Original Research Article

Influence of coral-reef complexity on species richness and the hierarchical structuration of species abundances in reef fish communities: a case study in south-east Brazil

Abstract

Increasing complexity of coral habitat is expected to increase resource partitioning among co-occurring reef fish and, thereby, reduce to some extent the mean competitive intensity, with correlative consequences on the internal structuring of species in reef fish communities, in particular regarding species richness and species abundance unevenness. Accumulating dedicated case studies are necessary, however, to get further empirical confirmations. The present analysis aims to contribute in this respect, comparing two coral-reef settings that markedly differ in their degree of morphological complexity. Available samplings remaining incomplete (as is often the case in practice), numerical extrapolations were implemented, providing least-bias estimates for both total species richness and the exhaustive distribution of species abundances in each two compared reef fish communities. As expected, the total species richness is found to increase with higher level of coral habitat complexity, while the species abundance unevenness decreases. This decrease in abundance unevenness – reflecting the corresponding relaxation of the mean level of competitive intensity – is partly due to the direct, negative influence of species richness on abundance unevenness, as an overall trend. Beyond that, however, the relaxation is further strengthened by an additional "genuine" contribution – this time independent from the variation in species richness – and, as such, idiosyncratically attached to the improvement in habitat complexity.

Key-words: species diversity, ranked species abundance distribution, evenness, incomplete sampling, numerical extrapolation, Itaipu

1. INTRODUCTION

Coral reefs as a whole, and the associated reef fish communities in particular, are considered embodying among the highest levels of diversity and biological complexity on Earth [1-6]. This high diversity is still enhanced by the tight relationships binding reef fishes to the surrounding coral settings [7, 10]. On the other hand, tropical marine ecosystems, especially those hosted by coral reefs, are under increasing threat, being particularly sensitive to ongoing anthropogenic deteriorations of environment. This, in turn, urges to monitor the progressive alteration of these ecosystems, especially focusing on the on-going reduction in species richness as well as the increased unevenness of species abundances [4].

Yet, detrimental anthropogenic activities are not the unique source of modification in the detailed structuring of species within animal communities. Other, *non-anthropogenic* ecological and environmental determinants may also be involved, whose own influences need to be assessed, in order to be able to disentangle, *in fine*, what is the genuine contribution of anthropogenic degradation of the environment from what is the mere consequence of "natural" causes. Therefore, it is necessary, first, to improve our knowledge regarding the influence of different kinds of "natural" factors, such as, for example, the degree of structural complexity of coral setting [7-15]. Hence the necessity to collect as much data as possible on this subject by accumulating dedicated case studies.

2. MATERIALS AND METHODS

2.1 – The reported field data

The present study is based on two partial samplings of reef fish communities conducted on two small islands ("Pai" island and "Mae" island) of Itaipu Sound, Niteroi, RJ, Brazil (22°58'S - 43°02'W) and reported in reference [16]. All details regarding the precise locations of the compared habitats and the sampling procedure are provided in the open-access reference above 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 extrapolations. These extrapolations are indeed required because the subsistence of species recorded only once ("singletons") suggests that reported samplings remain incomplete, as was indeed confirmed later. 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.

The coral habitat complexity, measured in term of chain link rugosity index [11], proves being significantly higher at "Mae" island than at "Pai" island [16] (a third reported community, at "Menina" island is not considered here, as it suffers intensive fishing and important coastal runoff due to its proximity to the main shore [16]).

2.2 - The Numerical Extrapolation procedure and its exploitation

To avoid making seriously biased inferences regarding the main structural descriptors of ecological communities (such as total species richness and abundance unevenness), it is required to rely upon (sub-) exhaustive inventories [17–21]. Yet, incomplete samplings are almost unavoidable in practice, with species-rich communities having very uneven distribution of abundances, as is most often the case with reef fish communities. Hence, the need to complete the available partial samplings by implementing a reliable procedure of *numerical extrapolation* [22] that can provide least-biased estimates regarding the number of the still unrecorded species, as well as the distribution of the abundances of these unrecorded species. This is all the more important that rare species, that often escape recording in practice, may yet disproportionately contribute to the functional structuring of communities in the wild: [23-33], the latter with numerous references therein. In particular, neglecting rare species can seriously reduce the capacity to detect ecological changes when analyzing species communities comparatively; thus "rare species are critical for bio-assessment" [33].

