecorded species.Only the taxonomic identities of these undetected species escape, of course,to any attempt to highlight them. In turn, once numerically *completed* (and *only* when it is so: [4]), the Species Abundance Distribution ("S.A.D.") can then providesynthetic pieces of information about the process (either deterministic or stochastic) that drive the hierarchical structuring of species abundances within community[5 – 9]. Accordingly, some light can thus be shed, both qualitatively and quantitatively, on the biological and ecological determinants of the internal structuration among species within community.

Although no further details may be extracted from this synthetic overview, the latter has, yet, the advantage of being straightforward, as it does not require the long and tedious analytical approachthat would be required otherwise to go deeper in the details of structuring process. As such, this synthetic overviewcan serve as a convenient preliminary approach.

Hereafter, I report and discuss the results from the numerical extrapolationof the partial inventories of twosea-stars communities(Echinodermata: Asteroidea) associated to coral reefs surrounding the small neighboring islets of Terumbu Siput ("Erica reef") and Terumbu Peninjau("Investigator shoal"),located in the Central South China Sea, off the Malaysian coast. Such marine ecosystems, in tropical shallow waters, are of major interest to ecologists and conservationists, as they are considered as embodying remarkably high levels of biological complexity [10 – 12].

2. MATERIALS AND METHODS

2.1 Materials

Coral reefssurrounding small islands dispersed in the Central South China Sea are home to a rich sea-stars fauna, reported as countingoverall no less than 230 species[13]. Yet, inventories at the local scale of sea-stars communities in China Sea, additionally listing the abundances of the recorded species, remain very scarce at the *local scale*. A recent report by KWANG*et al.*[12], however, opportunely provides such a series of local inventories of sea-stars from the Archipelago of Beting Patinggi Ali to Pulau Layang-Layang in the Malaysian waters ofCentral

South China Sea.Yet, the high proportion of singletons (species detected only once during sampling) that subsist in these inventories strongly suggests that samplings remain substantially incomplete[14 – 16], thus requiring *numerical extrapolation* to take full advantages of the as-recorded data and avoid the risk of erroneous inference.
Hereafter, I focus ontwo of these investigated sea-starscommunities,those having the highest number of recorded species (16 and 9 species) respectively. These two communities are located in two small neighboring coral islets:*Terumbu Siput* ("Erica reef") and *Terumbu Peninjau* ("Investigator shoal"), both being part of "Spratly Islands", off the coasts of the Philippines, Malaysia, and southern Vietnam. Further information regarding the precise locations, the environment and the practical details ofthe sampling procedure are provided in open reference [12].

2.2 Numerical extrapolation procedure

2.2.1 Total species richness

The least-biased estimation of the number of still undetected species after partial sampling and the resulting least-biased estimation of the true, total species richness of apartially sampled community are derived according to the procedure defined in [17, 18]and briefly summarized in Appendix 1, on the basis of the numbers f_x of species recorded x-times during partial sampling: Figures A.1 and A.2).

2.2.2Completed Species Abundance Distribution:

To accurately exploit its full potential, the as-recorded Species Abundance Distribution ("S.A.D.") requires[19, 20]:
- first, to be *corrected* for the statistical sampling bias resulting from the finite size of samplings;
- second, but still more importantly,to be *completed* by numerical extrapolation to the extent that the sampling is suspected to be incomplete (as revealed by the subsistence of several singletons).

After being *corrected* and *completed by numericalextrapolation*, the S.A.D.:
- 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
- butalso, can help addressing important questions regarding (i) the kind of causesthat determine the hierarchical structuration of species abundances, (ii) the resulting degree of abundance unevenness and (iii) the genuine intensity of the hierarchical structuring process (which by no means identifies to the degree of unevenness, contrary to a commonly held opinion).

The appropriate procedures of correction and, then, numerical extrapolation of the "S.A.D." beyondits as-recorded part, are described in details in reference [20] and briefly summarized in Appendix 2. Also, a concrete example of implementation of the procedure is commented in details in reference [21].
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, the latter being 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 having S_t species).

2.2.3 species abundance structuration- (i) the apparent pattern: abundance unevenness

The “S.A.D.” (either being exhaustive or completed by numerical extrapolation) conveys all the relevant quantitative data required to address the internal organization of member-species within a local community, especially the hierarchical structuration of species abundances. In particular, it is always advisable to use such species-abundance plots to quantify the degree of evenness or, more suggestively, the degree of *unevenness* of species abundances [22]. Indeed, following [23], it is the degree of *unevenness* – rather than evenness itself – that should be preferred to address properly the hierarchical structuring of species abundances in communities. Optionally, the “S.A.D.” may be synthetically reduced to its two major descriptors: the *total species richness* S_t and the degree U of*abundance unevenness*.

According to the aforementioned, classical mode of representation of “S.A.D.”, it goes natural to quantify the degree U of abundance unevenness as the average decreasing slope of the log-transformed abundance along the whole range of the abundance distribution, as already proposed by [24], that is:

$$U = [\log_{10}(a_1) - \log_{10}(a_{St})] / (S_t - 1) = [\log_{10}(a_1 / a_{St})] / (S_t - 1) \qquad (1)$$

2.2.4 species abundance structuration- (ii)origin and intensity of the underlying process

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 (i) the kind of *mechanism* involved in the process driving the hierarchical structuration of abundances and (ii) the *intensity* of this structuring process.

As regards the kind of *mechanism* 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 strongly predominant* factor or (ii) from the combined contributions of *many mutually independent factors* acting together. This can be tested by checking the conformity of the “S.A.D.” to either the *log-series* model or the *log-normal* model respectively [5, 25 – 28].

Now, as regards the genuine *intensity* of the structuring process, it is first necessary to remind that the degree of unevenness U does not univocally mirror the intensity of the structuring process, since it is *also* mathematically dependent (negatively) upon the species richness S_t [29, 30, 31]; see also Appendix 3.

One possible solutionto cancel this mathematical influence is to compare the slope of the “S.A.D.” with the slope of a theoretical distribution involving a *constant* structuring process, remaining *strictly independent*ofthe species richness. The “broken-stick” distribution meets precisely this requirement [32]. Accordingly, an index “I_{str}”, attempting to disentangle the part of unevenness which vary *independently of species richness*can be defined by standardizing 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[33 - 35], that is:

$$I_{str} = U/U' = [\log_{10}(a_1/a_{St})/(S_t - 1)] / [\log_{10}(a'_1/a'_{St})/(S_t - 1)]$$

that is finally:

$$I_{str} = \log_{10}(a_1/a_{St}) / \log_{10}(a'_1/a'_{St}) \qquad (2)$$

with a_1 and a_{St} standing for the highest and the lowest abundances in the studied community and a'_1 and a'_{St} standing for the highest and the lowest abundances in the corresponding “broken-stick” distribution computed for the same species richness S_t.

As the *invariable type* of structuring process involved in the “broken-stick” distribution is the process of random allocation of abundances to species [32], the index I_{str} highlights the *intensity* of the *structuring process* in the focused community by comparison to the intensity of this stochastic process, taken as a reference.

It is even possible to continue the analysis even further in the same direction. Beyond comparing the average slopes of the actual "S.A.D." to the corresponding "broken-stick" model, it isadditionally informative to operate the comparison separately for each of the two extremal points that support the slopes – i.e. the maximum and the minimum abundances, a_1 and a_{St}. Thus, the ratio $A_1 = (a_1/a'_1)$ mirrors the intensity of those kind(s) of factors which control the abundance a_1 of the more frequent species (especially the most frequent one) while the ratio $A_{St} = (a_{St}/a'_{St})$ mirrors the intensity of those (presumably different) kind(s) of factors which control the abundance a_{St} of the less frequent species (especially the least frequent one).

Splitted that way, the comparison with the "broken-stick" model (synthetically expressed by the index I_{str}), highlights even better the underlying structuring *process* and its *genuine* intensity, beyond the immediately apparent pattern of abundance unevenness U. This is briefly detailed in the following section.

2.2.5 analyzing the determinants of the species abundance structuration

Focused on quantitative terms, the "S.A.D." can be synthetized by three main descriptive parameters, S_t, U, a_{St} (the fourth descriptive parameter, the higher abundance a_1, being entirely defined by the three preceding parameters through equation (1)).Now, which "determinants" are actually constraining the values of S_t, a_1 and a_{St}?

Let consider first the case where the community has hypothetically reached its saturation level in term of species richness S_t, i.e. no more species may be added in the community without causing extinction(s) [36]. This means that both the abundance unevenness U and the lowest abundance a_{St} have reached their respective minimal threshold values that would necessarily be crossed over if any additional colonization would succeed in increasing species richness beyond the saturation level. Accordingly, in case of saturation,the species richness S_t is determined internally, the parameters U and a_{St} playing the role of determinants.

Now, it is widely admitted that saturation in species within a community is very uncommon [36, 37, 38], so that non-saturation should be hypothesized first. In non-saturated communities, species richness S_t is no more determined internally but externally, the determinant being the limitation in the colonizing flux of those species having characteristics compatible with the habitat, a limitation which depend on both dispersal abilities and the richness of the regional stock of species [37, 38, 39]. And, by contrast with the case where community is supposed being saturated, here, the parameters U and a_{St} are no more involved as the determinants of S_t. On the contrary, in this situation of limited availability of new colonizing species, it is the resulting limitation of species richness S_t which contributes to constrain the possible ranges of values of the triplet of parametersU, a_{St} and a_1, through equation (1).And, finally, it is I_{str}which is ultimately constrained, according to equation (2),asare the ratios $A_1 = (a_1/a'_1)$ and $A_{St} = (a_{St}/a'_{St})$.

