



Influence of Environmental Heterogeneity on the Species Composition, Species Richness and Species Abundances Unevenness in Reef-associated *Conus* Communities (Neogastropoda) from Papua New-Guinea

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Author's contribution

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

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ABSTRACT

To what extent differences in species composition, species richness and species abundance unevenness between marine communities are attributable to heterogeneities of the surrounding environment and/or to inter-community distance is a fundamental issue to be addressed, in order to more deeply understand the functioning of marine ecosystems. A comparison between six reef-associated *Conus* communities, differing more or less in both their surrounding environment and their mutual geographical distance, offers a relevant opportunity to address these questions. As expected, environmental heterogeneities prove having a *significant influence* on the dissimilarity in *species composition*, whereas distance-decay in similarity reveals comparatively negligible, at least within the investigated range of distances, up to 60 km. Less expectedly, more homogeneous surrounding environments between communities tend, here, to increase the dissimilarity in *species richness*. At last, here, difference in species abundance unevenness between communities seems unrelated to either environmental heterogeneity or inter-community distance.

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From a methodological point of view, these results could not have been reliably established without the prior implementation of a least-biased procedure of *numerical extrapolation* applied to the available *incomplete* samplings. Also, the relevant assessment of dissimilarity in species composition required using a *modified* Jaccard index, rendered insensitive to bias-induced differences in communities species richness.

Keywords: *Numerical extrapolation; incomplete sampling; diversity; evenness; Jaccard index; distance decay of similarity; neutral theory of biodiversity.*

1. INTRODUCTION

The genus *Conus* makes an emblematic and attractive group of marine Gastropods [1,2] and reef-associated communities of *Conus* deserve specific attention as regards the *internal structuring of species* within these communities, in terms of species composition, species richness and the degree of unevenness of species abundance distribution. Moreover, among all other marine Gastropods, *Conus* species are considered as especially important biodiversity indicators, in the context of tropical reef ecosystems [3-5]. This gives *Conus* communities a specific interest as a dedicated means of monitoring the impact of human activities on reef ecosystems. However, in order to distinguish between what is specific to anthropogenic influences from what is dependent on other, *naturally occurring* influences, there is a need to better understand the *proper, respective contributions* of the latter, i.e. the influences of purely “natural origin”.

Among such presumably influent natural causes, the degree of *environmental heterogeneity* at the local scale, in the vicinity of communities, is expected to be instrumental as regard observed differences in the internal structuring of species within communities [3,4], including in particular differences in species richness, species composition and, possibly, in the degree of unevenness of species abundance distribution. Also, the *geographical distance* separating communities is expected to play some role on the observed dissimilarity between more or less distant communities (beyond what is directly related to the corresponding differences in environmental conditions).

A recently published survey of a set of six *Conus* communities, differing in both the degree of heterogeneity of the surrounding environment and the inter-community distances [5], provides the basic field data appropriate for such an analysis. Yet, as substantial levels of incompleteness actually subsist in the reported

samplings (as is almost unavoidable with relatively species-rich communities including a good part of rare species), these incomplete samplings were completed using *numerical extrapolation*, prior to further analysis. This, in order to avoid biased inferences that may likely result from ignoring the rare species that had remained unrecorded [6]. Indeed, unrecorded species – in spite of their relative rarity – may yet disproportionately contribute to the functional structuring of communities, as emphasized in many reports [7-17]. As quoted in [17], “rare species are critical for bio-assessment”.

After implementation of the required numerical extrapolations, the five following points are mainly addressed, for each of the six studied *Conus* communities:

- the estimated true (total) species richness of each community,
- the exhaustive (numerically completed) distribution of species abundances, with related considerations regarding the intensity of the hierarchical structuring of species abundances and the kind of process involved,
- the estimated degree of dissimilarity in species composition between communities compared two by two (pairwise dissimilarity).

Then, based on the assessment of these *descriptive* aspects, I have dealt with the ins and outs of three major *functional* issues regarding the internal organization among species within community:

- how different levels of species richness among communities are actually *accommodated* by the respective contributions of (i) the degree of relaxation in mean competition intensity among co-occurring species and (ii) the extent of the overall range of species abundances;
- to what extent variations observed in relation to (i) the local environment around each studied *Conus* community and (ii) the

inter-community distance, can respectively influence the degree of dissimilarity between communities, in terms of each of the descriptive factors mentioned above: species composition, species richness, species abundance unevenness.

2. MATERIALS AND METHODS

2.1 The Reported Field Data

The present study is based on the survey of six *Conus* communities from Papua New Guinea, located at the northern tip of New Ireland, around the city of Kavieng. The number N_0 of collected individuals and the number R_0 of recorded species in each six communities are given in Table 1. All additional details regarding the precise localizations of the compared habitats and the implemented sampling procedure are provided in the open-access reference [5] and need not being repeated here any further. Yet, it is essential, here, to underline that the authors of the field study immediately distinguished, *a priori*, two groups among these six communities, on the basis of environmental distinctions: three communities, N1, N2, N3, belong to “an area displaying a rich environmental heterogeneity” (including barrier reef, fringing reef, reef shelves, patch reefs and subtidal reef flats), while the three other communities, E8, E9, E10, are in an area “displaying less environmental heterogeneity” (fringing reef), as emphasized in reference [5]. This provides an excellent opportunity to study the influence of the heterogeneity in the surrounding environment of each community upon the species organization within this community.

Now, using quasi exhaustive inventories is recommended to avoid making seriously biased inferences regarding the main structural descriptors of ecological communities, in particular, total species richness and abundance unevenness [18–22]. And, if this reveals impossible in practice, to rely on *numerical extrapolation* of incomplete samplings [23] (when, as here, far excessive additional sampling efforts would be needed to approach completeness).

2.2 The Numerical Extrapolation Procedure and Its Exploitation

Accordingly, a reliable, least-biased numerical extrapolation procedure is appropriately applied,

here, to the six, incompletely sampled *Conus* communities under study. Implementing numerical extrapolation procedure requires knowing the respective abundance of the recorded species, which, fortunately, were reported in reference [5].

Beyond estimating the number of unrecorded species, the numerical extrapolation can even provide, in addition, the least-biased estimates of the respective abundance of each of these unrecorded species, as detailed below. And this is of major interest since, once properly numerically completed (and *only* when it is so [20]), the distribution of species abundances can provide synthetic data, in both *qualitative* and *quantitative* terms, regarding the underlying process that drives the hierarchical structuring of species abundances within community [24–28].

