Variations in total species richness and the unevenness of species abundance distribution between two distant *Conus* communities (Neogastropoda): a case study in Mannar Gulf (India)

Original Research article

Abstract

The genus *Conus* forms a conspicuous and rather homogeneous group within marine Gastropods. This makes it all the more interesting to focus on the sub-communities formed by *Conus* species and to analyze the potential specificities in the internal organization of species in these communities, in particular species richness, species abundance distribution and the effect of geographical distance between communities on differences in their respective species composition. Accordingly, two *Conus* communities along the coast in Mannar Gulf (India), separated by 80 km, are considered. Reliable analysis requires, first, to treat exhaustive data from complete samplings or else – as here – to implement an appropriate extrapolation procedure to complete numerically the partial sampling. Substantial differences were highlighted between the two communities, not only in terms of true (total) species richness but, even more, as regards the profile and the average unevenness of the distributions of species abundance. Also, significant dissimilarity in species composition was found between the two communities, that may be tentatively attributed to either "deterministic" distance decay in similarity of species composition or, alternatively, to the persistence in the stochastic process of species recruitment from the regional stock of *Conus* planktonic larvae. This preliminary study yet requests to be complemented by other similar case studies, before drawing any safer interpretative conclusions.

Key-words: species diversity, ranked species abundance distribution, evenness, distance decay in similarity, incomplete sampling, numerical extrapolation, recruitment stochasticity.

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1. INTRODUCTION

Among all marine gastropods, the genus *Conus* makes an emblematic and attractive group to study, rather homogeneous in morphological aspect and very specific in its predation behavior [1, 2]. Less attention, however, has been devoted to the genus *Conus* as a subset (sub-community) within the marine gastropod communities in which they are included. Yet, it may be of interest to check whether or not *Conus* sub-communities are specific and singular as regards their internal structuration, highlighting in particular the relationship which can exist between the *species richness* and the *unevenness of species abundances*. Fortunately, several quantified inventories devoted to this group have already been reported which can provide basic data necessary to address the goal ~~I have just~~ stated above. Less fortunate however, these inventories most often remained incomplete, as evidenced from the subsistence of a substantial proportion of singletons, i.e. species recorded only once during sampling. Indeed, incomplete samplings are often unavoidable in practice when having to deal with species rich communities including numerous rare species. Numerical extrapolation of such incomplete samplings represents, however, an alternative solution to compensate for incompleteness, provided that during partial sampling, the respective abundances of recorded species are also registered. When this is the case, numerical extrapolation offers a useful surrogate to sampling incompleteness, especially when an appropriate extrapolation procedure is implemented, which allows to estimate not only the number of unrecorded species but also the abundances of each unrecorded species [3-5]. Numerical completion of partial samplings is all the more necessary that, contrary to what may be thought, rare species, that often escape recording in practice, may yet disproportionately contribute to the functional structuring of communities in the wild [6-16]. In particular, neglecting rare species can seriously reduce the capacity to detect ecological changes when analyzing species communities comparatively; so that “rare species are critical for bio-assessment” [16].

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As part of a series of other reports devoted to this project [17-25], ~~I consider~~, hereafter, cosiderations are taken on the partial inventories of two *Conus* communities located in the Gulf of Mannar (India) and separated from each other by a distance of 80 km, as reported by Gugulothu et al. [26].

After implementation of the required numerical extrapolations, I address the following points, for each two *Conus* sub-communities, i.e. the estimated true (total) species richness, the exhaustive (i.e. numerically completed) distribution of species abundances, with related considerations regarding the kind of process involved in the hierarchical structuring of abundances and the estimated mean competitive intensity within each sub-community, the relation between species richness and species abundance unevenness, directly derived from the comparison between the two *Conus* sub-communities, the degree of dissimilarity in species composition between the two compared sub-communities and what can be deduced in terms of either distance decay in similarity or stochasticity of species recruitment at the local scale (since both causes can possibly contribute to the observed dissimilarity in species composition).

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2. MATERIALS AND METHODS

2.1 – The reported field data

The present study is based on two partial samplings of *Conus* communities conducted at two localities, “Therespuram” and “Keelakarai”, distant from each other by ≈ 80 km, along the coast of Mannar Gulf National Reserve (south east India). All details regarding the precise locations of the compared habitats and the sampling procedure are provided in the open-access reference [26] and need not being repeated here. An important point is that the numbers of individual occurrences have been recorded for each species, thus making possible to implement numerical extrapolation in case of substantially incomplete inventory. Sampling incompleteness is revealed by the subsistence of “singletons” (species recorded only once), as indeed is the case for one of the inventories, at

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"Keelakarai". The number N_0 of collected individuals and the number R_0 of recorded species in each of the two communities are given in Table 1.

2.2 - The Numerical Extrapolation procedure and its exploitation

To avoid making seriously biased inferences regarding the main structural descriptors of ecological communities (i.e. total species richness and abundance unevenness), it is required to rely upon (sub-) exhaustive inventories [27–31]. However, when incomplete samplings only are available, a reliable procedure of *numerical extrapolation* can serve as an efficient surrogate [32]. Beyond estimating the number of unrecorded species, a newly developed extrapolation procedure can even provide, in addition, least-biased estimates of the respective abundance of each of these unrecorded species, as detailed in sections 2.2.1 to 2.2.3. Moreover, once properly numerically completed (and *only* when it is so [29]), 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 [33-37].