3. RESULTS

3.1 Estimation of the total species richness of eachsea-stars community

Based on the numbers $f_x$of species recorded x-times (with x = 1 to 5) at the end of the partial samplings (Figures A1 and A2 in Appendix 1), the selected, least-biased estimators of the number of undetected species are respectively Jackknife order 3 andJackknife order 5 for the communities at Terumbu Siput and Terumbu Peninjau (see selective keyin Appendix 1). The corresponding least-biased estimations of (i) the number Δ of undetected species, (ii) the resulting least-biased estimation of the total species richness $S_t$of the sampled communitiesand (iii) the level of completeness of the partial samplings, R_0/St, are provided in Table 1.

Table 1 – Numerical characteristics of thesea-stars communitiesassociated to coral reefs at Terumbu Siput, and Terumbu Peninjau: the sampling-size N_0, the number of detected species R_0 (= $R(N_0)$), the selected, least-biased estimator, the estimated number Δ of undetected species, the resulting evaluation ofthe total species richness S_t= R_0 + Δ and the level of sampling completeness R_0/St.

site	N_0	R_0	selected estimator	Δ	St	R_0/St
Terumbu Siput	52	16	Jack-3	8	24	67 %
Terumbu Peninjau	26	9	Jack-5	8	17	53 %

Due to the relatively low level of achieved sampling completeness (67% and 53%), further additional sampling could, alternatively, be considered of interest. In this perspective, the least-biased extrapolation of the Species Accumulation Curve can provide usefulpredictive information regarding the additional sampling efforts that would be required to obtain any desirable increase in sampling completeness. As an example, the expected increase in the number of detected species, R(N), as a function of growing sampling size N, is given in Figures1 and 2 for the sampling at Terembu Siput andFigures 3 and 4 for the sampling at Terembu Peninjau.

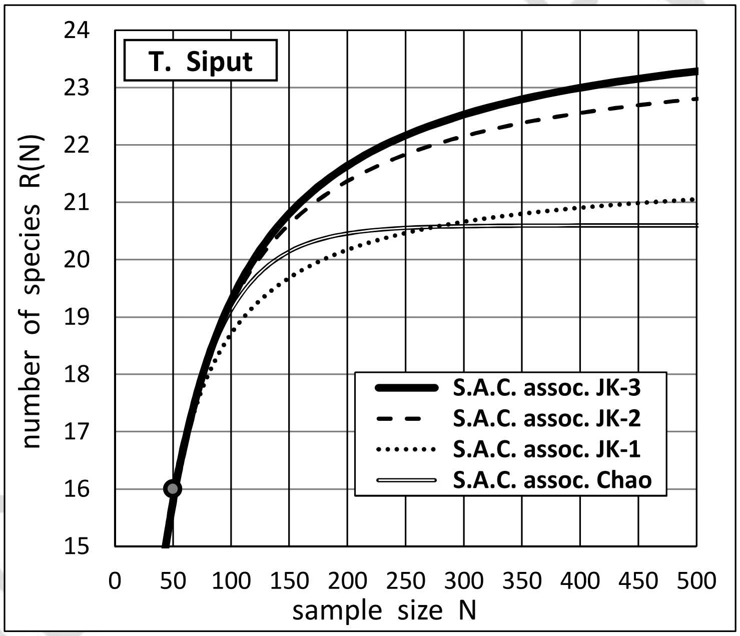


Figure 1 – Extrapolated part of the Species Accumulation Curve (S.A.C.) for the community at *Terembu Siput*, accounting for the increase of the number of detected species R(N) as a function of growing sample size N, beyond the actually achieved sampling (N_0 = 52, $R(N_0)$ = 16). Here, the selected, least-biased, nonparametric estimator of the number of undetected species is Jackknife-3, leading to a total species richness S_t = 16 + 8 = 24. The associated, least-biased extrapolation of the S.A.C. R(N) is plotted as the coarse solid line. Also plotted, for comparison, are the extrapolations of the S.A.C. associated to other, non-selected (as being more biased) estimators: Jackknife-2, Jackknife- 1, Chao1. The comparison highlights the practical importance of selecting the *least-biased* estimator.

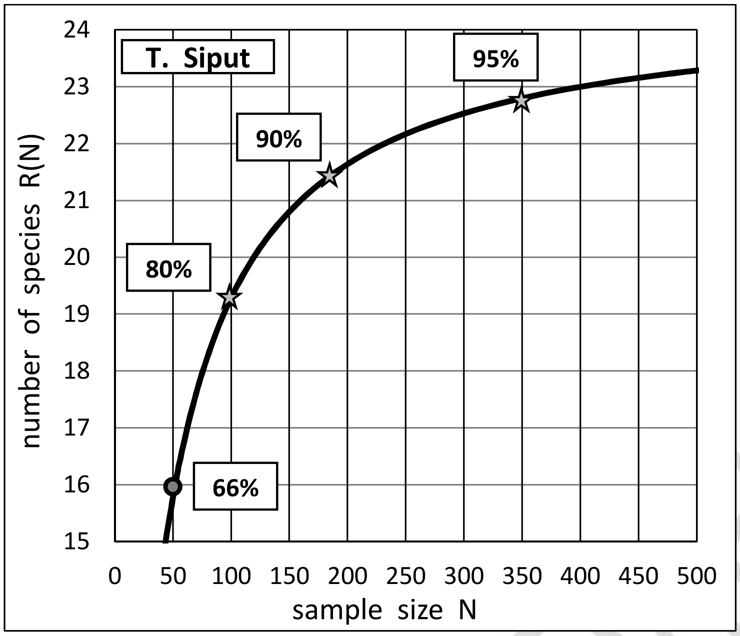


Figure 2 – Extrapolated part of the Species Accumulation Curve for the community at *Terembu Siput*, associated to the selected, least-biased, nonparametric estimator (here Jackknife-3). In practice, the least-biasedextrapolation of the Species Accumulation Curve allows to predict the expected additional sampling effort required to reach higher levels of sampling completeness (for example, the sample sizes required to reach 80%, 90% and 95% completeness would bearound N = 100, 180, 350 respectively).

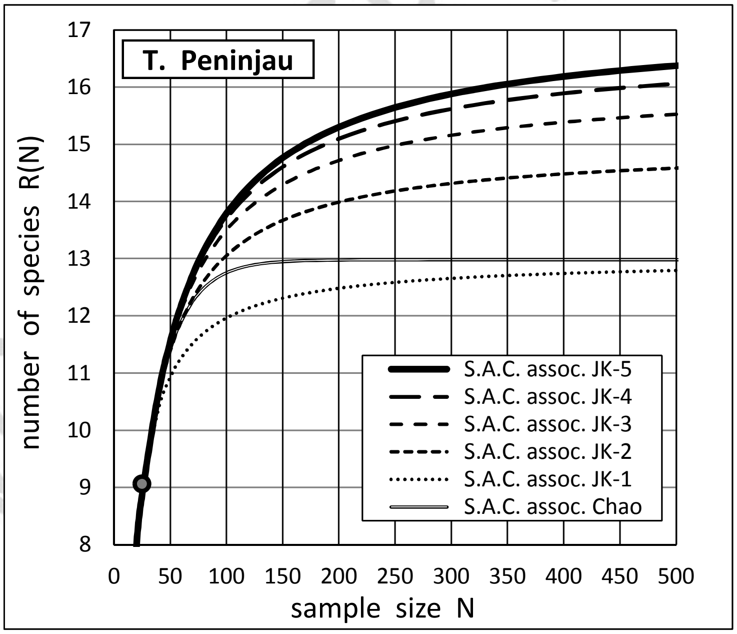


Figure 3 – Extrapolated part of the Species Accumulation Curve for the community at *Terembu Peninjau,* accounting for the increase of the number of detected species R(N) as a function of growing sample size N, beyond the actually achieved sampling (N_0 = 26, $R(N_0)$ = 9). Here, the selected, least-biased, nonparametric estimator of the number of undetected species is Jackknife-5, leading to a total species richness S_t = 9 + 8 = 17. The associated, least-biased extrapolation of the Species Accumulation Curve R(N) is plotted as the coarse solid line. Also plotted, for comparison, are the extrapolations of the S.A.C. associated to other, here non-selected (more biased) estimators: Jackknife 4, Jackknife 3, Jackknife-2, Jackknife- 1, Chao1. The comparison highlights the practical importance of selecting the *least-biased* estimator.