2.2.1 Practical implementation of the procedure of numerical extrapolation

Total species richness: a reliable, least-biased numerical extrapolation procedure has recently been proposed for the estimation of the number of still unrecorded species and the resulting total species richness of only partially sampled communities [29,30]. The computation procedure, argued and detailed in references [29, 30], is 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.

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 [31 - 34], the “S.A.D.” requires: (i) to be *corrected* for the bias resulting from drawing stochasticity during finite-size sampling and, still more importantly, (ii) to be *completed by numerical*

extrapolation, to the extent that sampling is suspected to be incomplete. The appropriate procedure of correction and least-biased numerical extrapolation of the as-recorded partial “S.A.D.” is described in details in reference [32], briefly summarized in Appendix 2 and concretely exemplified in details in [33]. Classically, the “S.A.D.” is graphically presented with the (log-transformed) abundances, a_i , plotted against the rank i of species, the species being ordered by their decreasing values of abundance (with, thus, a_1 and a_{S_t} respectively standing for the highest and the lowest abundances in a community of S_t species).

2.2.2 Abundance unevenness: The pattern of species abundance structuration

In practice, the “S.A.D.” can be synthetically summarized by two of its major features: the *total species richness* ‘ S_t ’ and the *degree* ‘ U ’ of *unevenness* of the abundance distribution. Indeed, following [35], 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.s”, 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 [36], that is:

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

with a_1 and a_{S_t} 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*, summarized by U , the underlying *process* involved in the hierarchical structuration of species 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 [24, 37-40].

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 [41-46]. The likely underlying ecological origin of this overall trend (behind its “mathematical-like” appearance) is discussed in detail by Béguinot [47]. 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 [45, 47]. As argued in detail [47], the direct, negative influence of species richness on abundance unevenness is adequately accounted for by the “broken-stick” theoretical distribution, originally conceptualized by MacArthur [48]. 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 [49]. This standardization highlights to what extent the rough abundance unevenness U of a community actually deviates from the common overall trend, resulting from the tendential, direct influence of species richness [41,42,45,47,49]. Accordingly, a *standardized unevenness index*, “ I_{str} ”, is defined by the ratio U/U' [45, 47]:

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

that is:

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

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

Thanks to this standardization – making I_{str} *free from the direct influence of species richness* –

this index allows for *relevant, unbiased and meaningful* comparisons between communities *differing from each other in their species richness*. I_{str} differs, in this, from 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 the particular species richness of this community. Basically, the *standardized abundance unevenness* I_{str} explicitly satisfies the condition required in references [43,50], that is: “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 more extensively detailed in reference [47]. And, in turn, the reciprocal of the rough unevenness ($1/U$) mirrors the degree of *relaxation of the mean competitive intensity* in the community.

In addition, the standardized structuring index I_{str} also reflects the mean competitive intensity, but standardized (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 [24,48], 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 index I_{str} offers an *evocative* benchmark to appreciate more concretely the level of the mean competitive intensity within community [41,47]. So that – in its *functional* sense as well as, above, in its *descriptive* acceptance – the standardized 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 in Each *Conus* Community

As was expected from the subsistence of singletons in samples, the least-biased numerical extrapolations confirm that all six studied *Conus* communities were only partially sampled, with an average 66% completeness level (Table 1).

Moreover, sampling completeness substantially differs among the six samplings, from 58% to 82% (Table 1). Thus, the six communities more strongly differ in true (total) species richness (13-20 species) than could be expected from their rather similar recorded species richness (10-12 species). Thus, based on recorded data alone, assumptions regarding the total species richness would be biased not only in *absolute* but even in *relative* terms, as a consequence of the disparity in sampling completeness. Which means that *rarefaction procedure would remain inefficient*.

3.2 Numerically Completed Species Abundance Distributions

The bias-corrected and numerically extrapolated Species Abundance Distributions (“S.A.D.s”) of the six studied communities (according to the procedure described in reference [32] and summarized in Appendix 2) are provided in Figs. 1 & 6. The (bias-corrected) abundances of *recorded* species are plotted as grey discs while the *extrapolated* part of the abundance distribution is plotted as a thick double line.

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

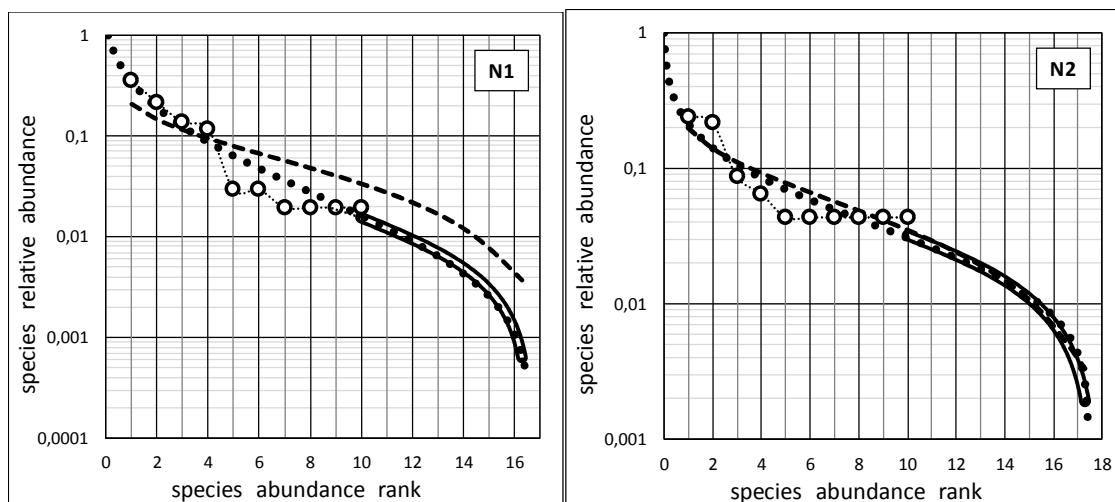
The numerically completed “S.A.D.s” of the six studied communities exhibits a more or less sigmoidal shape, which far better fit the typically sigmoidal shape of the “log-normal” model (Figs. 1 to 6) than the J shape of the “log-series” model (the latter not represented but see [33, 51-58]). Note that a slight deviation from the “log-normal” model is observed for the dominant species (rank 1) in communities E9 and E10 (Figs. 5 and 6). These deviations, which might be related, for example, to some negatively density dependent predation upon the dominant species, do not yet reach the threshold of statistical significance and may result, as well, from sampling stochasticity.