Fortunately, a recently developed procedure of numerical extrapolation takes into account these needs (sections 2.2.1 to 2.2.3). Moreover, 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, about the underlying process that drives the hierarchical structuring of species abundances within community [34-38].

2.2.1 - *implementation of the procedure of numerical extrapolation*

* *Total species richness*: the least-biased estimation of the number of still undetected species during partial sampling and the resulting estimation of the total species richness of the partially sampled community are derived according to the procedure defined in [39-40] 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.

* *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 [41, 42], 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 [42], briefly summarized in Appendix 2 and concretely exemplified in details in [43]. 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).

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 [44]. In turn, 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 [45], it is the degree of *unevenness* – rather than evenness – 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 [46], 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 [34, 47-50].

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 [51-55]. The likely underlying ecological origin of this overall trend (behind its "mathematical-like" appearance [51, 54]) is discussed in detail in [56]. 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 [55, 56]. As argued in detail in [56], the direct, negative influence of species richness on abundance unevenness is adequately accounted for by the "broken-stick" theoretical distribution, originally conceptualized by MacArthur [57]. 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 [58]. 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 [51, 52, 55, 56, 58]. Accordingly, a *standardized unevenness index*, "I_{str}", is defined by the ratio U/U' [55, 56]:

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

that is:

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

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, fully sensitive to this influence of species richness. In this respect, 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 [53, 59]: "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 [56]). 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 structure of most bird communities [34, 57], 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 [51, 56]. 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 community

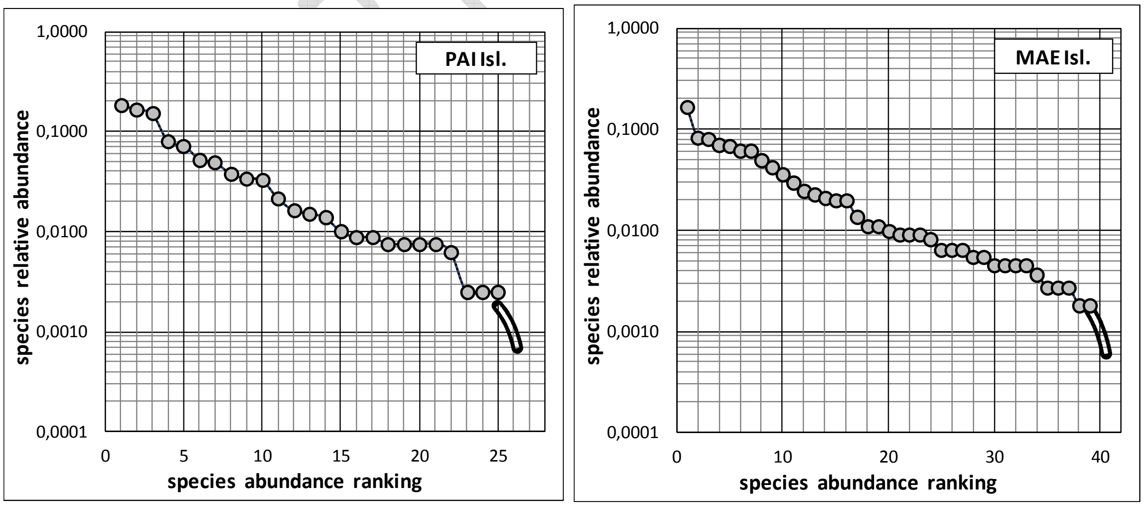
The two studied fish communities, at “Pai” and “Mae” islands, differ in their true (total) species richness, with *estimated* values $S_t = 26.2$ and $S_t = 40.5$ respectively (Table 1).

Table 1 – The number of collected individuals N_0, the number of recorded species R_0, the type of nonparametric estimator (Jackknife) selected as being the least-biased one, the estimated number 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.