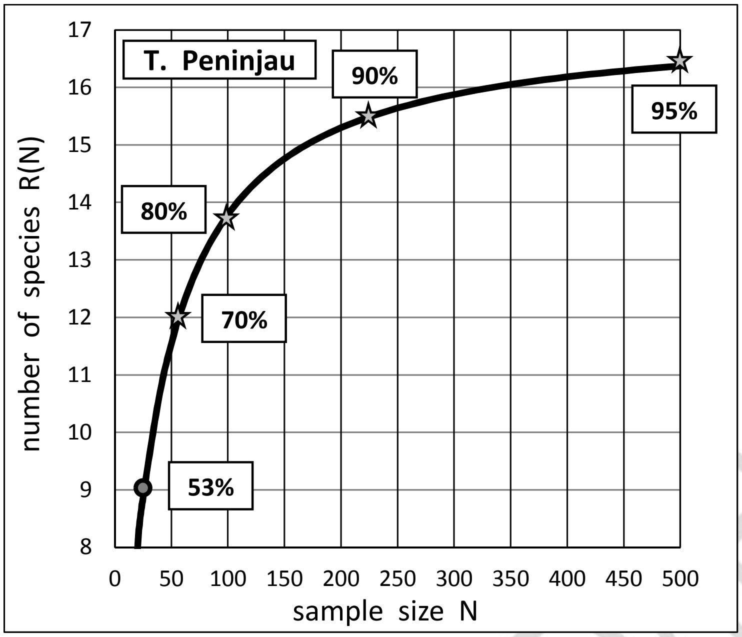


Figure 4 – Extrapolated part of the Species Accumulation Curve for the community at *Terembu Peninjau*, associated to the selected, least-biased, nonparametric estimator (here Jackknife-5). In practice, the least-biased extrapolation of the Species Accumulation Curve allows to predict the expected additional sampling effort required to reach higher levels of sampling completeness (for example, the sample sizes required to reach 70%, 80%, 90% and 95% completeness would be around N = 60, 100, 220, 500 respectively).

3.2 Correction and extrapolation of the Species Abundance Distributions

The bias-corrected and extrapolated Species Abundance Distributionsare plotted in Figure 5 (recorded part: ranks i = 1 to 16; extrapolated part from rank17 to 24) for the community at Terembu Siput and in Figure 6 (recorded part: ranks i = 1 to 9; extrapolated part from rank 10 to 17) for the community at Terembu Peninjau. Figures5and 6thus provide the *entire development* of the Species Abundance Distribution. Note that the *extrapolated* part of the distribution of abundances has no less importance than the *recorded* part since more or less rare species may have asequal ecological importance as more common ones [40 – 49]. Figure 7 allows to compare directly the Species Abundance Distributions of the two communities.

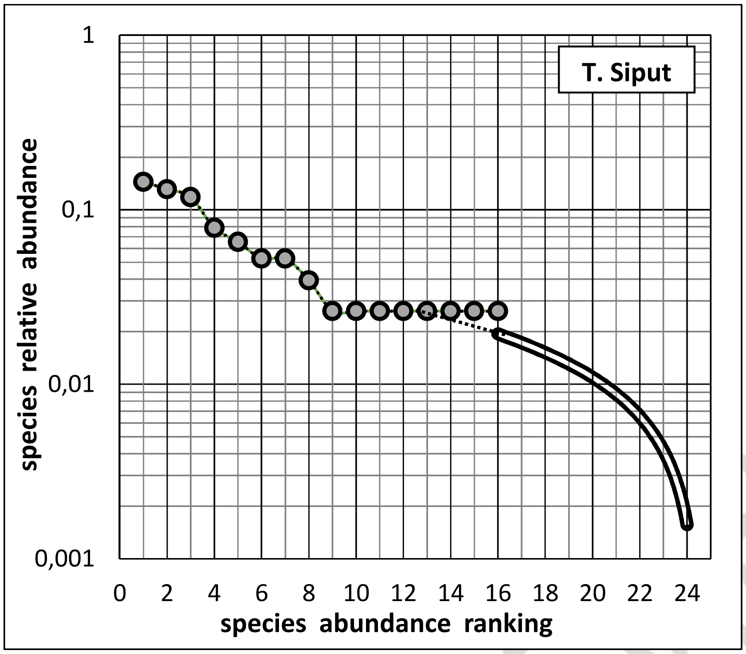


Figure 5 – The completed Species Abundance Distribution for the community at *Terembu Siput*, including the correction of the recorded part (involving the 16 detected species: grey discs) and the least-biased extrapolation of the unrecorded part (involving the 8 undetected species: coarse double line). Note logarithmic scale for relative abundances, a classical convention of graphical representation.

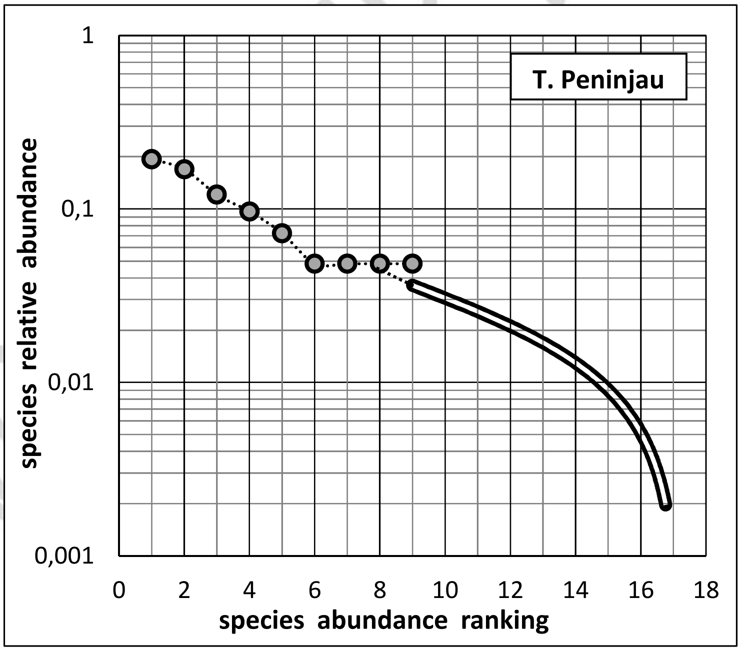


Figure 6 – The completed Species Abundance Distribution for the community at *Terembu Peninjau*, including the correction of the recorded part (involving the 9 detected species: grey discs) and the least-biased extrapolation of the unrecorded part (involving the 8 undetected species: coarse double line). Note logarithmic scale for relative abundances, a classical convention of graphical representation.

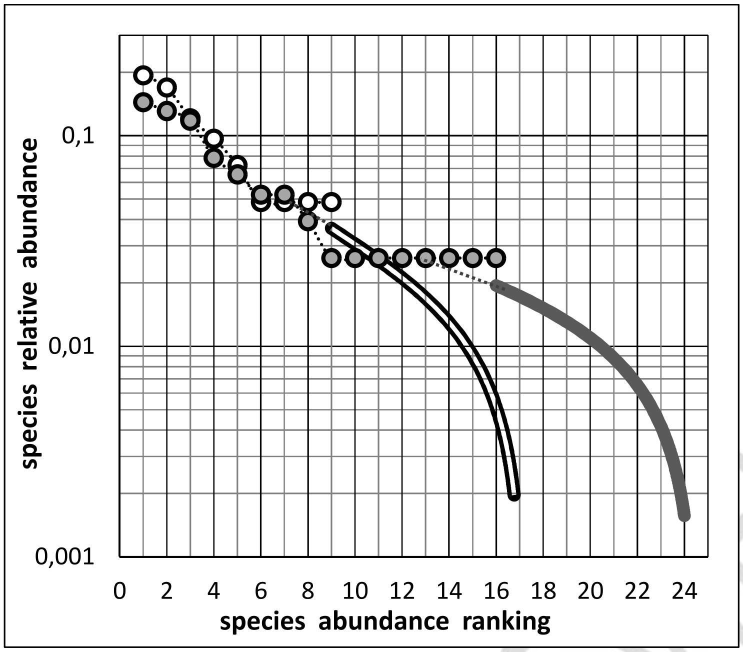


Figure 7 – Direct comparison between the completed Species Abundance Distributions of both communities - grey figures: *Terumbu Siput*; white figures: *Terumbu Peninjau*

3.3 Qualitative and quantitative characterizations of the hierarchical structuring of species abundances

3.3.1 the type of process likely involved in the hierarchical structuring of species abundances

In order to investigate which kind of structuring process is at work in thesesea-stars communities, two classical models of abundance distribution – the“log-normal”distribution and the “log-series”distribution – were tentatively fitted to the completed Species Abundance Distributions provided at Figures5 and 6. As shown in Figures 8 to 11, a fairly good fit is obtained with the *log-normal* model for both studied communities while the accordance with *log-series*model is comparatively unsatisfactory.

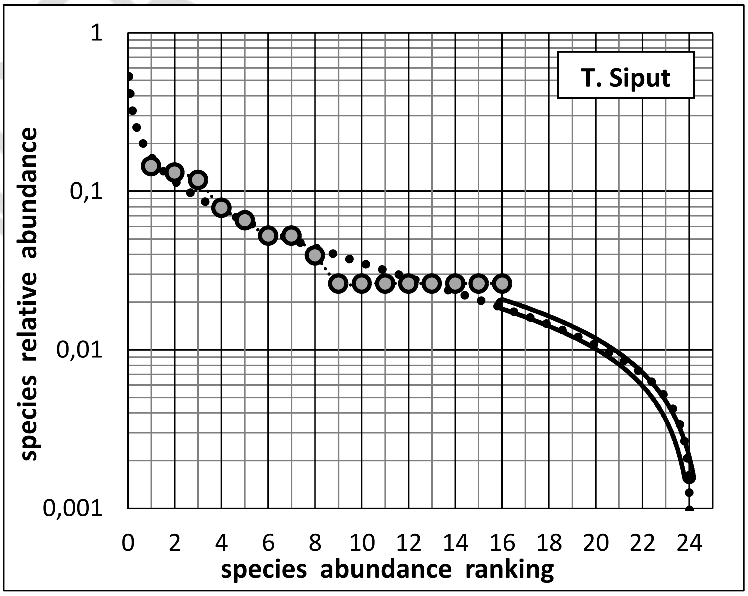


Figure 8 – The classical “log-normal” model (sigmoiddotted line) fitted to the completed Species Abundance Distribution of the community at *Terumbu Siput*.