3.4 Beyond the Abundance Unevenness Pattern, the Genuine Intensity of the Underlying Hierarchical Structuring Process

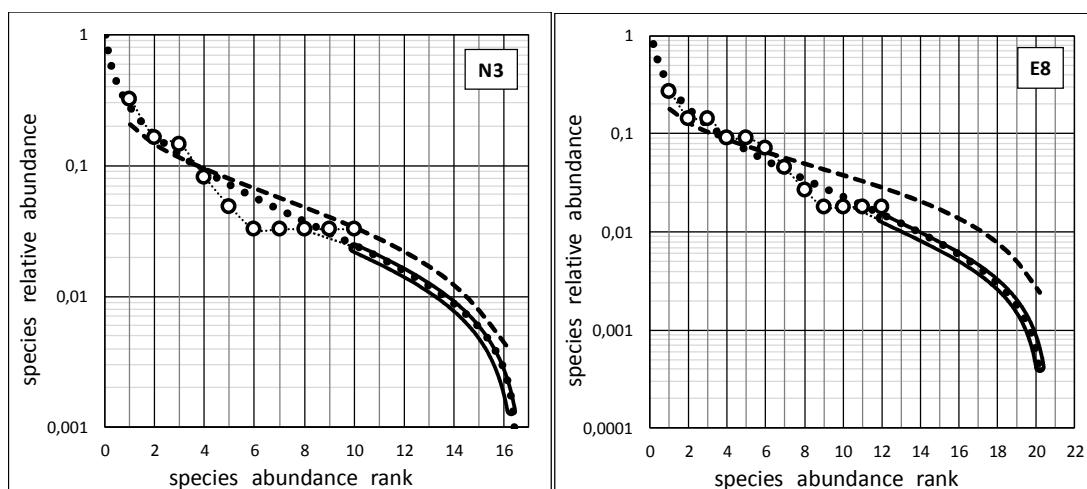
Figs. 1 to 6 allow to compare the average slope (U) of the “S.A.D.” to the average slope (U') of the corresponding “broken-stick” model, a comparison from which is derived the genuine standardized intensity, $I_{str} = U/U'$, of the underlying structuring process (equation (2)).

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 $S_t (= R_0 + \Delta)$, the resulting estimated level of sampling completeness R_0/S_t

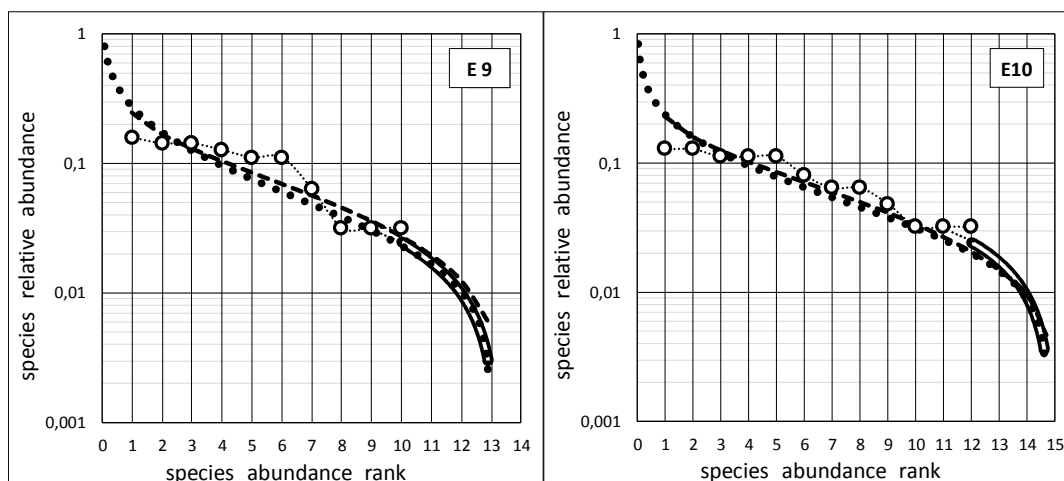
Conus community	N1	N2	N3	E8	E9	E10
nb. collected individuals N_0	88	30	47	94	50	47
nb. recorded species $R_0 = R(N_0)$	10	10	10	12	10	12
selected least-biased estimator	JK-5	JK-5	JK-5	JK-5	JK-4	JK-5
number unrecorded species Δ	6.3	7.3	6.3	8.2	2.9	2.6
Total species richness S_t	16.3	17.3	16.3	20.2	12.9	14.6
Sample completeness R_0/S_t	61%	58%	61%	59%	78%	82%



Figs. 1 and 2. The corrected and numerically completed species abundance distributions of the *Conus* communities N1 and N2 (white discs: recorded species, double line: numerically extrapolated part of the S.A.D.). For comparison, two classical models: “log-normal” (dotted line) and “broken-stick” (dashed line). Left: community N1, right: community N2



Figs. 3 and 4. The corrected and numerically completed species abundance distributions of the *Conus* communities N3 and E8 (white discs: recorded species, double line: numerically extrapolated part of the S.A.D.). For comparison, two classical models: “log-normal” (dotted line) and “broken-stick” (dashed line). Left: community N3, right: community E8



Figs. 5 and 6. The corrected and numerically completed species abundance distributions of the *Conus* communities E9 and E10 (white discs: recorded species, double line: numerically extrapolated part of the S.A.D.). For comparison, two classical models: “log-normal” (dotted line) and “broken-stick” (dashed line). Left: community E9, right: community E10

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_{S_t} of the most and least abundant species (species rank 1 and S_t) ; (iii) the same, a'_1 and a'_{S_t} , for the “broken-stick” model, (iv) the rough unevenness of abundances in the community: $U = \log(a_1/a_{S_t})/(S_t-1)$; (v) the unevenness of abundances in the corresponding “broken-stick” distribution: $U' = \log(a'_1/a'_{S_t})/(S_t-1)$ and (vi) the standardized unevenness index $I_{str} = U/U'$