2.2.1 - *Implementation of the procedure of numerical extrapolation*

* *Total species richness*: the least-biased estimation of the number of still unrecorded species during partial sampling and the resulting estimation of the total species richness of the partially sampled community are computed according to the procedure defined in [3, 4] and briefly summarized in Appendix 1, on the basis of the numbers f_x of species observed x-times during partial sampling (x = 1 to 5). The same procedure allows to derive the least-biased extrapolation of the "Species Accumulation Curve", which predicts the expected increase in the number of newly recorded species, R(N), as a function of the growing sampling size N (N: number of currently recorded individuals); see Appendix 1 for computation. In practice, this extrapolation allows to *forecast* the likely additional sampling efforts that would be required to obtain any desirable increment in sampling completeness.

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* *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 [5, 38], the "S.A.D." requires (i) to be *corrected* for the bias resulting from drawing stochasticity during sampling of finite size and, still more importantly, (ii) to be *completed* by *numerical extrapolation*, to the extent that sampling is suspected to be incomplete, as revealed by the subsistence of singletons. The appropriate procedure of correction and least-biased numerical extrapolation of the as-recorded partial "S.A.D." is described in details in reference [5], briefly summarized in Appendix 2 and concretely exemplified in details in [18]. Classically, the "S.A.D." is graphically presented with the (log-transformed) abundances, a_i, 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 of S_t species).

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2.2.2. *Abundance unevenness: the pattern of species abundance structuration*

Once numerically completed, the "S.A.D." conveys all the relevant quantitative data required to address the internal organization among species within a local community [39]. In turn, the "S.A.D." can be synthetically summarized by two of its major features: the

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total species richness 'S_t' and the *degree* 'U' *of unevenness* of the abundance distribution. Indeed, following [40], it is the degree of *unevenness* – rather than evenness itself – that should be preferred to address the hierarchical structuring of species abundances in communities. According to the mode of representation of "S.A.D.", it goes natural to quantify the degree of abundance unevenness U as the average slope of the log-transformed abundance decrease, as already proposed by [41], that is:

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

with a_1 and a_{St} standing for the highest and the lowest abundances in the studied community.

2.2.3. *Abundance unevenness: the underlying process of abundance structuration*

Beyond the unevenness *pattern* U, the underlying *process* of hierarchical structuration of abundances is worth being considered, in terms of (i) the kind of *mechanism* involved and (ii) what determines the *intensity* of this structuring process, from which follows the degree of abundance unevenness. Very schematically, the kind of *mechanism* driving 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 distinction can be tested by checking the conformity of the "S.A.D." to either the *log-series* model or the *log-normal* model respectively [33, 42-45].

As regards now the *intensity* of the process of hierarchical structuration, it should be first emphasized that species richness has a *direct*, negative influence on abundance unevenness U, *as a general trend*, a point already highlighted by several authors [46-50]. The likely underlying ecological origin of this overall trend (behind its "mathematical-like" appearance [46, 49]) is discussed in detail in [51]. Now, each particular community usually deviates more or less – often substantially – from this overall trend. So that it is appropriate to *consider and quantify separately*: (i) on the one hand, the contribution of this overall general trend and (ii) on the other hand, the more or less important deviation from this tendential influence, which specifically singularizes each particular community and is particularly significant ecologically [50, 51]. As argued in detail in [51], the direct, negative influence of species richness on abundance unevenness is adequately accounted for by the "broken-stick" theoretical distribution, originally conceptualized by MacArthur [52]. Accordingly, it looks relevant to standardize the "rough" abundance unevenness U to the corresponding rough abundance unevenness U' of the "broken-stick" distribution, computed for the same species richness [53]. Doing so highlights to what extent the rough abundance unevenness U of a community actually deviates from the common overall trend, dictated by the tendential, direct influence of species richness [46, 47, 50, 51, 53].

Accordingly, a *standardized unevenness index*, "I_{str}", is defined by the ratio U/U' [50, 51]:

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

that is:

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

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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.
Thanks to this standardization – making it free from the direct influence of species richness – the index I_{str} allows for relevant, unbiased and meaningful comparisons between communities *differing by their species richness* – contrary to the rough abundance, U, which is explicitly sensitive to this influence of species richness. In this respect, the index I_{str} deserves being considered as "genuinely" (idiosyncratically) attached to the corresponding community, *independently* of its particular species richness. Basically, the standardized abundance unevenness I_{str} satisfies the condition required in [48, 54]: "to *make sense*, (un)evenness must be independent of species richness".

Now, from a *functional* point of view, the abundance unevenness U reflects the "mean competitive intensity" in the community (with "competitive intensity" being understood *sensu latissimo*, in its broadest scope, including both biotic and abiotic factors, as detailed in [51]). Accordingly, the standardized structuring index I_{str} reflects the mean competitive intensity, normalized (i.e. compared) to what it is in the broken-stick distribution at the same level of species richness. As the broken-stick model often fits rather well the abundance distribution in most bird communities [33, 52], it follows that the mean competitive intensity in a community is equal to I_{str} times that in a *typical bird community having the same species richness*. Thereby, the standardized structuring index I_{str} offers an *evocative* benchmark to appreciate more concretely the mean competitive intensity within community [46, 51]. And, of course, in its *functional* sense, as well as in its *descriptive* acceptance, the index I_{str} allows for relevant, unbiased and meaningful comparisons between communities, *regardless of their respective species richness*.