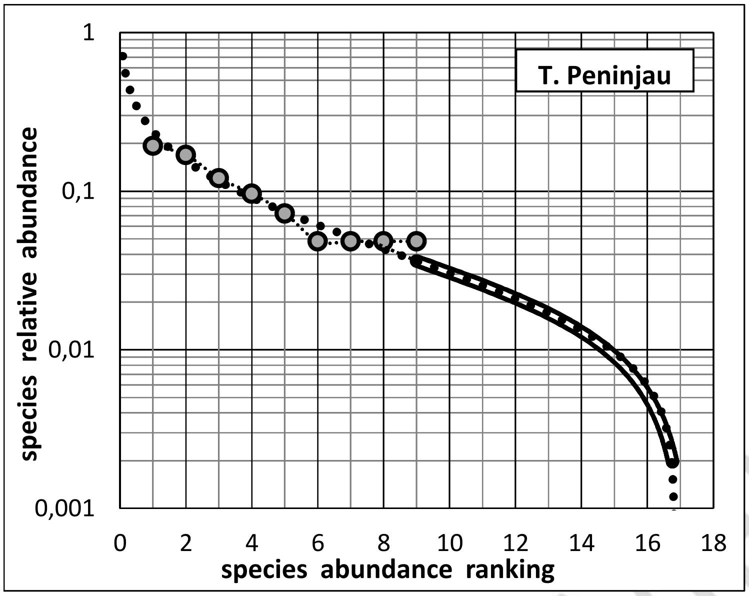


Figure 9 – The classical "log-normal" model (sigmoid dotted line) fitted to the completed Species Abundance Distribution of the community at *Terumbu Peninjau*.

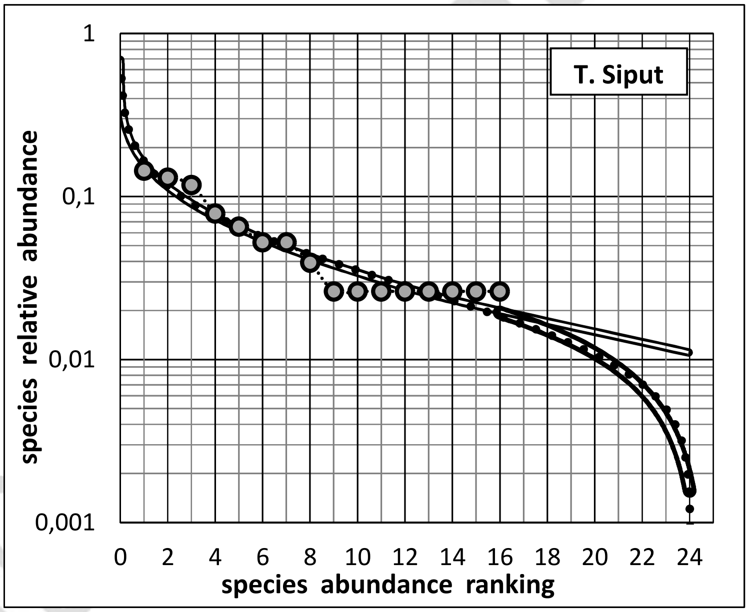


Figure 10 – The two classical models: "log-normal" (sigmoid dotted line) and "log-series" (fine double line) compared to the Species Abundance Distribution of the community at *Terumbu Siput*.Best fit is clearly obtained with the "log-normal" distribution. Note that considering the *recorded part* of the Species Abundance Distribution*only* would have led to the opposite conclusion: a "J" shaped model such as the "log-series" model would have fit the recorded part best than a "sigmoid" shapedmodel such as the "log-normal" model.

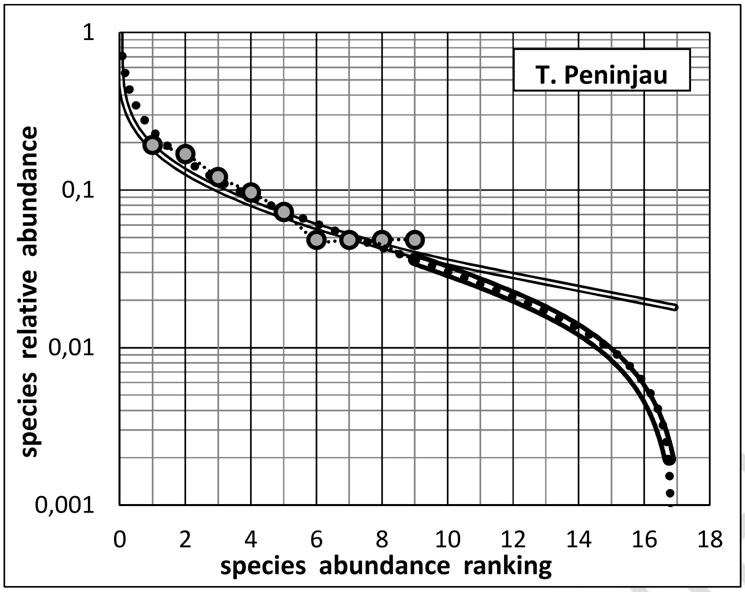
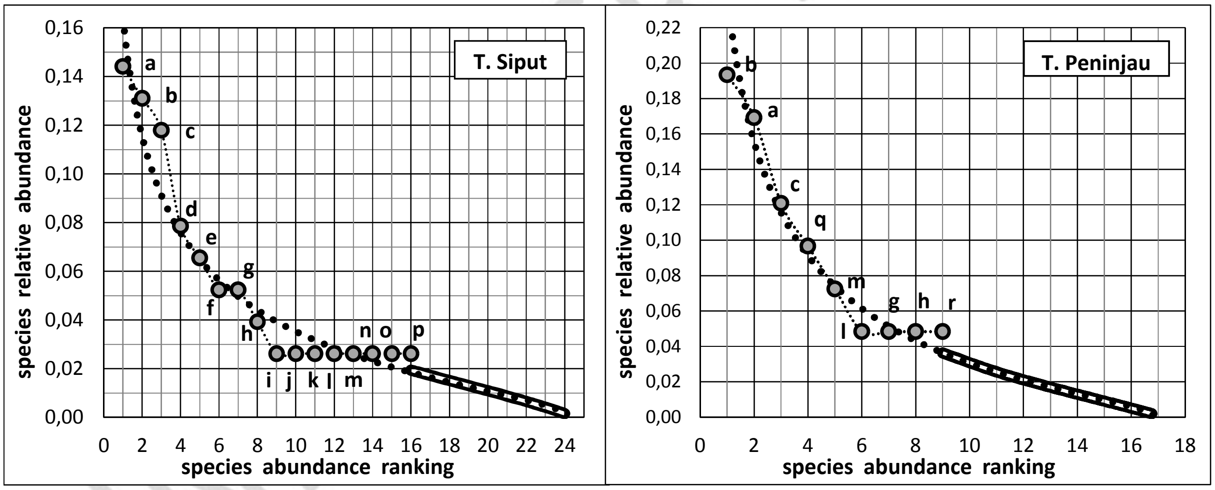


Figure 11 – The two classical models: “log-normal” (coarse dotted line) and “log-series” (fine double line) compared to the Species Abundance Distribution of the community at *Terumbu Peninjau*. Best fit is clearly obtained with the “log-normal” distribution. Note that considering the *recorded part* of the Species Abundance Distribution *only* would have led to the opposite conclusion: a “J” shaped model such as the “log-series” model would have fit the recorded part best than a “sigmoid” shaped model such as the “log-normal” model.



a: *Linckia laevigata* (Linnaeus 1758) –**b:***Linckia multifora*(Lamarck 1816)–**c**:*Culcita novaeguineae*Müller & Troschel 1842–**d**:*Linckia sp.* – **e:***Echinaster luzonicus*(Gray 1840)– **f:***Fromia monilis*(Perrier 1869)– **g:***Linckia guildingi*(Gray 1840)– **h:***Leiaster sp.*– **i:***Acanthaster planci*(Linnaeus 1758) – **j:***Asteropsis carinifera* (Lamarck 1816)–**k:***Echinaster callosus*Marrenzeller 1895 – **l:***Mithrodia fisheri*Holly 1932 –**m:***Fromia indica* (Perrier 1869) – **n:***Nordia sp.* –**o:** *Leiaster speciosus*von Martens 1866 –**p:***Ophidiaster hemprichi*Müller & Troschel 1842– **q:***Choriaster granulatus* (Lütken 1869) – **r:***Fromia* sp.

Figures 12& 13 – The same as Figures8&9, but, here, the species relative abundances are plotted untransformed (instead of being classically log-transformed: [32]) for a better visualization of the good general fit with log-normal model of the recorded part as well. The identities of the eighteen recorded species have been added.

3.3.2.the intensity of the hierarchical structuring process

According to the definitions provided in Methods section:

- the degree, U, of unevenness of species abundance distribution resulting from the process driving the hierarchical structuration of abundances is computed according to equation (1);

- the genuine intensity, I_{str}, 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. Figures14 and 15 allows this comparison, from which the genuine intensity I_{str} of the structuring process is derived according to equation (2).