Community	S_t	a_1	a_{S_t}	a_1/a_{S_t}	a'_1	a'_{S_t}	a'_1/a'_{S_t}	U	U'	I_{str}
N1	16.3	0.353	.00064	551	0.207	0.0038	54	0.179	0.113	1.58
N2	17.3	0.238	.00191	125	0.199	0.0033	60	0.129	0.109	1.18
N3	16.3	0.324	.00134	242	0.207	0.0038	54	0.156	0.114	1.37
E8	20.2	0.272	.00042	648	0.178	0.0025	71	0.146	0.097	1.51
E9	12.9	0.159	.00305	52	0.247	0.0060	41	0.144	0.135	1.07
E10	14.6	0.129	.00360	36	0.227	0.0047	48	0.114	0.124	0.92

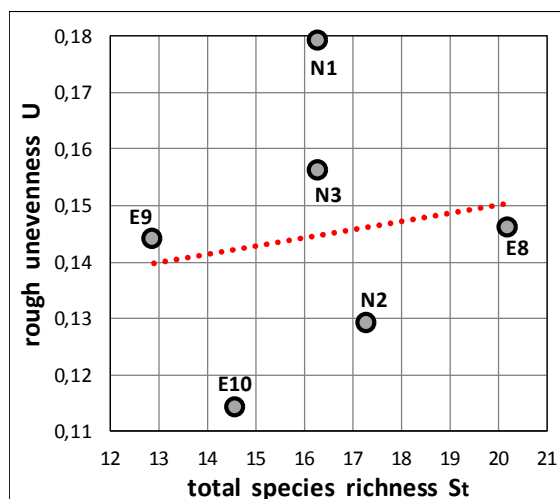


Fig. 7. The rough abundance unevenness U plotted against the total species richness S_t in six *Conus* communities ($r = 0.16$, $p = 0.38$)

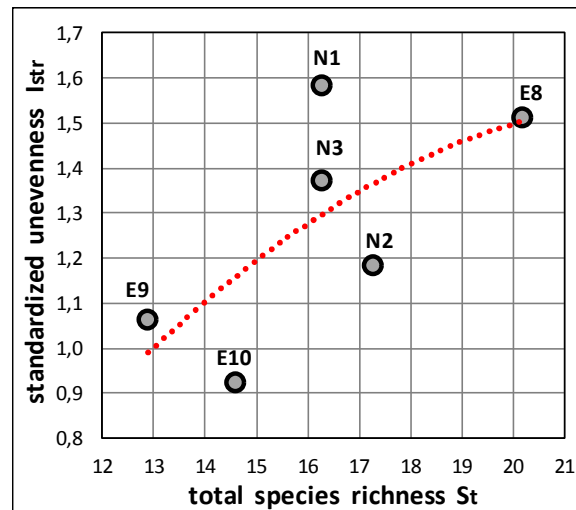


Fig. 8. The standardized abundance unevenness I_{str} plotted against the total species richness S_t in six *Conus* communities ($r = 0.68$, $p = 0.07$)

The main results derived from this comparison are summarized synthetically in Table 2 which highlights in particular the differences between the six communities in terms of: (i) the true total species richness S_t , (ii) the ratio a_1/a_{St} between the abundances of the commonest and the rarest species, (iii) the rough abundance unevenness U and, finally, (iv) the standardized unevenness I_{str} .

The variations of the rough abundance unevenness U and the standardized unevenness I_{str} according to total species richness S_t are plotted in Figs. 7 and 8. While there is no significant dependence of rough unevenness U upon S_t ($r = 0.16$, $p = 0.38$), the increase of the standardized unevenness I_{str} with S_t is approaching statistical significance ($r = 0.681$, $p = 0.07$).

3.5 Respective Contributions of an Improved Relaxation of Competition and a Broadened Range of Species Abundance to Accommodate Increasing Species Richness

The quasi-constancy (instead of the usual sharp decrease) of rough unevenness U with growing S_t (and the resulting – unusual – strong increase of I_{str} with S_t) both highlight the singular difficulty for *Conus* communities to accommodate growing species richness by further relaxing the mean competitive intensity (*sensu latissimo*) within community (relaxation of competitive intensity mirrored by the reciprocal ($1/U$) of the rough abundance unevenness U). So that, here, the

increasing species richness is almost entirely accommodated by the strong broadening of the range R_a of species abundances (Fig. 9, $r = 0.78$, $p = 0.03$), while the relaxation ($1/U$) remains substantially unchanged. This broadening of R_a being, in turn, essentially accommodated by the strong decrease of the minimum abundance a_{St} (Fig. 10, $r = 0.82$, $p = 0.02$).

Note that this progressively asymptotic decrease of a_{St} with S_t is likely announcing the involvement of some Allee effect (or the like), ultimately imposing some minimum threshold to the decrease of the minimum species abundance. So that a substantial further increase of species richness would likely become difficult, in these *particular set* of communities, since neither a substantial further improvement in the relaxation of mean competitive intensity nor a substantial further decrease in the minimum species abundance a_{St} , seem possible.

3.6 Influence of Variations in the Local Environment upon the Internal Organization of Species within Communities

As mentioned above, the communities N1, N2, N3, belong to “an area displaying a rich environmental heterogeneity” while the three other communities, E8, E9, E10, are in an area “exhibiting less environmental heterogeneity” [5]. Focused hereafter is the influence of the heterogeneity in neighboring environment among communities on (i) the degree of dissimilarity in species composition between communities,

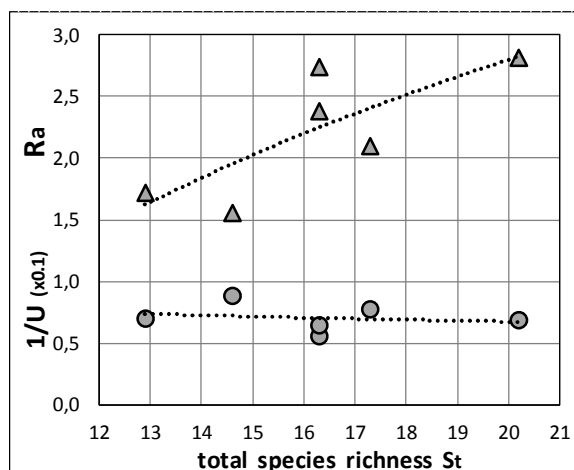


Fig. 9. The overall range R_a of species abundances (*triangles*) and the relaxation of the mean competitive intensity, mirrored by the reciprocal of rough unevenness [$1/U$] (*discs*), plotted against the total species richness S_t . The increase of R_a with S_t is statistically significant: $r = 0.78$, $p = 0.03$