3. RESULTS

3.1 Estimated total species richness of each Conus community

Although both studied *Conus* communities, at "Therespuram" and "Keelakarai", have the same recorded species richness (8 species) they actually differ in true (total) species richness. The sampling of the community at "Keelakarai" includes two singletons, thus denoting sampling incompleteness and, indeed, the numerical extrapolation suggests an estimated 3 unrecorded species. The total species richness at "Keelakarai" is thus estimated being equal to 11 species (Table 1).

Table 1 – The number of collected individuals N_0, the number of recorded species R_0, the type of nonparametric estimator (Jackknife series) selected as being the least-biased one, the estimated number Δ of unrecorded species, the resulting estimate of the "true" total species richness S_t (= R_0 + Δ), the resulting estimated level of sampling completeness R_0/S_t.

***Conus* community**	**Therespuram**	**Keelakarai**
nb. collected individuals N_0	201	113
nb. recorded species $R_0 = R(N_0)$	8	8
selected least-biased estimator	/	JK-3
number unrecorded species Δ	0	2.7
total species richness S_t	**8**	**10.7**
sample completeness R_0/S_t	100%	75%

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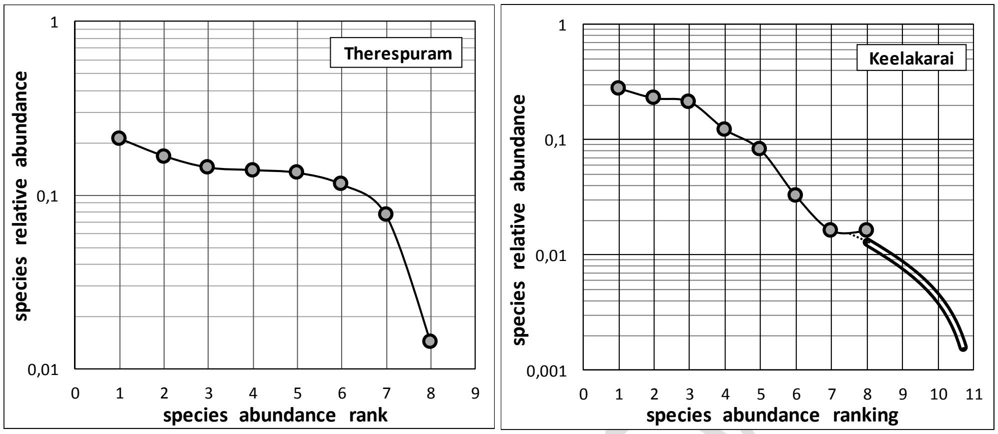
3.2 Species Abundance Distributions numerically completed

The bias-corrected and numerically extrapolated Species Abundance Distributions ("S.A.D.") of the two studied communities are provided in Figures 1 & 2.



Figures 1 & 2 – The corrected and completed Species Abundance Distributions of reef fish communities at "Therespuram" (left) and "Keelakarai", (right). *As recorded*: grey discs; *numerically extrapolated* part: double line.

The abundances of the *recorded* species are plotted as grey discs, while the *extrapolated* part of the abundance distribution is plotted as a thick double line. Of note is the exceptionally weak unevenness in abundances of the seven first species at "Therespuram", followed, however, by a sharp fall in abundance for the last species (rank 8). The difference, between the two communities, as regards the abundance unevenness for the seven first species (i = 1 to 7), is strikingly highlighted in Figure 3 or by comparing Figures 1 and 2. This difference is highly significant: $\chi^2 = 7.8$ (= 6.3 with Yates correction), p = 0.01.

3.3 Taxonomic dissimilarity between the two Conus communities

3.3.1 Shared and unshared species

The taxonomic identities of recorded species in both studied communities are provided in Figure 3, together with their relative abundances in each two communities. Based on recorded data only, four species are shared between the two communities (*Conus leopardus* Röding 1798, *C. eburneus* Hwass in Bruguière 1792, *C. textile* Linneaus 1758 and *C. striatus* Linneaus 1758, the abundances of these last two species being, a little unexpectedly, among the lowest. Specific to the community at "Keelakarai" are *Conus aulicus* Linneaus 1758, *C. lithoglyphus* Hwass in Bruguière 1792, *C. planorbis* Born 1780 and *C. nivalis* da Motta 1985. At last, *Conus virgo* Linneaus 1758, *C. betulinus* Linneaus 1758, *C. litteratus* Linneaus 1758 and *C. araneosus* Linneaus 1758 appear specific to the community at "Therespuram" although up to 3 of them may possibly be identical to the 3 unrecorded species at "Keelakarai" and thus be additionally shared by both communities.

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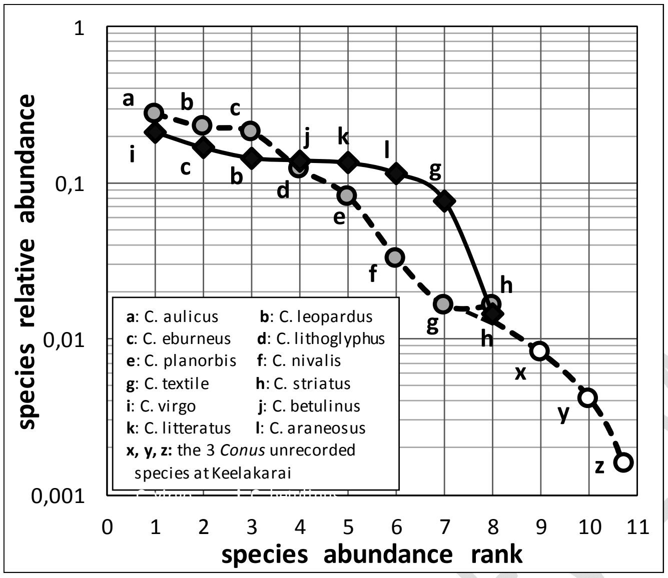

Figure 3 – Taxonomic identities and relative abundances of species in the two studied *Conus* communities, at "Therespuram" (diamonds) and "Keelakarai" (discs).