The corresponding results are summarized in Table 2 which highlights (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 and, finally, (iv) the genuine intensity I_{str} of the process driving the hierarchical structuration of species abundances. Note that the parameters U and I_{str}accounts for two complementary aspects of the hierarchical structuration of species abundances: while U quantifies the apparent *pattern* of species abundance structuration,I_{str}highlights the genuine intensity of the underlying *process* driving this structuration. Being understood that, in quantitative terms, the unevenness pattern is far from faithfully reflecting the structuring process itself, as already emphasized.

The ratios $A_1 = (a_1/a'_1)$ and $A_{St} = (a_{St}/a'_{St})$ (which mirror the intensity of those factors which control the abundances a_1 and a_{St} of the more and the less frequent species: see section Methods) are derived accordingly: $A_1 = 0.92$, $A_{St} = 0.90$ at Terembu Siput and $A_1 = 0.96$, $A_{St} = 0.57$at Terembu Peninjau (Figures 16 and 17).

Table 2 – A synthetic summary of the main quantitative features of the hierarchical organization 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 the least abundant species (species rank 1 and S_t) ; (iii) the unevenness of abundances in the community: $U = \log(a_1/a_{St})/(S_t-1)$; (iv) the unevenness of abundances in the corresponding "broken-stick" distribution: $U' = \log(a'_1/a'_{St})/(S_t-1)$, (v) the genuineintensity of the structuring process $I_{str} = U/U'$ and, at last, the ratios $A_1 = (a_1/a'_1)$ and $A_{St} = (a_{St}/a'_{St})$.

sites	**S_t**	**a_1**	**a_{St}**	**a_1/a_{St}**	**a'_1**	**a'_{St}**	**U**	**U'**	**I_{str}**	**A_1**	**A_{St}**
T. Siput	24	0.14422	0.00157	94	0.15733	0.00174	0.0854	0.0851	1.003	0.92	0.90
T. Peninjau	17	0.19341	0.00197	98	0.20233	0.00346	0.1246	0.1104	1.128	0.96	0.57

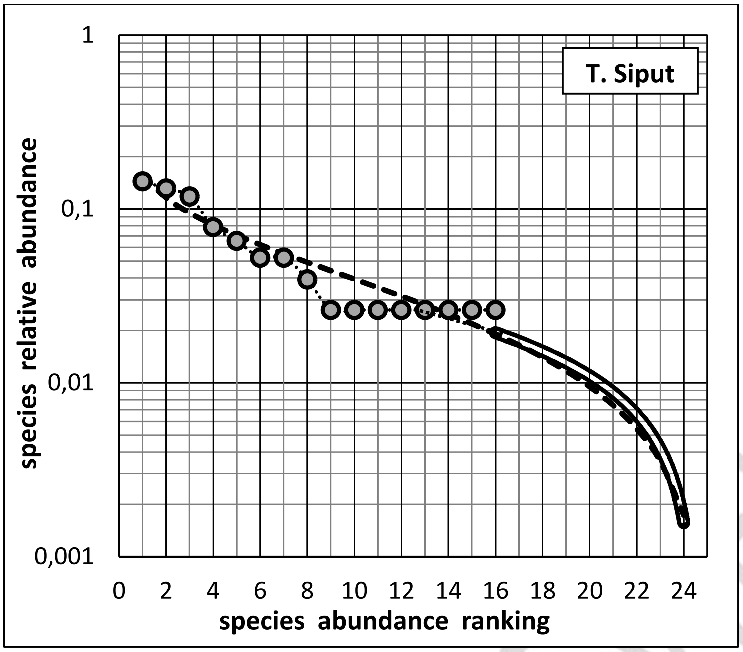


Figure 14 – The Species Abundance Distribution of the community at *Terumbu Siput*, plotted together with the corresponding "broken-stick" distribution (i.e. computed for the same species richness).

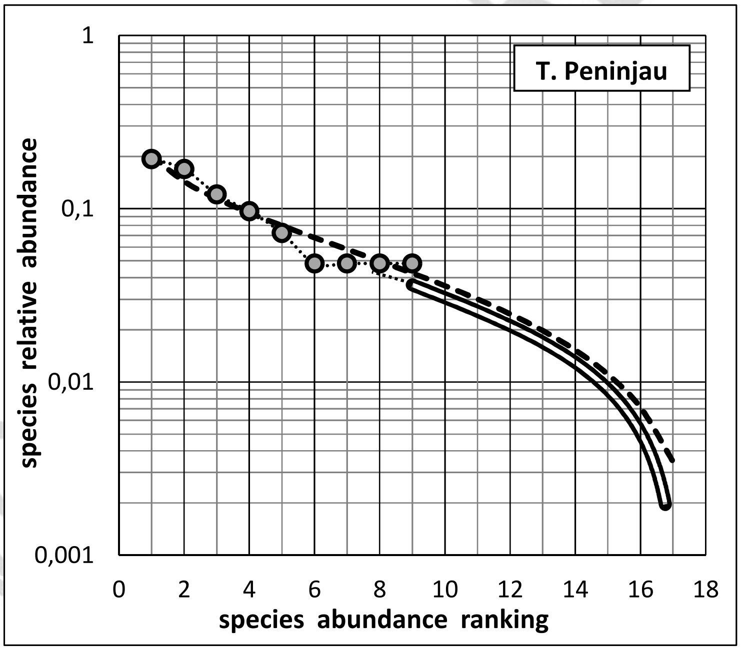
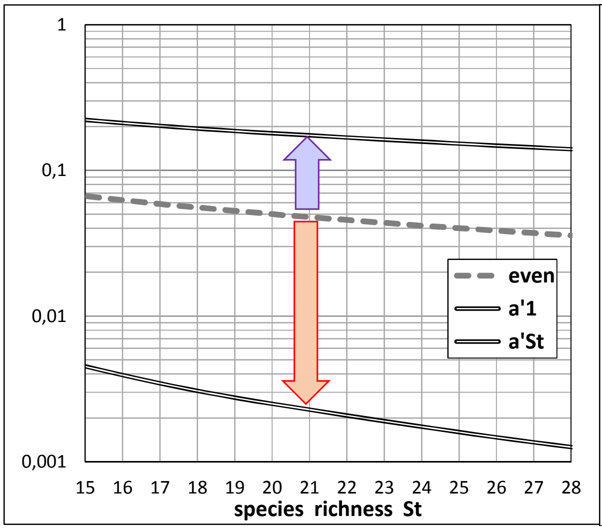


Figure 15 – The Species Abundance Distribution of the community at *Terumbu Peninjau*, plotted together with the corresponding "broken-stick" distribution (i.e. computed for the same species richness).



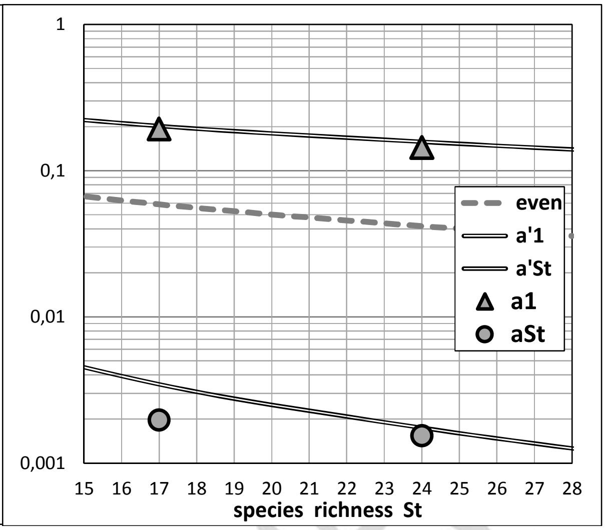
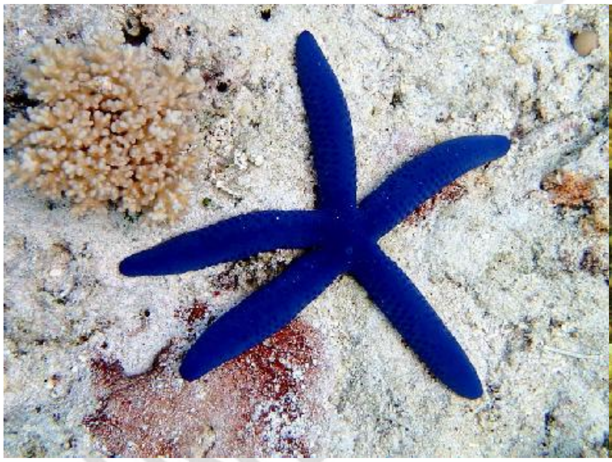
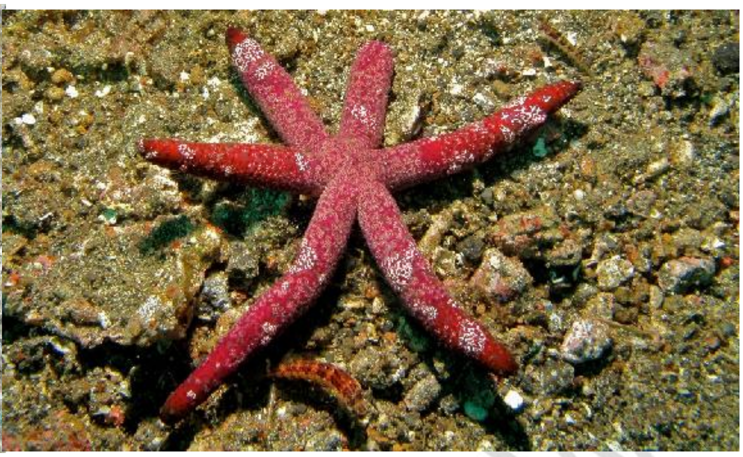


Figure 16 – The variations of the maximum and minimum abundances, a'_1 and a'_{St} of the “broken-stick” model (double lines) and the uniform abundance level (= $1/S_t$) of the perfectly “even” model (dashed line) as a function of the species richness S_t.