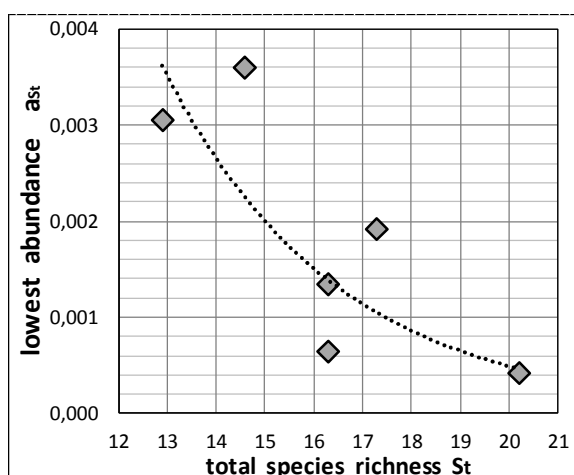


Fig. 10. The lowest species abundance a_{St} plotted against the total species richness S_t . The decrease of a_{St} with S_t is statistically significant: $r = 0.82$, $p = 0.02$

(ii) the total species richness of communities, (iii) the kind of mechanism involved in the hierarchical distribution of abundance and (iv) the sharpness of this hierarchical distribution.

3.6.1 Influence of variations of the local environment on the dissimilarity in species composition among communities

The Jaccard similarity index is one of the most commonly used metrics to quantify the degree of similarity / dissimilarity in species composition between two ecological communities: $J = a/(b + c - a)$, with 'a' as the number of shared species

and 'b', 'c', as the species richness of the two compared communities respectively. Yet, thus defined, the Jaccard index is regrettably sensitive, also, to the difference in species richness between communities [59,60]. For example, when one community is entirely nested into another one, similarity obviously reaches its maximum possible value while, the Jaccard index yet remains less than 1 and all the more so that the difference in species richness is large. To cancel this source of bias, it is appropriate to modify the Jaccard index so that the number of shared species is compared to the species richness of the less speciose among the two compared communities. Accordingly, an

appropriately *modified* Jaccard index of similarity could be $J_{mod} = a / \min\{b, c\}$, which, in particular, reaches unity when similarity reaches its maximum possible value, *regardless* of the difference in species richness $|b - c|$ between the two compared communities (see also [59]).

While using the usual, unmodified Jaccard index would remain almost acceptable, here, when using *as-recorded* data (since recorded species richness weakly differ between communities, Table 1); implementing the *modified* Jaccard index becomes highly recommendable here, since the levels of true species richness, estimated from *numerically completed* samplings, strongly differ between communities.

Fig. 11 provides the 15 values of the modified Jaccard similarity index, J_{mod} , computed for the six *Conus* communities compared two by two. As expected, the three communities E8, E9, E10 sharing similar environments, show greater similarity to each other ($J_{mod} = 0.77$ to 0.80) than the three communities N1, N2, N3 having contrasted environments ($J_{mod} = 0.65$). And, as expected also, intermediate levels of similarity ($J_{mod} = 0.61$ to 0.74) are obtained when comparing couple of communities respectively issued from each of the two sets, Ex and Ny.

Note that these strong variations, induced by the level of heterogeneity among local environments, largely outweigh the distance-decay in species-composition similarity, as will be further examined in section 3.7.

The importance of choosing an appropriate, bias-free metrics of similarity, advocated above, is highlighted in Fig. 12, where the usual, *non-modified* Jaccard index is implemented. The clear pattern relating composition dissimilarity to environment heterogeneity, shown in Fig. 11, is no longer exhibited when using the non-modified Jaccard index. Which retrospectively confirms the appropriateness of choosing the *modified* index.

3.6.2 Influence of variations in the surrounding environment on the species richness of communities

Rather unexpectedly, there is some trend for higher differences in true (total) species richness S_t between those communities having more similar species composition – that is placed in less heterogeneous environments (E8, E9, E10) – when compared to more dissimilar communities occurring among more heterogeneous environments (N1, N2, N3): Fig. 13.

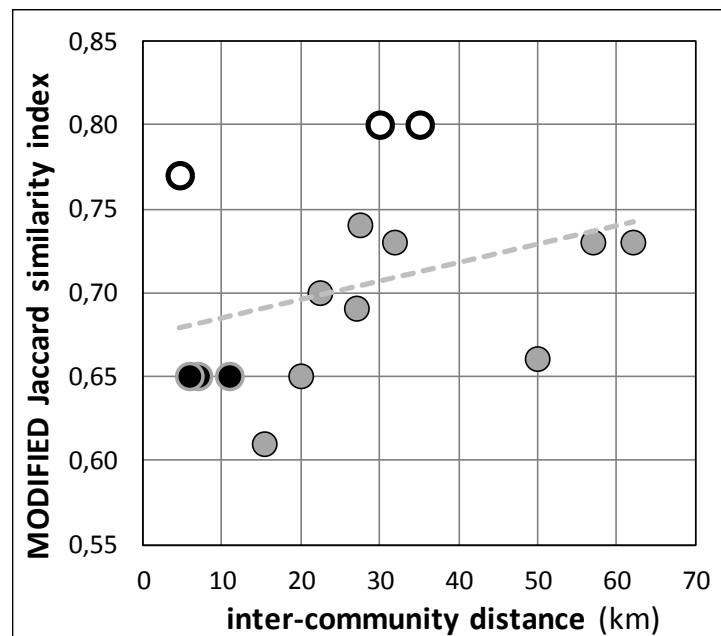


Fig. 11. The similarity in species composition (modified Jaccard index) between the six *Conus* communities compared two by two, plotted against inter-community distance

White discs: similarities between E8, E9, E10; black discs: similarities between N1, N2, N3 ; grey discs: similarities between E8, E9, E10 on the one hand and N1, N2, N3 on the other hand