Reef fish community	**PAI Isl.**	**MAE Isl.**
nb. collected individuals N_0	770	1063
nb. recorded species $R_0 = R(N_0)$	25	39
selected least-biased estimator	JK-2	JK-2
number unrecorded species Δ	1.2	1.5
total species richness S_t	**26.2**	**40.5**
sample completeness R_0/S_t	95%	96%

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



Figures 1 & 2 – The Species Abundance Distributions of reef fish communities at “Pai” island (left) and at “Mae” island (right). *Recorded*: discs; *numerically extrapolated* part: double line

3.3 Taxonomic dissimilarity between the two fish communities

3.3.1 Jaccard similarity index

Referring to recorded species lists, the fish community at "Pai" island is entirely nested taxonomically in the fish community at "Mae" island, the 25 recorded species in the former being all shared by the latter. Based on *recorded* data, the Jaccard similarity index is thus hypothetically evaluated as Jr = 25/(25 + 39 – 25) = 0.64. In turn, numerically extrapolated data (S_t = 26.2 and 40.5) allows to more surely specify that the actual Jaccard index is comprised between:

- at least, J = 25/(26.2 + 40.5 – 25) = 0.60, if no species are shared in common among the unrecorded species and

- at most, J = 26.2/(26.2 + 40.5 – 26.2) = 0.65, if unrecorded species in "Pai" island community is also shared by "Mae" island community.

That is – now more reliably based on numerically completed samplings – an estimated Jaccard similarity index comprised between 0.60 and 0.65.

3.3.2 Species exclusive to "Mae" community according to recorded data

Based on recorded data, 14 species (= 39–25) are considered exclusive to the community at "Mae" island and listed in [16]. Interestingly, the average relative abundance of these 14 exclusive species is 5 times lower than that of the 25 shared species (0.0071/0.0360). Although not surprising, this feature yet deserved being verified, as graphically highlighted in Figure 3.

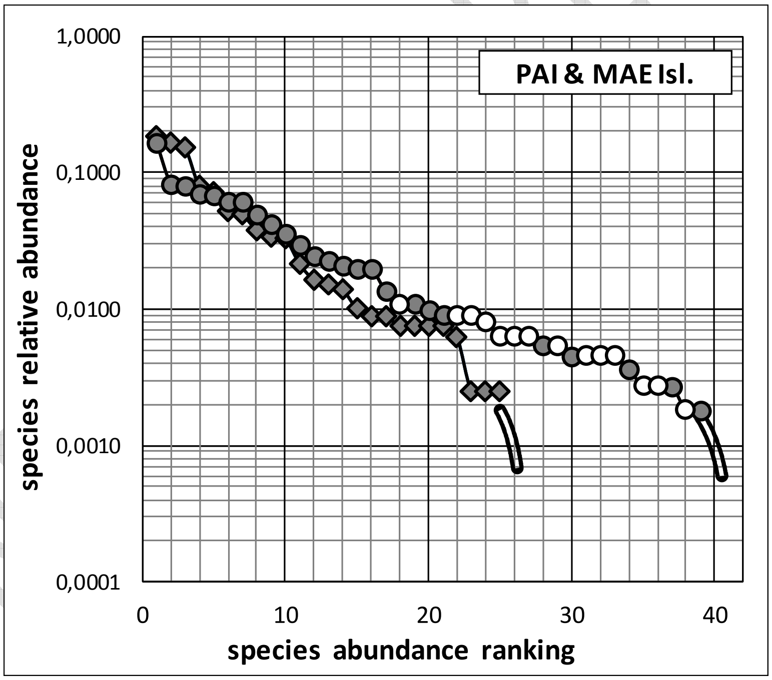
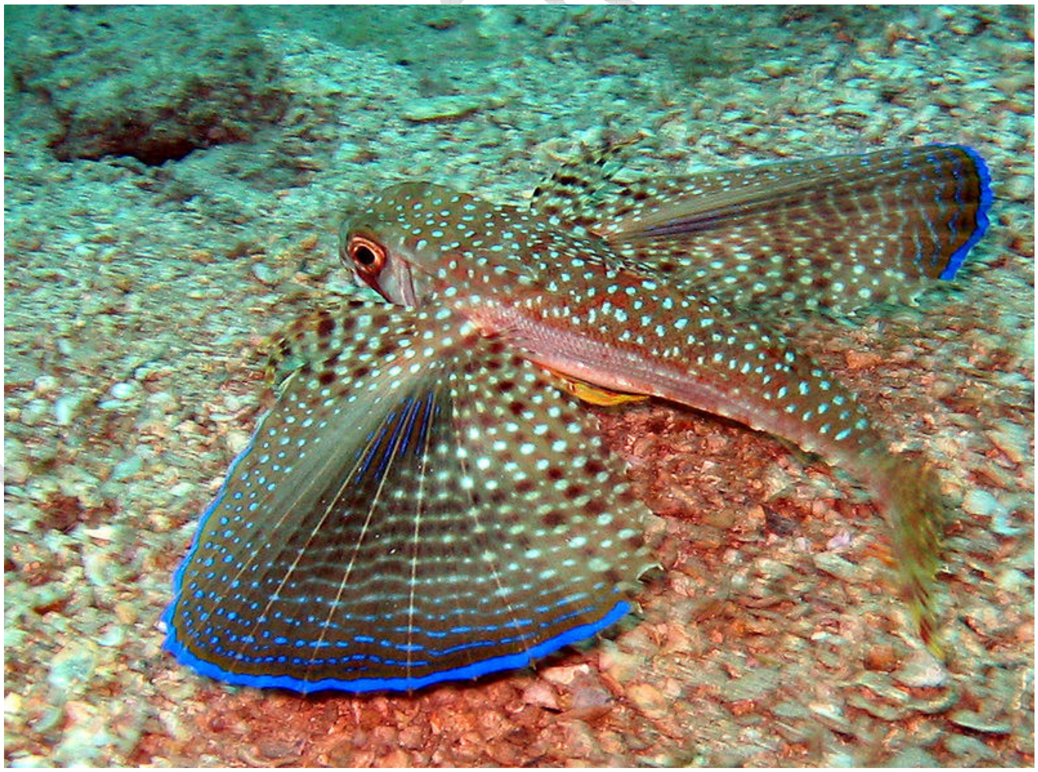