Figure 17 – The maximum and minimum abundances, a_1 and a_{St}, for each of the two studied sea-stars communities plotted jointly with the maximum and minimum abundances, a'_1 and a'_{St} of the “broken-stick” model and the uniform abundance level (= $1/S_t$) of the perfectly “even” model.

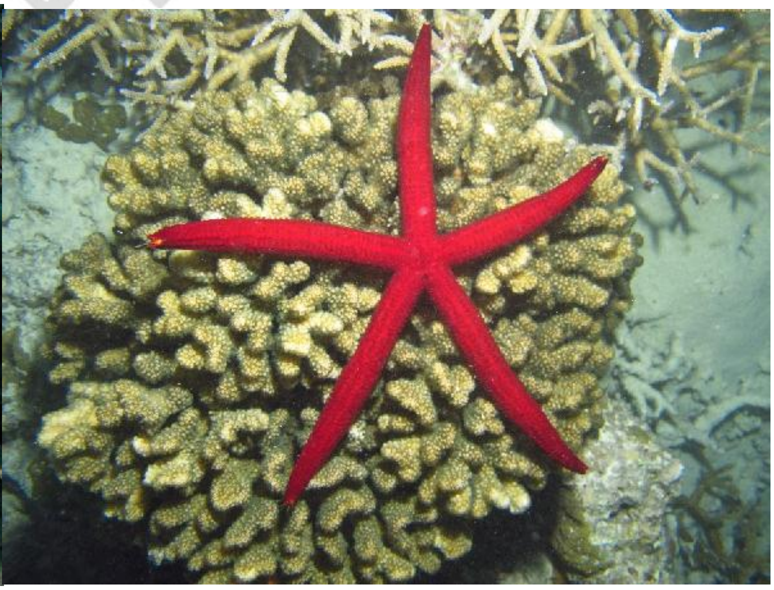


Linckia laevigata(Linnaeus 1758) © dr.scott.mills*Linckia multifora*(Lamarck 1816)© Frédéric Ducarme



*Culcita novaeguineae*Müller & Troschel 1842 © Shizhao *Echinaster luzonicus*(Gray 1840) © Bernard Dupont

Fromia monilis(Perrier 1869)© Hectonichus*Acanthaster planci* (Linnaeus 1758)© Michel Dammeron



*Echinaster callosus*Marrenzeller 1895© Nick Hobgood*Leiaster speciosus*von Martens 1866© MDC Seamark


Choriaster granulatus(Lütken, 1869) © Ed. Callaghan*Asteropsis carinifera*(Lamarck 1816) © Ph. Bourjon

4. DISCUSSION

Trying to get a comprehensive understanding – species by species – of the internal organization of species-rich communities would normally require long and tedious programs of field investigations, often beyond the usual practical possibilities.

Limiting the scope to the mere evaluation ofthe total species richness and the overall, synthetic characterization of the hierarchical structuring of abundances would yet still require the *exhaustive* sampling of the studied species assemblage.And even thisless demanding requirementis often difficult to reach in practice, especially when having to deal with species-rich communities including a lot of rare species, as is, for example, often the case with invertebrate faunas.

Fortunately, the implementation of appropriate methodsof numerical extrapolation can “force”incomplete samplings and partial inventories to reveal *much more information* than one wouldhave expected*a priori*. Indeed, proper numerical extrapolations of both the Species Accumulation Curve and the Species Abundance Distribution can provide an unexpectedly richset of additional information relative to those species remaining *undetected*after partial sampling. This, in turn, allows to tackle the main issues relative to the evaluation of true (total) species richness and the hierarchical organization of species abundance,even whencommunities are only partially sampled – all subjects that otherwise would have requiredexhaustiveinventories.

A thorough analysis of twosea-starscommunities associated to coral reefs, located in the Central South China Sea,has been 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 procedure of numerical extrapolation implies selecting the *least-biased* estimator of the number of undetected species. Here, estimators Jackknife-3 and Jackknife-5 are selected for the communities at Trembu Siput and Terembu Peninjau respectively.Accordingly, the total species richness estimated this way reaches 24 species at Trembu Siput and 17 speciesat Terembu Peninjau(Table 1),which substantially exceeds the recorded numbers (16 and 9 species respectively).This confirms the limited levels of sampling completeness (67% and 53% respectively)and thus justifies, *a posteriori*, the need for implementing numerical extrapolations of these inventories.The importance of selecting for each community thecorresponding*least-biased* estimator of the number of undetected species – and the associated least-biased extrapolation of the Species Accumulation Curve – is advocated at Figures1 and 3, which both highlight the marked differences that separate the extrapolations of the Species Accumulation Curve associated to different types of estimators. In particular, here, Jackknife-1 and Chao estimators prove being strongly biased negatively (Figures 1 and 3). Although the least-biased numerical extrapolationcan provide a lot of additional interesting information regarding the set of still unrecorded species, further sampling effort, aiming at increasing the completeness of inventories, might alternatively be considered. In this perspective, reliable forecasts of the additional sampling effortsin order to meet anytargetedgain in sampling-completeness would be useful for the optimal planning of the additional efforts to be implemented. The least-biased extrapolation of the Species Accumulation Curve answers appropriately this demand, as shown in Figures 2 and 4). Clearly, further improvements of sampling completeness would rapidly requirevery substantial additional efforts. For example, increasing completeness at Terembu Siput, fromthe actual 67% level upto 80%, 90%, 95% completeness levels would require multiplying the actual sample-size (N_0 = 52) by a factor2, a factor 3.5, a factor7, respectively. Being able to reliably estimate the required additional efforts, as shown above, is of obvious prime interest to rationally decide whether to continue sampling operation any further orto rely only on actual partial inventories, subsequently completed by numerical extrapolation.

4.2 Correction and extrapolation of the Species Abundance Distribution

As-recorded Species Abundance Distributionsneed correction and extrapolation because both are (i) slightly *biased* due to sampling stochasticity and (ii) most importantly, *incomplete*, as no less than eight species had remained undetected, in each studied community.After correction and extrapolation are applied, the complete development of the Species Abundance Distributions, including the estimated distribution of the abundances of the still undetected species, is made available: Figures5, 6, 7. Note that complementation of Species Abundance Distribution to include the (undetected) less abundant species may be more important than it might seem at first glance. Indeed, less abundant species may possibly have ecological importance no less than more common species,as it hasalready been repeatedly emphasized [40 – 49]. Inaddition, considering the*full range*of the Species Abundance Distributionis 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 as well as the genuine intensity of this structuring process. Indeed, answering these questions properly requires comparing the *full range* ofSpecies Abundance Distribution to different theoretical models [5], at the risk, otherwise, to provide severely erroneous inferences.

4.3 Inferring the type of process driving the hierarchical structuring of species abundances

Considered full range, the Species Abundance Distributions of bothstudied communitiesclearly fit bestthe "log-normal" distribution than the "log-series" distribution (Figures8 to 11). This suggests that the *processof structuration* of thesesea-starscommunitiesis likely driven by the combined contributions of many independent factors, rather than by only one (or very few) dominant factor. This, in fact, might well be a rather general trend, as already argued elsewhere [5, 25, 26 – 28]. Moreover, the fairly goodfitto the "log-normal" model standsas good within the range of most abundant species (i.e. for lower ranks i). Thissuggeststhat, in these sea-stars communities, no additionalnegatively (resp. positively) density-dependent factor actually occurs that, otherwise, would have depressed(resp. increased) the levels of abundance of the most abundantspecies.

At last, it is also worth noting that relying *only*upon the recorded part of the Species Abundance Distribution would have led to the *opposite conclusion*: indeed, the “J” shape of the “log-series” model fits the *recorded* part best than does the “sigmoid” shape of the “log-normal” model. This is a new confirmation that relyingupon incomplete distributions of abundances *only* (i.e. neglecting the numerical extrapolation when required) may often leads to *erroneous diagnostics*, as already emphasized by several authors [4, 6, 20, 27, 50, 51].

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 subset of the still undetected species but, also, to make possible the standardization of the Species Abundance Distribution slope to the corresponding “broken-stick” reference (Figures 14 & 15). As argued above, this is a key-condition to unveil the *genuine intensity*$I_{str}$of the process driving the hierarchical structuration of species abundances.

Here (Table 2), the intensity of the structuring process is very close to 1(i.e. very similar to the intensity in the “broken-stick” model) for the community at Terembu Siput (I_{str} = 1.003), while in the community at Terembu Peninjau,the intensity of the structuring process is somewhat (12%) stronger (I_{str} = 1.128). In turn, this stronger structuring intensityis only marginally related to the level of dominance of the most abundant species (since the values of$A_1 = (a_1/a'_1)$for both communities are very similar: Table 2, Figure 17). Instead, the stronger structuring intensity is mainly due to the lower value of $A_{St} = (a_{St}/a'_{St})$ (0.90 at Terembu Siput and 0.57 only at T. Peninjau: Table 2, Figure 17). In other words, the larger intensity of the structuring process highlighted in the community at Terembu Peninjau mainly involves the right-hand part of the abundance distribution, that is the set of less abundant species.