3.3.2 Jaccard similarity index

Referring to recorded species lists only, the Jaccard similarity index between the two studied communities (separated from each other by ≈ 80 km) would be J = 4/(8+8-4) = 0.33. This is close to the expected value of Jaccard index for the null hypothesis of random assignment of 12 species among two communities: Figure 4, adapted from statistical tables for Jaccard index in reference [55]. Now, accounting for the real species richness (St = 11) in the community at "Keelakarai", it comes:

- J= 4/(8+11-4) = 0.27, if all 3 unrecorded species at "Keelakarai" differ from the 8 species at "Therespuram";
- J = 7/(8+11-7) = 0.58, if all 3 unrecorded species at "Keelakarai" are among the 8 species at "Therespuram".

So that, in place of the definite – but hypothetical – value J = 0.33 based on incomplete data, it can be more safely concluded that, in fact, 0.27 < J < 0.58 (average value J = 0.43).

Beyond its merely descriptive aspect, the value taken by the Jaccard index can be checked in term of whether it denotes a statistically significant similarity or dissimilarity, according to statistical significance of Jaccard index [55]. Similarity/dissimilarity is tested against the null hypothesis of a random assignment of species between the two compared communities: (coarse solid line in Figure 4). The threshold levels of statistical significance, for either similarity or dissimilarity, are plotted against the number N of species in the compared communities pooled together.

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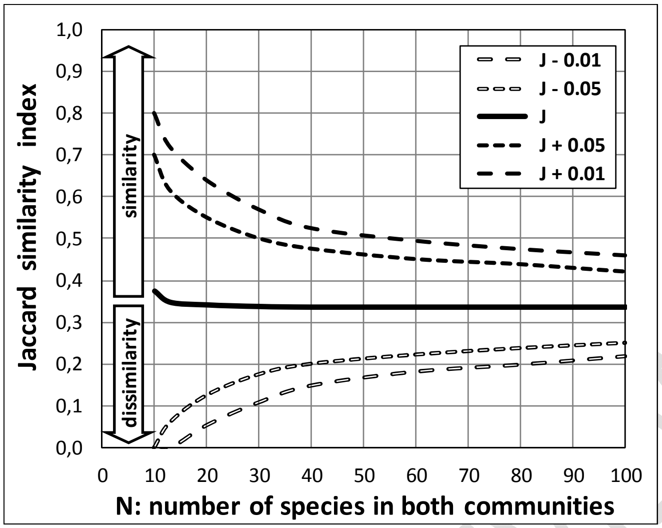

Figure 4 – The significance of Jaccard similarity index plotted against the number N of species in the pooled compared communities (adapted from Real [55] Table 1, i.e. according to the simplified option of reversibility). *Thick solid line*: Jaccard index for the null hypothesis of random assignment of N species to the two compared communities. *Dashed lines*: the thresholds at p = 0.05 and p = 0.01 for statistically significant similarity (J+0.05 & J+0.01) and statistically significant dissimilarity (J-0.05 & J-0.01).

Here, the range of confidence for Jaccard index, $0.27 < J < 0.58$, suggests a trend for some positive taxonomical similarity between the two communities: J is rather larger than the null hypothesis level 0.34 (Figure 5). This trend, yet, does not exceed the critical value $J_{+0.05} \approx 0.6$ for minimal statistical significance at $p = 0.05$.

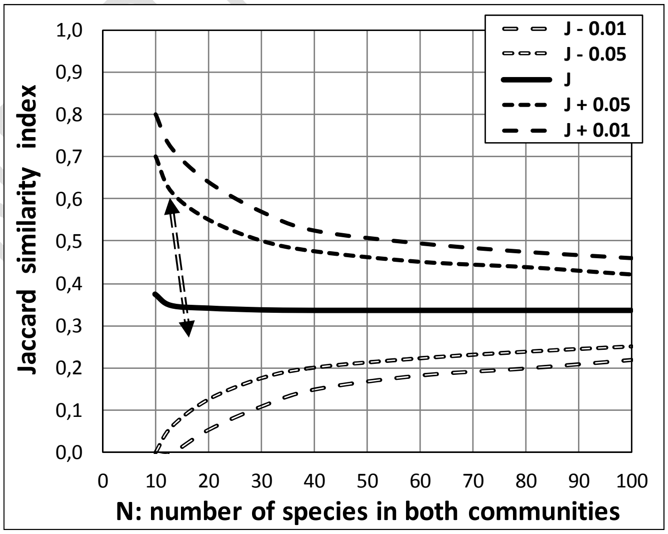

Figure 5 – Test of statistical significance of the estimated range for the Jaccard index (*dashed line with arrows*) between the two communities at “Therespuram” and “Keelakarai”: J = 0.27 (N = 8+11-4 =15) to J = 0.58 (N = 8+11-7 = 12).