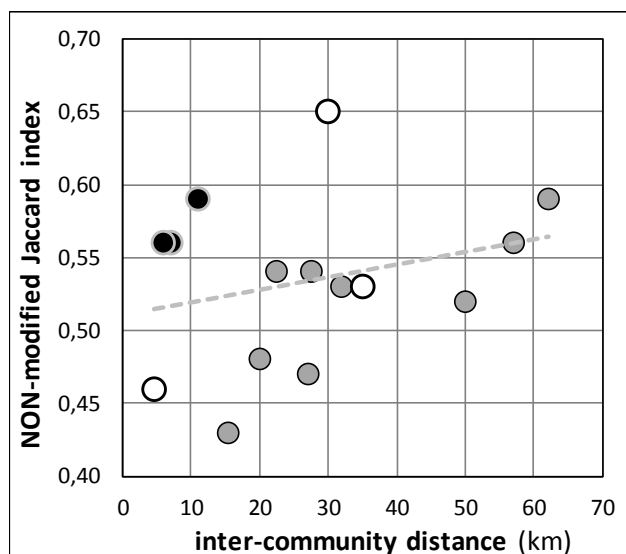


Fig. 12. Values of the non-modified Jaccard index of similarities between the six *Conus* communities compared two by two, plotted against inter-community distance
 White discs: similarities between E8, E9, E10; black discs: similarities between N1, N2, N3 ; grey discs: similarities between E8, E9, E10 on the one hand and N1, N2, N3 on the other hand

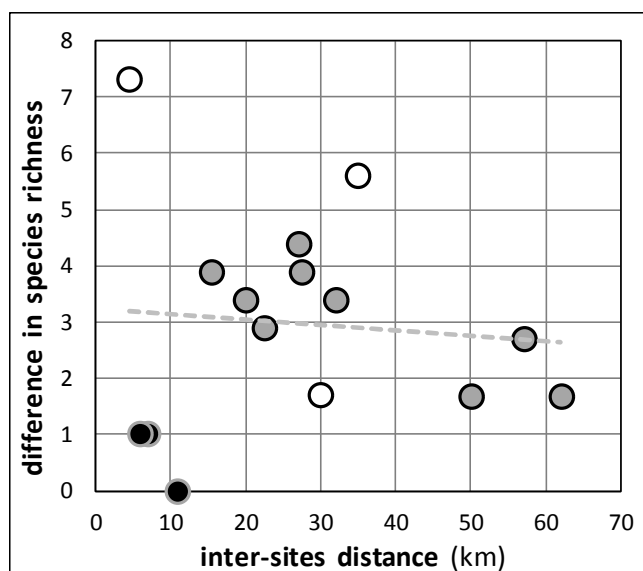


Fig. 13. Difference in true (total) species richness S_t between the six *Conus* communities compared two by two, plotted against inter-community distance
 White discs: between E8, E9, E10; black discs: between N1, N2, N3; grey discs: between E8, E9, E10 on the one hand and N1, N2, N3 on the other hand

3.6.3 Influence of variations in the local environment on abundance unevenness

As the compared communities substantially differ in total species richness, it is advisable to consider the standardized abundance unevenness I_{str} (free from the direct influence of species richness, see section 2), rather than the

rough abundance unevenness U (which is not). As shown in Fig. 14, the differences in standardized abundance unevenness I_{str} between the six communities are substantially unrelated to the degree of heterogeneity in the surrounding environments ($r = 0.29$, $p = 0.15$). Indeed, no particular relationship was expected in this respect.

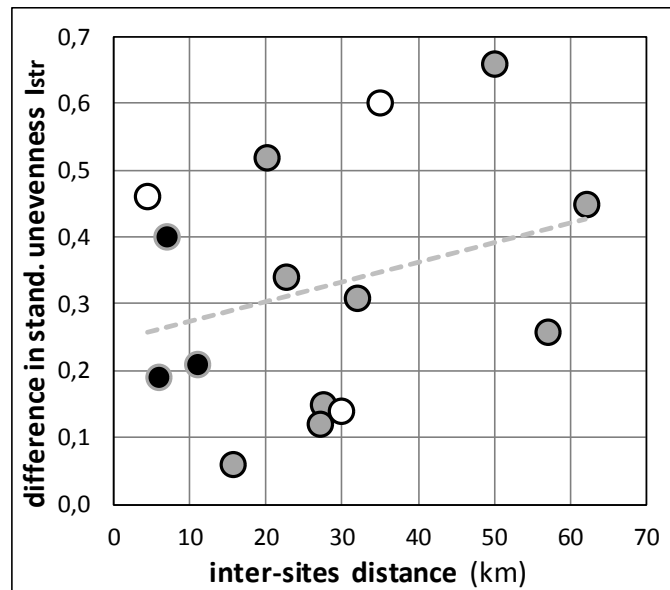


Fig. 14. Difference in standardized abundance unevenness I_{str} between the six *Conus* communities compared two by two, plotted against inter-community distance ($r = 0.29$, $p = 0.15$)

White discs: between E8, E9, E10; black discs: between N1, N2, N3; grey discs: between E8, E9, E10 on the one hand and N1, N2, N3 on the other hand

3.6.4 Influence of variations in the local environment on the type of process involved in the hierarchical distribution of species abundance

As shown in section 3.3 (Figs. 1 to 6), the same type of mechanism is involved in each of the six studied communities, whatever the differences in the respective surrounding environments of these communities.

3.7 About the “Distance-decay” in Species-composition Similarity

Here, no distance decay in the degree of similarity in species composition is observed (considering the modified- as well as the unmodified- Jaccard index): Figs. 11 and 12. In fact, if any decay in species composition similarity actually occurs, it is more than largely outweighed by the influence of the degree of heterogeneity of the surrounding environment among communities. Moreover, even focusing on the subset of communities having similar environments (E8, E9, E10), still no distance decay is apparent. Incidentally, and as expected, the difference between communities, regarding their species richness and their standard unevenness, are both insensitive also to inter-community distance (Fig. 11).

4. DISCUSSION

Muttenhaller *et al.* [5] reported detailed field data relative to six reef-associated *Conus* communities from New Ireland (Papua New-Guinea), that more or less differ between each other as regards (i) their respective surrounding environment and (ii) their mutual geographical distance. Also reported in [5] are substantial differences among the six studied communities, as regard three major aspects of the organization of species within each of these communities: (i) species composition, (ii) species richness and (iii) abundance unevenness. Highlighting to what extent these recorded differences may possibly result from the contextual differences cited above (i.e. surrounding-environment and/or inter-community distance) was the major purpose of the present investigation. Analysis in this respect is favored by the likely similar initial conditions of colonization among the six communities, due to the likely well-mixed regional pool of *Conus* species from which all six communities have recruited their respective lot of species. This well-mixed regional pool is expected, in turn, from the likely homogenizing effect of the New-Guinea Coastal Current [61].