Another interesting question is: how the structuring intensitiesI_{str}in these two sea-stars communities would compare withthe structuring intensities in other types of marine invertebrates communities. The currently available data in this respectremains still limited [21, 34, 35], but yetsuggests that tropical marine gastropod communities tend to be more stronglystructured than the two studied sea-stars communities.

As regards the *unevenness pattern*, the difference in the degree of unevenness U between the two studied communitiesproves being still far larger (> 46%, Table 2) than is the difference in the genuine intensity of the structuring process (12%). As already emphasized, such discrepancy between the pattern (U) and the underlying process (I_{str}) is the mere mathematical consequence of the difference in species richness between the two communities.

At last it should be noted that if the three more abundant species are the same in both communities (labelled a, b, c: see Figures 12 &13); the taxonomic composition of less abundant species is, on the contrary, very different – at least as regards the set of recorded species. Yet, this cannot be considered as firmly conclusive, as it might well be possible that this difference would be less pronounced if the taxonomic identities of the unrecorded species were unveiled. In this respect, numerical extrapolation finds its limit and only further sampling can actually provide a sound answer. An answer, however, at a very substantialextra-cost in term of additional sampling effort. Additional effort that the numerical extrapolation of the Species Accumulation Curvescan efficiently help to predict (Figures 2 & 4).

5. CONCLUSION

When dealing with substantially incomplete species inventories, the numerical extrapolations of (i) the *Species Accumulation Curve* and (ii)the *Species Abundance Distribution* offer remarkable opportunities to unveil an unexpectedly rich sum of information relative to the set of undetected species. In turn, thanks tothe resulting access to the *full range* of the Species Abundance Distribution, interesting additional information may be derived, regarding the process driving the hierarchical organization of species abundances within a partially sampled community. The numerical extrapolations – hereappliedto the partial inventories of two sea-stars communities – demonstrate concretely the wide range of ecological questions that may be addressed and successfully answered, even when no less thanone third up to almost half of the member-species had remained unrecorded.

In short, this clearly highlights the potential interest of numerical extrapolations applied to partial inventories, in the context of increasingly frequentpractice of "quick assessments" of biodiversity, especially when having to deal with highly species-richassemblages, as is often the case with invertebrate faunas under tropical climates.

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, 52, 53]:

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

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 $R_{\mathbf{x}}(N)$ that respectively satisfy the mathematical constraint (A1.1), considering increasing orders x of derivation $\partial^x R_{(N)}/\partial N^x$. Each solution $R_{\mathbf{x}}(N)$ is appropriate for a given range of values of f_1 compared to the other numbersf_x, according to [17]:

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

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

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

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

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

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

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

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

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

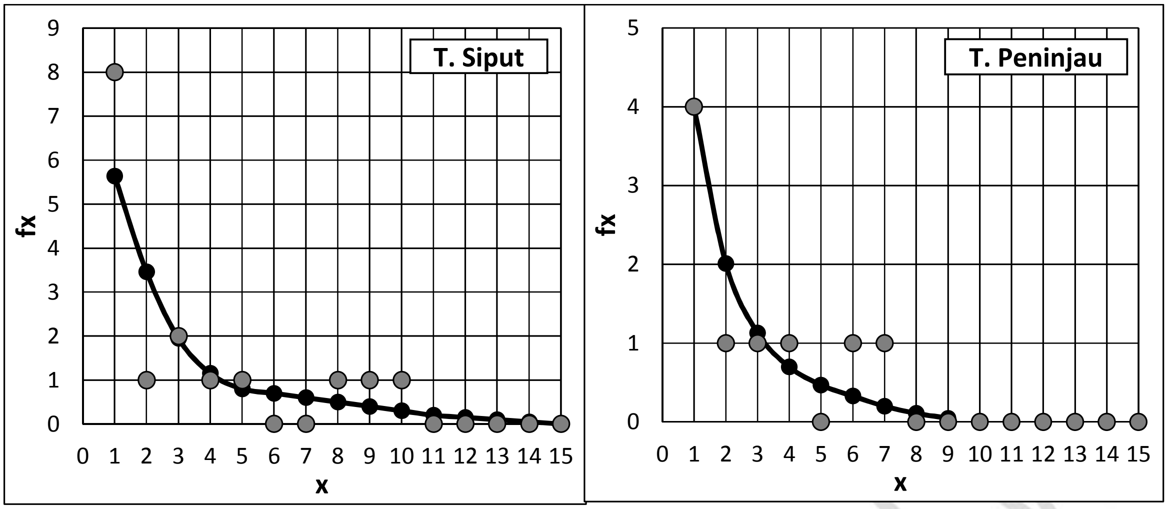
* $3f_2 - 3f_3 + f_4 < \mathbf{f_1} \leq 4f_2 - 6f_3 + 4f_4 - f_5 \rightarrow \quad \Delta_{J4} = 4f_1 - 6f_2 + 4f_3 - f_4$; $\quad R_4(N)$

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

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 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 [2, 3, 15, 16, 54]. Also, this shows that the approach initially proposed by BROSE *et al.*[55] – which has regrettably suffered from its somewhat difficult implementation in practice – might be advantageously reconsidered, now, in light of the very simple selection key above, of *far much easier practical use*.

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

N.B. 3: For f_1 falling beneath 0.6 x f_2 (that is when sampling completeness closely approaches exhaustivity), then Chao estimator may be selected: see reference [18].



Figures A1 & A2 – 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 during sampling.

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 [20].

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

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

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

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

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

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

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

which, in practice, comes down to:

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

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: Figure A3

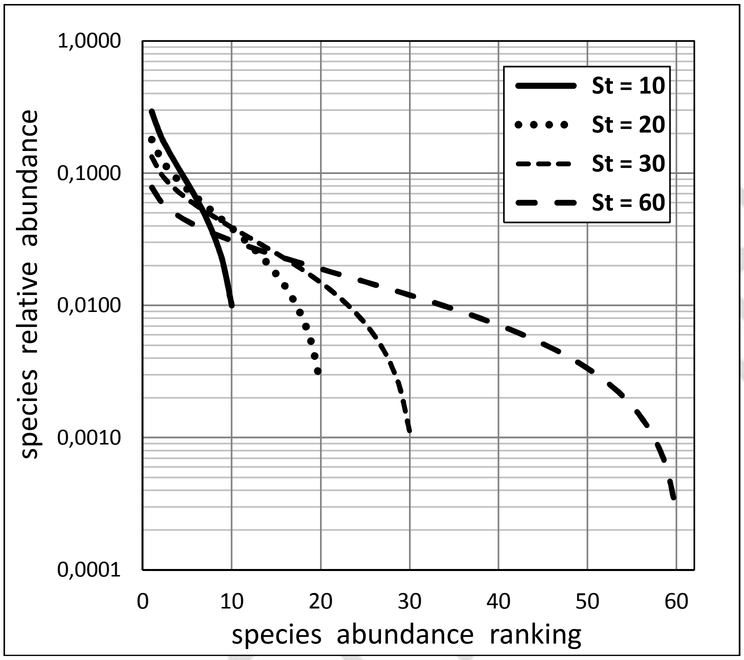


Figure A3 – The "broken-stick" distribution model applied to species communities with increasing species richness S_t = 10, 20, 30, 60. Although the theoretical structuring process involved in the "broken-stick" model remains unchanged (random apportionment of relative abundances among member species),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

COMPETING INTERESTS

Author has declared that no competing interests exist.

References

1. CamE, Nichols JD, Saue JR & Hines, JE.On the estimation of species richness based on the accumulation of previously unrecorded species. Ecography. 2002; 25: 102-108.

2. Rajakaruna H, Drake DAR, Chan FT & Bailey SA.Optimizing performance of nonparametric species richness estimators under constrained sampling. Ecology and Evolution. 2016; 6: 7311-7322.

3. ChenY& Shen TJ.Rarefaction and extrapolation of species richness using an area-based Fisher's logseries. Ecology and Evolution. 2017; 7: 10066-10078.

4. Connolly SR, Hughes TP & Bellwood DR. A unified model explains commonness and rarity on coral reefs. Ecology Letters. 2017; 20: 477-486.

5. May RM. Patterns of species abundance and diversity. InCody M.L. & Diamond J.M. Ecology and Evolution of Communities. 1975; The Belknap Press of Harvard University: 81-120.

6. McGill BJ, Etienne RS, Gray JSet al. Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. Ecology Letters. 2007; 10: 995-1015.

7. Ulrich W, Ollik M& Ugland KI.A meta-analysis of species-abundance distributions. Oikos. 2010; 119:1149-1155.

8. Komonen A& Elo M. Ecological response hides behind the species abundance distribution: community response to low-intensity disturbance in managed grasslands. Ecology and Evolution. 2017; 7: 8558-8566.

9. Wang X, Ellwood F, Ai D, Zhang R& Wang G.Species abundance distributions as a proxy for the niche-neutrality continuum. Journal of Plant Ecology. 2017; rtx 013.