Figure 3 – The Species Abundance Distributions of reef fish communities at "Mae" island (discs) and at "Pai" island (diamonds). Grey figures: species shared in common by both communities; white figures: species exclusive to the community at "Mae" island

Chaetodon striatus Linnaeus 1758, *common* to both fish communities © Bernard E. Picton

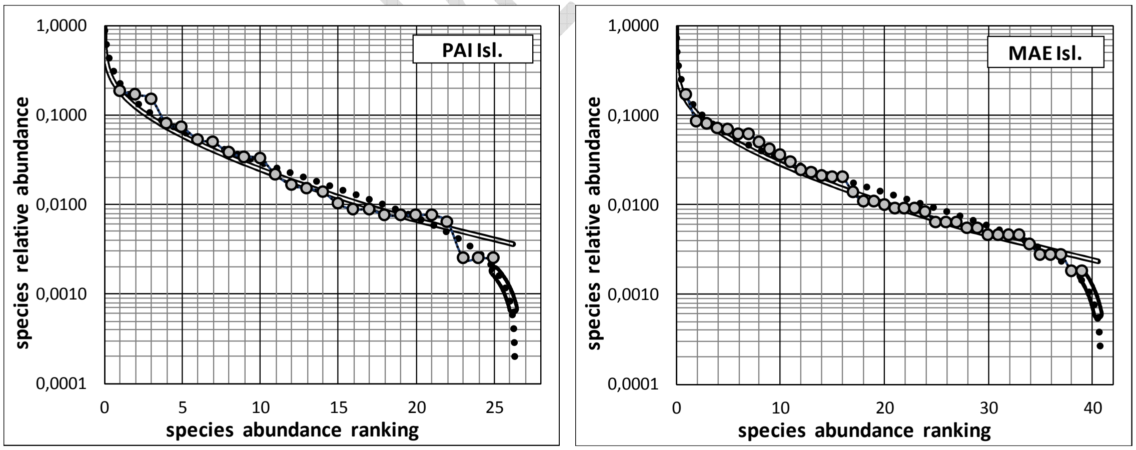


Dactylopterus volitans (Linnaeus 1758), *common* to both fish communities © Carlos Henrique

Pomacanthus paru (Bloch 1787), recorded from Mae community *only* © Brian Gratwicke