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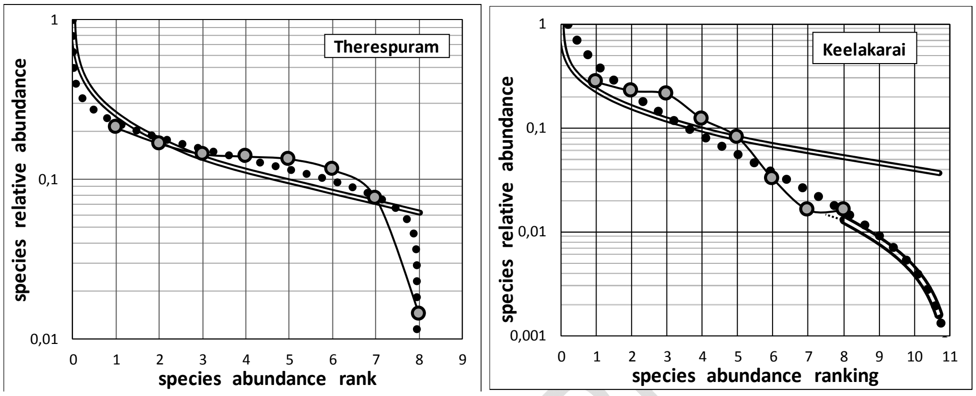
3.4 Testing for the type of process involved in the structuring of species abundances

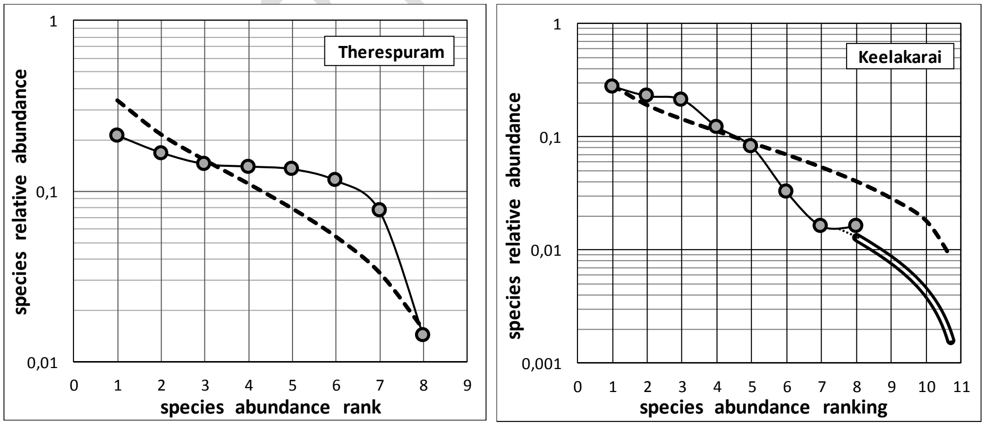
The numerically completed "S.A.D.s" of both studied communities clearly fit better the "log-normal" model than the "log-series" model (Figures 6 & 7). For the community at "Keelakarai", this would have remained uncertain from incomplete sampling and becomes clear only after considering the numerically completed distribution of abundances.



Figures 6 & 7 – Two classical models: "log-normal" (coarse dotted line) and "log-series" (fine double line) compared to the complete or numerically completed Species Abundance Distributions of each of the two studied communities. Best fit is with the "log-normal" distribution for both communities.

3.5 Beyond the rough abundance unevenness, the genuine intensity of the hierarchical structuring process

Figures 8 and 9 compare the average slope (U) of the "S.A.D." to the average slope (U') of the corresponding "broken-stick" model, a comparison from which is derived the genuine intensity I_{str} = U/U' of the underlying structuring process (equation (2)).



Figures 8 & 9 – The Species Abundance Distribution for each studied community compared to the corresponding "broken-stick" model (dashed line) computed for the same species richness respectively.

The main results derived from this comparison are summarized synthetically in Table 2 which highlights in particular the differences between the two communities in terms of:

(i) true total species richness S_t, (ii) ratio a_1/a_{St} between the abundances of the commonest and the rarest species, (iii) the rough abundance unevenness U and, finally, (iv) the standardized unevenness I_{str}.

Table 2 – A synthetic summary of the main quantitative features of the hierarchical organization of species abundances within community, as derived from numerically completed "S.A.D.s" : (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 same, a'_1 and a'_{St}, for the "broken-stick" model, (iv) the rough unevenness of abundances in the community: $U = \log(a_1/a_{St})/(S_t-1)$; (v) the unevenness of abundances in the corresponding "broken-stick" distribution: $U' = \log(a'_1/a'_{St})/(S_t-1)$ and, at last, (vi) the standardized unevenness index $I_{str} = U/U'$.

community	S_t	a_1	a_{St}	a_1/a_{St}	a'_1	a'_{St}	a'_1/a'_{St}	U	U'	I_{str}
Therespuram	8	.2105	.01435	15	.3397	.0156	22	.1666	.1910	0.872
Keelakarai	10.7	.2760	.00157	176	.2825	.0086	33	.2313	.1556	1.486