However, to properly address all these interesting issues – given the actual, and

practically unavoidable, incompleteness of the available reported samplings – the required implementation of *numerical extrapolation* of each of these sampling was achieved first.

4.1 The True (Total) Species Richness of Communities

The extrapolated values of total species richness of the six studied communities (from 13 to 20 species) are typically in the range of what was assessed for reef-associated *Conus* assemblages at the local scale: 8 to 10 species in Mannar Gulf (India) [58], 20 species at Suva Island (Fiji's) [52].

4.2 The Distribution of Species Abundances within Community

Once numerically completed, the Species Abundance Distributions in all six studied communities show sigmoidal shapes, which all comply fairly well with the corresponding *log-normal* model (Figs. 1 to 6), thus suggesting that in all these communities, the distribution of abundances is driven by the cooperation of numerous mutually independent factors, which, indeed, is the usual case [33,47,51-58]. This compliance of the species abundance distributions with the log-normal, rather than with the log-series distributions does not support the relevance of the *Neutral Model of Biodiversity* (at least in its strong version) as a mean to explain the structuration of these communities, a point further confirmed independently in section 4.4.4.

What, indeed, is less usual, is the constancy of the rough abundance unevenness U – and, accordingly, the sharp increase of the standardized abundance unevenness I_{str} – along with increasing species richness S_t (Figs. 7 and 8). This is in deep contrast with the usual trend of sharp decrease of U with S_t [33,41,42,51-57]. A usual trend which, according to our current series of studies [33,51-58], finds only one other exception which – interestingly – also involves *Conus* communities: see reference [58].

4.3 The Accommodation of Increasing Species Richness

Directly related to the previous observation, the relaxation of mean competition intensity – mirrored by $(1/U)$ – thus plays no role at all in the accommodation of growing species richness along the range $S_t = 13$ to 20, covered by the six

studied communities (Fig. 9). Accordingly, here, growing species richness is entirely accommodated by the broadening of the overall abundance range R_a which, in turn, is essentially accommodated by the decrease of the minimum abundance a_{st} (Fig. 10). As already underlined above, this is in marked contrast with the usual accommodation process, involving the shared contributions of, at first, some relaxation in the mean competitive intensity (especially thanks to improved “resource partitioning” [47]) subsequently complemented, as far as necessary, by the enlargement of the abundance range. When first observed in a couple of *Conus* communities from the Gulf of Mannar [58], this non-involvement of the relaxation in competitive intensity was tentatively attributed to the remanence of recruitment stochasticity (see [58], section 4.3). Yet, the same non-involvement, reiterated here among six new *Conus* communities, now calls for an alternative, more deterministic assumption: a true difficulty, within these *Conus* communities, to further relax competition intensity (typically by improving “resource partitioning”) beyond some upper threshold, seemingly rapidly reached. And this, although the genus *Conus* is known for its propensity to more or less specialize on specific prey, thereby improving resource partitioning. In fact, this limitation in the possibility of further competitive relaxation might ultimately be related to *local conditions*, namely some limitation in the available stock of *Conus* species at the local scale, from which to recruit colonizing species to sustain the development of communities. Local stock limitation seems more likely involved, since some other *Conus* communities yet show stronger relaxation of competitive intensity, that is lower abundance unevenness U : for example, in the Fiji's with $U = 0.09$ [52].

Yet, additional case studies, involving other *Conus* communities, remain necessary to better substantiate this second hypothesis.

4.4 What Makes Communities More or Less Different from Each-other: The Respective Roles of Difference in Surrounding Environment and Inter-community Distance

Several causes – in particular the difference in surrounding environment and the distance that separates communities – can explain the differences which singularize each of the six studied *Conus* communities, in terms of species

composition, species richness, level of abundance unevenness.

4.4.1 Causes of difference in species composition among communities

As expected, and clearly highlighted in Fig. 11, differences in the surrounding environment between communities contribute to increase the degree of dissimilarity in species composition among these communities. Thus, communities N1, N2, N3, distributed within an area displaying a strong environmental heterogeneity, differ more sharply from one another in this respect than do communities E8, E9, E10, the latter being placed in similar types of environment. This demonstration had required, however, the implementation of an appropriately modified expression of the Jaccard index, necessary to cancel the confusing effect of difference in species richness, to which the usual, unmodified Jaccard index is sensitive (Fig. 12).

As regards the influence of the distance separating communities, within the range from 4 km to 60 km (the so-called “distance-decay in similarity”), this influence is clearly negligible as compared to the consequence of varying local environments (Figs. 11 and 12). Of course, this observation does not call into question the distance-decay in similarity as a general phenomenon. It merely suggests that, for distances of the order of a hundred kilometers or less, the amplitude of distance-decay in similarity remains quite limited, compared with other causes of dissimilarity, such as varying local environment, as already emphasized in references [51,58,60,62].

4.4.2 Causes of difference in species richness

Rather surprisingly, *higher* similarity in surrounding environment between the studied *Conus* communities (*viz* E8, E9, E10) seems going with *lower* similarity in their respective species richness (Fig. 13), which, indeed, looks rather counterintuitive. Yet, correlation does not necessarily reveal causality: this negative correlation may well be only circumstantial. Additional case studies in this respect are required before being able to reliably identify what is really involved in this unexpected result.

Less surprising, the distance between communities has negligible role on the difference in species richness (as above for species composition): Fig. 13.

4.4.3 Causes of difference in abundance unevenness

Here, neither the differences in the surrounding environments between communities nor the inter-community distance have any distinct influence on the dissimilarity in species abundance unevenness between communities: Fig. 14.

4.4.4 An additional comment on the pre-eminence of deterministic over stochastic drivers, as responsible for the internal structuration of these *Conus* communities

The influential *Neutral Theory of Biodiversity* [63] duly emphasized – but probably too much exclusively consider – the relative importance of stochastic events and processes (dispersal, historicity of colonization events, hardly predictable resulting demography) in the internal structuring of biological communities. In this respect, trying to relevantly disentangle what comes from *deterministic*, “niche-based” ecological filtering, from what likely results from *stochastic* events and processes, is necessary to gain a deep and reliable understanding of community structuring. Yet, when considering a couple of communities, obviously differing from each other as regards their ecological conditions, it remains difficult to decide to what extent these ecological differences have actually contributed to the difference in the structuration of the two communities. And which complementary contribution is of purely stochastic nature: i.e. unpredictable events and hardly predictable outcome of demographic processes.