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

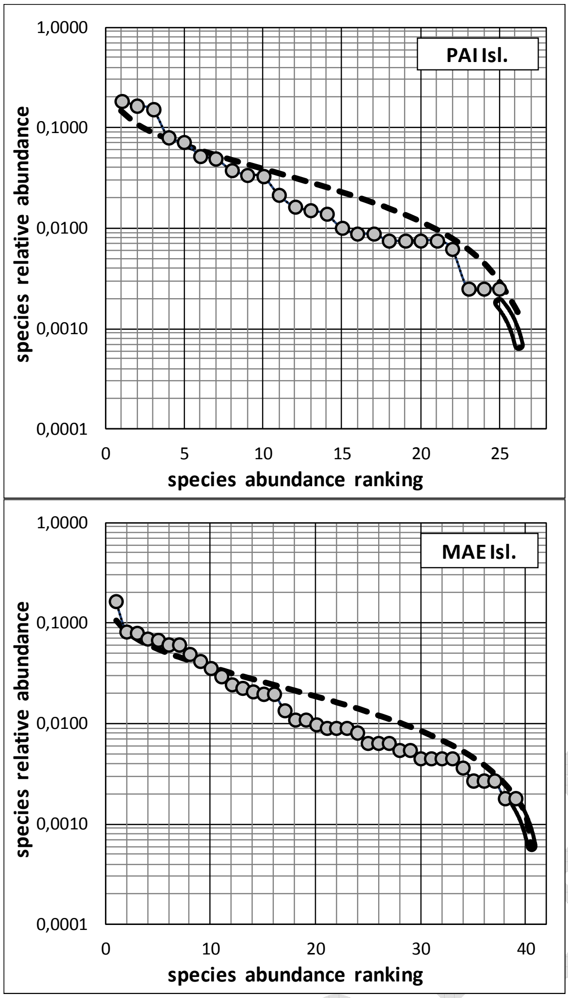
The numerically completed "S.A.D.s" of both studied communities clearly fit better the "log-normal" model than the "log-series" model (Figures 4 & 5). This remained rather uncertain as long as based exclusively upon recorded data and becomes quite clear only after considering the numerical extrapolation of abundance distributions.



Figures 4 & 5 – Two classical models: "log-normal" (coarse dotted line) and "log-series" (fine double line) compared to the 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 6, 7 and 8, allow to compare the average slope (U) of the "S.A.D." to the average slope (U') of the corresponding "broken-stick" model (§ 2.2.2 & 2.2.3), from which is derived the genuine intensity of the underlying structuring process $I_{str} = U/U'$ (equation (2)).



Figures 6 & 7 – The Species Abundance Distribution for each studied community compared to the corresponding "broken-stick" model (dashed line) computed for the same species richness.

The main results derived from this comparison are summarized synthetically in Table 2 which highlights in particular the variations of the true total species richness S_t, the ratio a_1/a_{St} between the abundances of the commonest and rarest species, the rough abundance unevenness U and, finally, 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}
PAI isld.	26.2	.1858	.000683	272	.1471	.00146	101	.0966	.0795	1.22
MAE isld.	40.5	.1657	.000599	277	.1063	.00061	174	.0615	.0565	1.09

The numerically completed Species Abundance Distributions of both fish communities are plotted together in Figure 8, for a more straightforward appreciation of the effect of coral habitat complexity on the hierarchical structuration of species abundances. Rough abundance unevenness U is substantially less at “Mae” than at “Pai”, due to both:

(i) the greater species richness at “Mae”, which negatively influence unevenness as a general overall trend and

(ii) the additional relaxation of the mean competitive intensity (leading to a corresponding additional reduction of abundance unevenness) allowed by the more complex habitat at “Mae” island, likely offering additional differentiated ecological niches and, thereby an easier resource partitioning among co-occurring species.

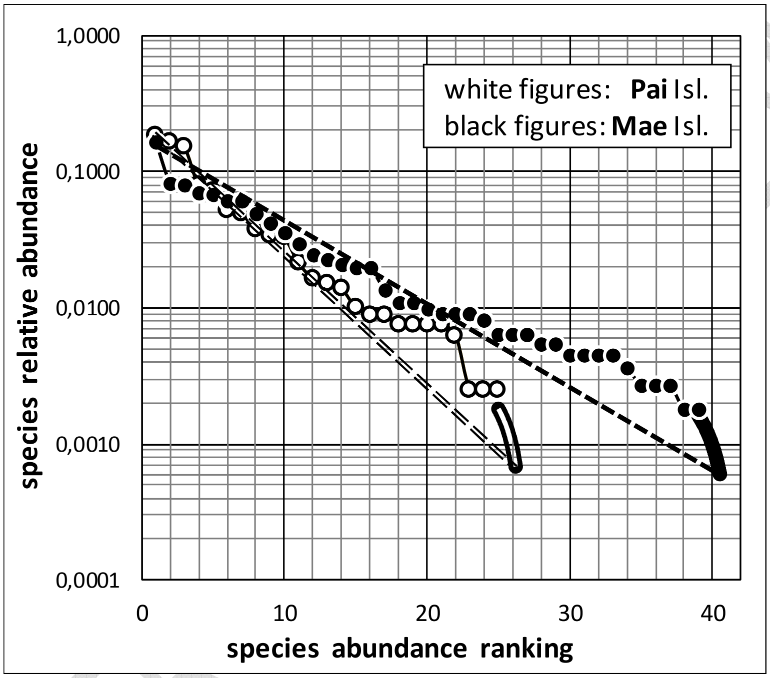


Figure 8 – The Species Abundance Distributions of both fish communities plotted together to allow direct comparison of the influence of the coral habitat complexity, higher at “Mae” Island than at “Pai” island.