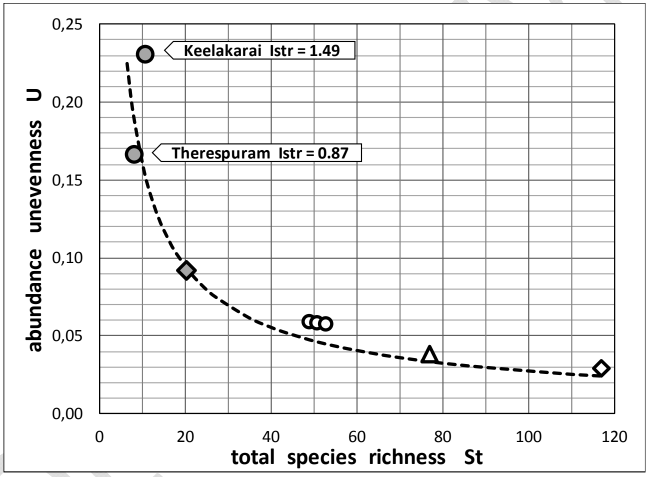


Figure 10 – Rough abundance unevenness U versus total species richness S_t in a series of marine gastropod communities. *Grey discs*: the two studied *Conus* communities at Mannar Gulf ("Therespuram" and "Keelakarai") ; *grey diamond*: *Conus* community in Fiji archipelago [20] ; *white discs*: three Gastropod communities at Mannar Gulf [19] ; *white triangle*: Gastropod community in Andaman Island [18] ; *white diamond*: Gastropod community in Fiji archipelago [20]. Dashed line: the rough abundance unevenness U' in the "broken-stick" distribution plotted against species richness.

Figure 10 provides an overview of reported values of the rough abundance unevenness U versus the total species richness S_t for a series of marine gastropod communities and for the genus *Conus* only, as a subset of gastropods as a whole. Compared to others, the community at "Keelakarai" singles out by its comparatively large deviation from the broken-stick standard (i.e. singles out by its relatively high structuring intensity I_{str}).

Consistent with the preceding observation, Figure 11 highlights the relative increase, with species richness S_t, of the rough abundance unevenness U and the still stronger relative increase of the standardized unevenness I_{str}.

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This situation is deeply contrasting with the usual trend [17-24], according to which (i) the rough unevenness U strongly *decreases* – instead of increase – with species richness S_t and (ii) the standardized unevenness I_{str} remains approximately *stable* or varies rather slightly, but does not strongly increase with S_t as observed here.

The usual trend (U strongly decreasing with growing species richness) has received a likely explanation [51]: an improved resource partitioning among co-occurring species in a community would arguably (i) result in some relaxation of the mean competitive intensity within community, leading to some decrease in abundance unevenness U and (ii) favor the co-occurrence of a larger number of species, i.e. a higher species richness S_t. Hence the usual trend for a negative correlation between rough unevenness U and species richness S_t. The unusual, opposite situation observed here suggests that the mechanism above was either rather ineffective in that case or, at least and more likely, did not come to an end. In turn, this could mean that, here, the *in situ* ecological conditions have not yet achieved their decisive role as drivers of the competitive interactions among species. And that, consequently, the sequence of past-recruitment of species is still playing a critical role in the local distribution of species abundances.

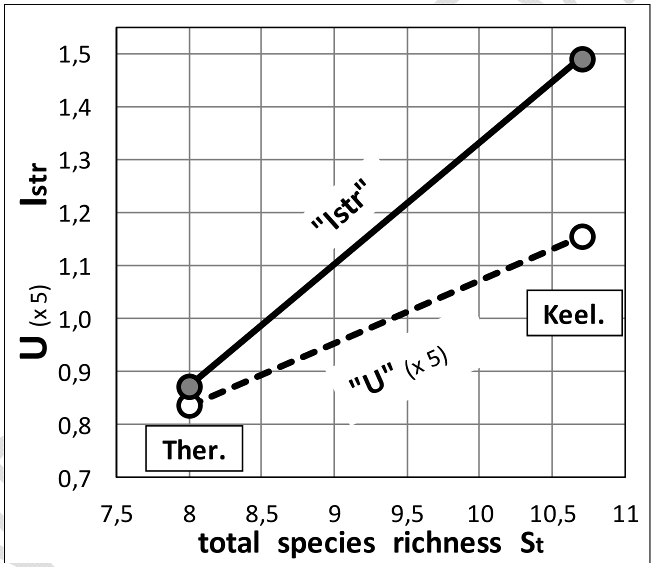

Figure 11 – Rough abundance unevenness U and standardized abundance unevenness I_{str} plotted against total species richness S_t for the two studied *Conus* communities at "Therespuram" and "Keelakarai" (U is multiplied by 5 to make easier comparison between the relative variations of U and I_{str}).

3.5 Distance decay of similarity in species composition

Table 3 and Figure 12 provide data relative to the degree of dissimilarity between the two studied *Conus* communities – separated from each other by ≈ 80 km – and, for comparison, for three couples of Gastropods communities, also located in Mannar Gulf [19]. While the strong dissimilarity in species composition (average Jaccard = 0.43) between the two *Conus* communities might tentatively be attributed to their separation distance by 80 km, comparatively weak decays (average Jaccard = 0.77, 0.75, 0.72), are observed for the three Gastropod communities, almost independently of distances, from 5 km up to 100 km. This apparent inconsistency in results is discussed further.

Table 3 – Jaccard similarity index computed for four reef associated communities in Mannar Gulf National Reserve: two *Conus* communities at "Therespuram" and "Keelakarai"; three marine Gastropod communities at "Koswari" isl., "Vaan" isl., "Hare" isl. (from reference [19]). Provided are the estimated range of Jaccard index, the corresponding number N of species in pooled communities, the corresponding level of significance of similarity between compared communities (cf. Figure 12) and the geographical distance between compared communities.