Things become a little bit less complex when having the opportunity to compare two *sets of communities* (instead of simply two *communities*) that differ from each other as regards their respective ecological conditions. Indeed, relying on a set of communities, rather than on a community alone, contributes to reduce the relative influence of stochasticity and help disentangling the specific contribution of deterministic – niche-based – ecological mechanisms. Thus, having the opportunity to deal with sets of communities, obviously helps to uncover ecologically-based explanations. The present case study offers such an opportunity, with its two sets of communities (E8, E9, E10 *versus* N1, N2, N3) that clearly differ from each other, in terms of their respective surrounding environments [5]. As already pointed out, the

results highlighted in section 3.6. support the idea that, in these *Conus* communities, *ecological drivers* play a more decisive role than *stochastic events and processes* – even if the latter should in no way be neglected. Indeed, the limited relevance of the *Neutral Theory of Biodiversity*, at least in its strong version, had already been pointed out by several authors, in the context of coral reef communities: see in particular reference [64].

5. CONCLUSION

Addressing empirically the relationships linking the internal organization of species within community to a series of external factors – such as heterogeneity in surrounding environment or inter-community distance – obviously requires implementing *dedicated investigation tools* avoiding different sources of bias that, otherwise, would undermine the reliability of the derived results and interpretations. Thus, here, both the validity and the significance of the results reported above are entirely conditioned by the *prior numerical extrapolation* of the (unavoidably) incomplete available samplings. Also, implementing an appropriately *modified Jaccard index* proves necessary to relevantly cancel the bias induced by the difference in species richness among communities, to which the usual Jaccard index is especially sensitive.

It follows from the preceding remarks that these results make a new original contribution to the knowledge of the structural organization within *Conus* communities associated to tropical coral reefs, by *ensuring to encompass the full set of co-occurring species*. Indeed, to our best knowledge, this is the first time that a least-biased numerical extrapolation procedure is applied to reef-associated *Conus* communities, as a surrogate to compensate for the practically unavoidable sampling incompleteness.

One major finding regarding the internal organization of species within these *Conus* communities is the fair constancy of the rough abundance unevenness, regardless of species richness and, accordingly, the sharp increase of the standardized abundance unevenness I_{str} with increasing species richness. This, indeed, is in *striking contrast with the common trend*, repeatedly highlighted in most marine communities, including both invertebrate and vertebrate faunas. In turn, the functional significance of this unusual pattern in species abundance unevenness is that such *Conus*

communities likely show a very limited capacity to further relax the average level of inter-specific competition, as would be required to accommodate additional increment in species richness. In other words, this suggests that these *Conus* communities appear to have reached (or at least have approached) an upper threshold limit as regards the “resource partitioning” among species. Accordingly, in these *Conus* communities, the increase in species richness becomes almost entirely accommodated by the enlargement of the overall range of species abundances, that is by the corresponding decrease of the abundance level of the rarest species.

Another interesting point, argued in sections 4.2 and 4.4.4, is the rather weak adequacy of the Neutral Theory of Biodiversity – in its strong version – to convincingly explain the internal structuration of these *Conus* communities.

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COMPETING INTERESTS

Author has declared that no competing interests exist.

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Appendix 1

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

Consider the survey of an assemblage of species of size N_0 (with sampling effort N_0 typically identified either to the number of recorded individuals or to the number of sampled sites, according to the inventory being in terms of either species abundances or species incidences), including $R(N_0)$ species among which f_1, f_2, f_3, f_4, f_5 , of them are recorded 1, 2, 3, 4, 5 times respectively. The following procedure, designed to select the less-biased solution, results from a general mathematical relationship that constrains the theoretical expression of *any* theoretical Species Accumulation Curves $R(N)$ [see [29,65,66]:

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

Compliance with the mathematical constraint (equation (A.1)) warrants *reduced-bias* expression for the extrapolation of the Species Accumulation Curves $R(N)$ (i.e. for $N > N_0$). Below are provided, accordingly, the polynomial solutions $R_x(N)$ that respectively satisfy the mathematical constraint (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 [29]:

- * for f_1 up to $f_2 \rightarrow R_1(N) = (R(N_0) + f_1) - f_1.N_0/N$
- * for larger f_1 up to $2f_2 - f_3 \rightarrow R_2(N) = (R(N_0) + 2f_1 - f_2) - (3f_1 - 2f_2).N_0/N - (f_2 - f_1).N_0^2/N^2$
- * for larger f_1 up to $3f_2 - 3f_3 + f_4 \rightarrow R_3(N) = (R(N_0) + 3f_1 - 3f_2 + f_3) - (6f_1 - 8f_2 + 3f_3).N_0/N - (-4f_1 + 7f_2 - 3f_3).N_0^2/N^2 - (f_1 - 2f_2 + f_3).N_0^3/N^3$
- * 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:

- * $f_1 \leq f_2 \rightarrow \Delta_{J1} = f_1 ; R_1(N)$
- * $f_2 < f_1 \leq 2f_2 - f_3 \rightarrow \Delta_{J2} = 2f_1 - f_2 ; R_2(N)$
- * $2f_2 - f_3 < f_1 \leq 3f_2 - 3f_3 + f_4 \rightarrow \Delta_{J3} = 3f_1 - 3f_2 + f_3 ; R_3(N)$
- * $3f_2 - 3f_3 + f_4 < f_1 \leq 4f_2 - 6f_3 + 4f_4 - f_5 \rightarrow \Delta_{J4} = 4f_1 - 6f_2 + 4f_3 - f_4 ; R_4(N)$
- * $f_1 > 4f_2 - 6f_3 + 4f_4 - f_5 \rightarrow \Delta_{J5} = 5f_1 - 10f_2 + 10f_3 - 5f_4 + f_5 ; R_5(N)$

N.B. 1: As indicated above (and demonstrated in details in [29]), 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 [20,22,

67-69]. Also, this shows that the approach initially proposed by [70] – which has regrettably suffered from its somewhat difficult implementation in practice – might be advantageously reconsidered, now, in light of the very simple selection key above, of *far much easier practical use*.

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

N.B. 3: For f_1 falling beneath $0.6 \times f_2$ (that is when sampling completeness closely approaches exhaustivity), then Chao estimator may alternatively be selected: see reference [30].

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 [32].

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

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

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

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

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

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

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

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

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

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