10. Wells JW.Coral reefs: 609-632; in J.W. Hedspeth editor, Treatise on marine ecology and paleoecology. 1957; Geological Society of America. Mem. 67.

11. Glynn PW.High complexity food webs in low-diversity eastern Pacific reef-coral communities. Ecosystems. 2004; 7: 358-367.

12 Kwang SY, Shau-Hwai AT & Yasin S. The diversity and abundance of the Sea Stars (Echinodermata: Asteroidea) from coral reefs of the Central South China Sea. The Nagisa Westpac Congress. 2008; 25-36.

13 Purwati P & Lane DJW. Asteroidea of the Anambas Expedition 2002. The Raffles Bulletin of Zoology. 2004; suppl. n° 11: 89-102.

14. Coddington JA, Agnarsson I, Miller JA, Kuntner M & Hormiga G. Undersampling bias : the null hypothesis for singleton species in tropical arthropod surveys. Journal of Animal Ecology. 2009; 78: 573-584.

15. Gotelli NJ & Colwell RK. Estimating species richness. pp. 39-54 in: Biological Diversity: Frontiers In Measurement And Assessment. A.E. Magurran and B.J. McGill (eds.). 2010; Oxford University Press, Oxford. 345 pp.

16. Gotelli NJ & Chao A. Measuring and Estimating Species Richness, Species Diversity, and Biotic Similarity from Sampling Data. In: Levin S.A. (ed.) Encyclopedia of Biodiversity. 2013; second edition, volume 5, pp. 195-211. Waltham, MA: Academic Press.

17. Béguinot J.Theoretical derivation of a bias-reduced expression for the extrapolation of the Species Accumulation Curve and the associated estimation of total species richness. Advances in Research. 2016; 7(3): 1-16. doi: 10.9734/AIR/2016/26387 ; <hal-01367803>

18. Béguinot J. Extrapolation of the Species Accumulation Curve associated to “Chao” estimator of the number of unrecorded species: a mathematically consistent derivation. Annual Research & Review in Biology. 2016; 11 (4): 1-19 doi: 10.9734/ARRB/2016/30522; <hal 01477263 >

19. Chao A, Hsieh T, Chazdon RL, Colwell RK & Gotelli NJ. Unveiling the species-rank abundance distribution by generalizing the Good-Turing sample coverage theory. Ecology. 2015; 96(5): 1189-1201.

20. Béguinot J.How to extrapolate species abundance distributions with minimum bias when dealing with incomplete species inventories. Advances in Research. 2018; 13(4): 1-24. doi: 10.9734/AIR/2018/39002.

21. Béguinot J. 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). Asian Journal of Environment and Ecology. 2018; 6(4): 1 – 23. doi: 10.9734/AJEE/2018/41293 <hal-01807454>

22. Heip CHR, Herman PMJ & Soetaert K. Indices of diversity and evenness. Océanis. 1998; 24(4): 61-87.

23. Strong WL. Assessing species abundance unevenness within and between plant communities. Community Ecology. 2002; 3(2):237-246· doi: 10.1556/ComEc.3.2002.2.9

24. Grzès IM. Ant species richness and evenness increase along a metal pollution gradient in the Boleslaw zinc smelter area. Pedobiologia. 2009; 53: 65-73.

25. Loreau M. Species abundance patterns and the structure of ground-beetle communities. Ann. Zool. Fennici. 1992; 28: 49-56.

26. Magurran AE & Henderson PA. Explaining the excess of rare species in natural species abundance distributions. Nature. 2003; 422: 714-716.

27. Connolly SR, Hughes TP, Bellwood DR & Karlson RH. Community structure of corals and reef fishes at multiple scales. Science. 2005; 309: 1363-1365.

28. Ulrich W, Soliveres S, Thomas AD, Dougill AJ & Maestre FT. Environmental correlates of species rank-abundance distributions in global drylands. Europe PMC Funders Group. 2016; 20: 56-64.

29. Smith B & Wilson JB. A consumer’s guide to evenness indices. Oikos. 1996;76: 70-82.

30. Loiseau N & Gaertner JC. Indices for assessing coral reef fish biodiversity: the need for a change in habits. Ecology and Evolution. 2015; 5(18): 4018-4027.

31. MacDonald ZG, Nielsen SE & Acorn JH. Negative relationships between species richness and evenness render common diversity indices inadequate for assessing long-term trends in butterfly diversity. Biodiversity Conservation. 2017; 26: 617-629.

32. MacArthur RH. On the relative abundance of bird species. Proceedings of the National Academy of Sciences U.S.A. 1957; 43: 293-295.

33. Béguinot J. The hierarchical structuring of species abundances within communities: disentangling the intensity of the underlying structuring process behind the apparent unevenness pattern. Advances in Research. 2018; 16(1): 1-12. doi: 10.9734/AIR/2018/43918.

34. Béguinot J. The full hierarchical structuration of species abundances reliably inferred from the numerical extrapolation of still partial samplings: a case study with marine snail communities in Mannar Gulf (India). Asian Journal of Environment and Ecology. 2018; 7(3): 1-27. doi: 109734/AJEE/2018/36831.

35. Béguinot J. Analyzing 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). International Journal of Environment and Climate Change. 2018; 8(3): 200-233. doi: 109734/IJECC/2018/44913.

36. Pinto-Sanchez NR, Crawford AJ & Wiens JJ. Using historical biogeography to test for community saturation. Ecology Letters.2014; 17(9): 1077-1085.

37. Cornell HV. Unsaturation and regional influences on species richness in ecological communities: a review of the evidence. Ecoscience. 1999; 6(3): 303-315.

38. Loreau M. Are communities saturated? On the relationship between alpha, beta and gamma diversity. Ecology Letters. 2000; 3: 73-76.

39. Diamond JM. Assembly of species communities. In Cody M.L. & Diamond J.M. 1975 Ecology and Evolution of Communities. The Belknap Press of Harvard University: 81-120.

40. Novotny V& Basset Y. Rare species in communities of tropical insect herbivores: pondering the mystery of singletons. Oikos. 2000; 89: 564-572.

41. Harte J.Tail of death and resurrection. Nature. 2003; 424: 1006-1007.

42. Bracken M & Low N. Realistic losses of rare species disproportionately impact higher trophic levels. Ecology Letters. 2012; 15: 461-467.

43. Mouillot D, Bellwood DR, Baraloto C, Chave J, Galzin R, Harmelin-Vivien M, Kulbicki M, Lavergne S, Lavorel S, Mouquet N, Paine CET, Renaud J & Thuiller W. Rare species support vulnerable functions in high-diversity ecosystems. PLoS Biol. 2013; 11(5): e1001569.

44. Stuart-Smith RD, Bares AE, Lefcheck JS, Duffy JE, Baker SC, Thomson RJ, Stuart-Smith JF, Hill NA et al. Integrating abundance and functional traits reveals new global hotspots of fish diversity. Nature. 2013; 501:539-541.

45. Jain M, Flynn DFB, Prager CM, Hart GM, DeVan CM, Ahrestani FS, Palmer MI, Bunker DE, Knops JHM, Jouseau CF & Naeem S. The importance of rare species: a trait-based assessment of rare species contribution to functional diversity and possible ecosystem function in tall-grass prairies. Ecology and Evolution. 2014; 4(1): 104-112.

46. Henderson PA& Magurran AE.Direct evidence that density-dependent regulation underpins the temporal stability of abundant species in a diverse animal community. Proceedings of The Royal Society B. 2014; 281. doi: 10.1098/rspb.2014.1336.

47. Low-Decarie E, Kolber M, Homme P, Lofano A, Dumbrell A, Gonzalez A & Bell G. Community rescue in experimental communities. Proceedings of the National Academy of Sciences USA. 2015; 112(46): 14307-14312.

48. Leitao RP, Zuanon J, Villéger S, Williams SE, Baraloto C, Fortunel C, Mendonça FP & Mouillot D. Rare species contribute disproportionately to the functional structure of species assemblages. Proceedings of The Royal Society B. 2016; 283: 2016 0084 ; doi: 10.1098/rspb.2016.0084

49. Violle C, Thuillier W, Mouquet N, Munoz F, Kraft NJB, Cadotte MW, Livingstone SW & Mouillot D. Functional rarity: the ecology of outliers. Trends in Ecology. 2017; doi 10.1016/j.tree.2017.02.002

50.Magurran AE.Species abundance distributions: pattern or process? Functional Ecology. 2005;19: 177-181.

51. Matthews TJ& Whittaker RJ.On the species abundance distribution in applied ecology and biodiversity management. Journal of Applied Ecology. 2015; 52: 443-454.

52. Béguinot J.An algebraic derivation of Chao's estimator of the number of species in a community highlights the condition allowing Chao to deliver centered estimates. ISRN Ecology. 2014; vol. 2014 : article ID 847328, doi:10.1155/2014/847328 ; <hal-01101415>

53. Béguinot J.When reasonably stop sampling? How to estimate the gain in newly recorded speciesaccording to the degree of supplementary samplingeffort. Annual Research & Review in Biology. 2015; 7(5): 300-308. doi : 10.9734/ARRB/2015/18809 ; <hal-01228695>

54. O'Hara RB. Species richness estimators: how many species can dance on the head of a pin? Journal of Animal Ecology. 2005; 74: 375-386.

55. Brose U, Martinez ND & Williams RJ. Estimating species richness: sensitivity to sample coverage and insensitivity to spatial patterns. Ecology. 2003; 84(9): 2364-2377.