	Conus Theresp. & Keelak.		marin. **Gastropods** Koswari & Vaan		marin. **Gastropods** Koswari & Hare		marin. **Gastropods** Vaan & Hare	
range Jaccard	0.27	0.58	0.58	0.96	0.50	0.93	0.54	0.96
nb. sp. N	15	12	66	53	68	53	65	51
similarity	non-sign. (p>0.05)		signific. (p<0.01)		signific. (p<0.01)		signific. (p<0.01)	
distance	≈ 80 km		≈ 5 km		≈ 100 km		≈ 100 km	

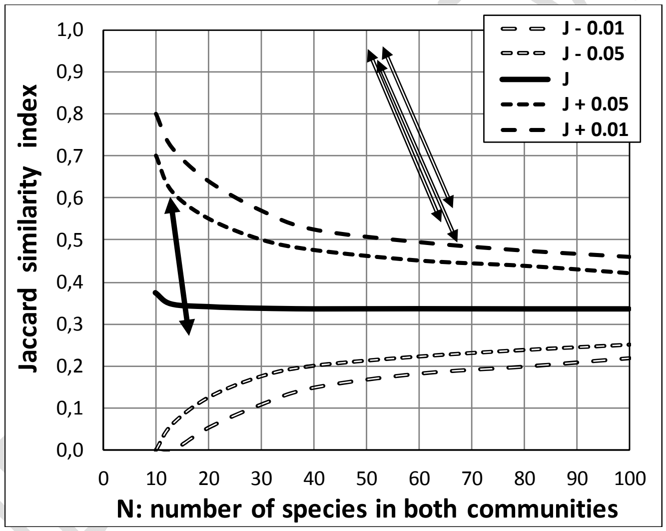

Figure 12 – Test of statistical significance of the Jaccard index (i) between the two *Conus* communities at "Therespuram" and "Keelakarai" (*coarse solid line with arrows*) and (ii) between the three marine Gastropod communities at "Koswari", "Vaan" and "Hare" (*fine double lines with arrows*) : see Table 3. Positive similarity in all cases, but non-significant for the first comparison (p > 0.05) and highly significant for the following three comparisons ($p \leq 0.01$).

4. DISCUSSION

The Conus genus is an emblematic group - and very interesting from a behavioral point of view - which deserves, as such, special attention among all marine gastropods, which, as a whole, contribute so strongly to animal diversity in tropical coral reefs. Thus, in addition to a previous study of reef-associated gastropod communities in the Gulf of Mannar [19], the present study aimed to further clarify the specificities of the *Conus* group in the context of the Gulf of Mannar.

4.1 Numerical extrapolation as a mean of deriving reliable information from incomplete samplings

As expected from the subsistence of singletons in one of the studied *Conus* communities, implementing numerical extrapolation proved necessary to obtain reliable inferences on species organization within community. The resulting estimations of total species richness, Jaccard similarity level and the completed distribution of species abundance, including unrecorded species (Table 1 and Figures 1 to 3) are further discussed below.

4.2 Dissimilarity in species composition: distance decay or recruitment stochasticity?

Although numerical extrapolation leaves us unaware of the identities of the unrecorded species, it provides a reliable range of values for the Jaccard similarity index (instead of the undeterminably biased value derived from incomplete samplings). This range is, however, sufficient to highlight a rather low similarity in species composition between the two studied *Conus* communities, with a Jaccard index in the range of 0.27-0.58 (average 0.43) for a distance of 80 km between the two studied community (Figures 4 and 5). This, however, is deeply contrasting with what is assessed for three marine Gastropod communities (also located in Mannar Gulf), which appear particularly insensitive to any decay in similarity over a 5 to 100 km range of distances (with average Jaccard remaining comprised between 0.71 and 0.77: Table 3, Figure 12).

Yet, it should be noted that dissimilarity in species composition between two distant communities, as established here for the two *Conus* communities, should not necessarily be assigned to inter-community distance *per se*. For example, stochasticity in the process of local recruitment of species – which can contribute to significant difference in species composition between communities, as well – is not expected to be dependent upon the distance between communities. And precisely, *stochastic recruitment* of species is likely to be especially influential in highly dynamic ecosystems, as are coral reefs [56]. Also, more deterministic causes, such as between-sites differences in ecological conditions, are not necessarily correlated to distance, even if such correlation could be expected and must possibly occur more or less frequently.

In fact, definitely demonstrating a true distance decay in similarity should obligatory require to consider not only two but a sufficiently numerous series of communities with varied inter-community distance, in order to check whether the Jaccard similarity index actually decreases more or less monotonically with increasing inter-community distances. Thus, here, the relatively low similarity between the two *Conus* communities may possibly have no linkage with their mutual distance. As just mentioned, this limited similarity may result, as well, from the remaining influence of the stochastic recruitment of species and/or from subsequent ecological sorting of species according to differences in local ecological conditions that do not depend on geographical distance.

In fact, what may seem perhaps more surprising – at least at first sight – is the opposite situation, highlighted between the three marine Gastropod communities in Mannar Gulf, that share so high similarities in species compositions despite their mutual distances. Surprising because, at least, the stochasticity in species recruitment – even from an ideally homogeneous available species stock – might be expected to generate substantial dissimilarity between communities, whatever their mutual distance.

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4.3 Species abundance distributions

The two *Conus* communities sharply differ as regards their respective distribution of species abundance and, once again, reliable assessments in this regard could only be derived by implementing numerical extrapolation. Both communities not only differ (by 37%) in their true (total) species richness (St = 8 and 11) but, still more, as regard the shape of their respective distributions of abundances. First, although being free from the influence of the difference in species richness, the standardized abundance unevenness I_{str} is markedly stronger at "Keelakarai" than at "Therespuram": $I_{str} = 1.49$ against 0.87 (Table 2, Figures 8 to 10). Second, the (log-transformed) representation of ranked abundances is far more irregular at "Therespuram" than it is at "Keelakarai" (Figure 3), with an almost even distribution of abundances for species ranks i = 1 to 6: the average ratio of abundance between each of these six species is only $\approx 2^{(1/5)} \approx 1.15$, which, indeed, is rather low all along a continuous series of six species (although this is partially compensated by a sharp final fall in abundance between species at ranks 7 and 8). While, on the contrary, species abundances are much more regularly decreasing at "Keelakaria" (Figure 3).

In spite of these crude differences, both communities appear being governed by the same kind of mechanisms regulating the distribution of abundances: for both communities, the hierarchical distribution of species abundances likely results from the combined contributions of *many mutually independent factors* acting together, rather than by the determinant role of one major factor only, as suggested by the better fit of their "S.A.D.s" to the *log-normal* than to the *log-series* model (Figures 6 and 7). This, indeed, complies with what is very commonly observed [17-24].

At last, the patterns of variation with species richness S_t of (i) the rough abundance unevenness U and (ii) the standardized abundance unevenness I_{str} (Figure 11) both look rather unusual: an increase of, not only the standardized unevenness I_{str}, but even the rough unevenness U with species richness. This is in full contrast with what have been consistently observed elsewhere: until now, only a strong decrease of U with S_t was documented, while I_{str} shows very limited variations, at most no more than a very slight increase with species richness [17-24].

The usual situation has received a likely explanation [51], based upon increasing species richness S_t being allowed by an improved relaxation of the mean competitive intensity, thanks to a better resource partitioning among co-occurring species. Here, the opposite suggests that this expected – and usually realized – mechanism is not involved, or at least not achieved. Which would likely suggest that, here, the in-situ ecological conditions – responsible for ultimate species sorting – have not yet been able to play their full role, thus still letting the local specificities of past-recruitment in species keeping the major influence. In other words, the *stochasticity* in species recruitment would still predominate, here, as compared to the *determinism* of species sorting by local ecological conditions. According to this way of thinking, it seems likely that marine currents along the coast [57] could contribute to the continuous renewal of species recruitment of *Conus* species, at their planktonic larval stage [58], thereby slowing down the contribution of ecological sorting.

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5. CONCLUSION

The genus *Conus* is arguably original among all other marine Gastropods, at both biological and behavioral points of view. I highlight that, here, the genus *Conus* makes also quite a singular subset within the marine Gastropod communities in which they are embedded, especially as regards the structuration of their species abundances. Thus, considering the two studied sub-communities of *Conus*, a greater species richness corresponds to a stronger unevenness in species abundances, which is quite the opposite of the usual trend of decreasing abundance unevenness with increasing species richness.

Also, an apparently strong sensitivity to distance decay of similarity is highlighted between the two studied *Conus* sub-communities; which strongly contrasts with the comparatively weak sensitivity observed at the level of Gastropod communities as a whole. It remains yet not clear whether this strong dissimilarity is really attributable to distance decay or, alternatively, results simply from species recruitment stochasticity, independently of distance.

Anyway, all these remain tentative, provisional conclusions which require additional confirmations from several other similar case studies, before more definitive conclusions can be reached.

Comment [u6]: Put this in the end of discussion

Appendix 1

Comment [u7]: You could refer it to references. You do not allow present appendix

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 [3, 59, 60]:

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

Compliance with the mathematical constraint (equation (A.1)) warrants *reduced-bias* expression for the extrapolation of the Species Accumulation Curves R(N) (i.e. for $N > N_0$). Below are provided, accordingly, the polynomial solutions R_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_x (N) is appropriate for a given range of values of f_1 compared to the other numbers f_x, according to [3]:

* *for* f_1 *up to* f_2 → $R_1(N) = (R(N_0) + f_1) - f_1.N_0/N$

* *for larger* f_1 *up to* $2f_2 - f_3$ → $R_2(N) = (R(N_0) + 2f_1 - f_2) - (3f_1 - 2f_2).N_0/N - (f_2 - f_1).N_0^2/N^2$

* *for larger* f_1 *up to* $3f_2 - 3f_3 + f_4$ → $R_3(N) = (R(N_0) + 3f_1 - 3f_2 + f_3) - (6f_1 - 8f_2 + 3f_3).N_0/N$ –

$(-4f_1 + 7f_2 - 3f_3).N_0^2/N^2 - (f_1 - 2f_2 + f_3).N_0^3/N^3$

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

* *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:

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

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

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

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

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

N.B. 1: As indicated above (and demonstrated in details in [3]), 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 [29, 31, 61-63]. Also, this shows that the approach initially proposed by [64] – which has regrettably suffered from its somewhat difficult implementation in practice – might be advantageously reconsidered, now, in light of the very simple selection key above, of *far much easier practical use*.

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

N.B. 3: For f_1 falling beneath 0.6 x f_2 (that is when sampling completeness closely approaches exhaustivity), then Chao estimator may alternatively be selected: see reference [4].

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 [5].

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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:

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

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 $i > R_0$):

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

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.

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