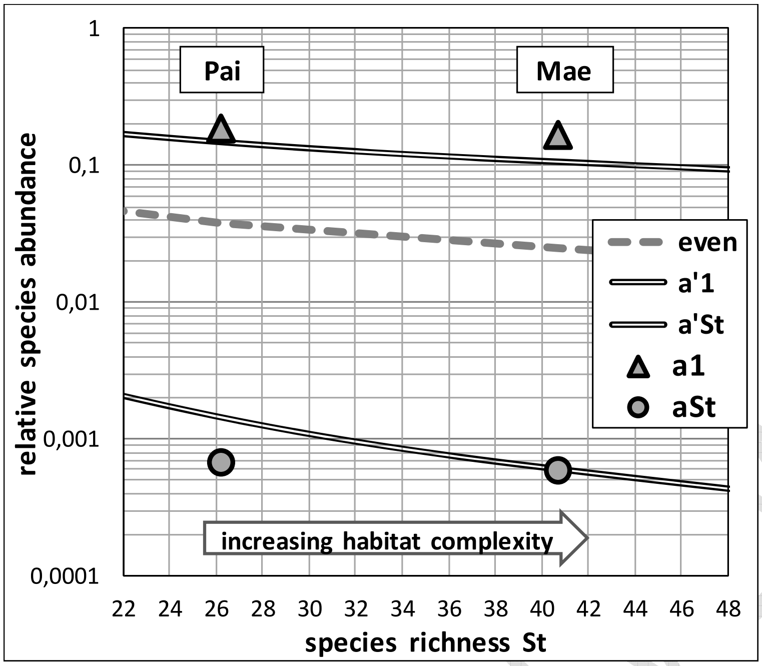


Figure 9 – The maximum and minimum abundances, a_1 and a_{St}, for each of the two studied reef fish communities plotted jointly with the maximum and minimum abundances, a'_1 and a'_{St} of the "broken-stick" model and the uniform abundance level (= $1/S_t$) of the perfectly "even" model. The range of species abundance (a_1/a_{St}) remains almost unchanged (+2%) from "Pai" to "Mae" while the corresponding range of species abundance in the broken-stick model (a'_1/a'_{St}) substantially increases (+73% for a_1/a_{St}) (cf. Table 2). This is at the origin of the decrease of I_{str} from "Pai" to "Mae" (Table 2).

As a complement, Figure 9 highlights graphically how the highest and lowest abundances, a_1 and a_{St}, vary with increasing levels of species richness accompanying higher habitat complexity. Comparison is allowed with two theoretical referential models: the broken-stick distribution and the ideally even abundance distribution. Note that here, both a_1 and a_{St}, remain remarkably stable in spite of the substantial increase of species richness, contrasting in this with the two referential models. This stability emphasizes the efficacy of the relaxation of mean competitive intensity, likely allowed by the higher habitat complexity at "Mae": this relaxation makes compatible a strong increase in species richness with a practically unchanged range of species abundances (i.e. without decreasing a_{St} nor increasing a_1).

At last, the results in Table 2 highlight how each of the three structural parameters, S_t, U and I_{str} , respond respectively to the significant complexification of habitat at "Mae" as compared to "Pai":

(i) the *species richness* S_t increases by $\Delta S_t/S_t$ ($=(S_{t2}-S_{t1})/½(S_{t2}+S_{t1})$) = 43%, which, in turn, corresponds to a variation $\Delta U'/U'$ = –33% of the abundance unevenness for the broken-stick distribution (the latter accounting for the tendential negative influence of species richness on abundance unevenness: *cf.* section 2.2.3).

(ii) the *rough abundance unevenness* U decreases by $\Delta U/U$ = –44%

(iii) the *standardized abundance unevenness* I_{str} decreases by $\Delta I_{str}/I_{str}$ = –11%.

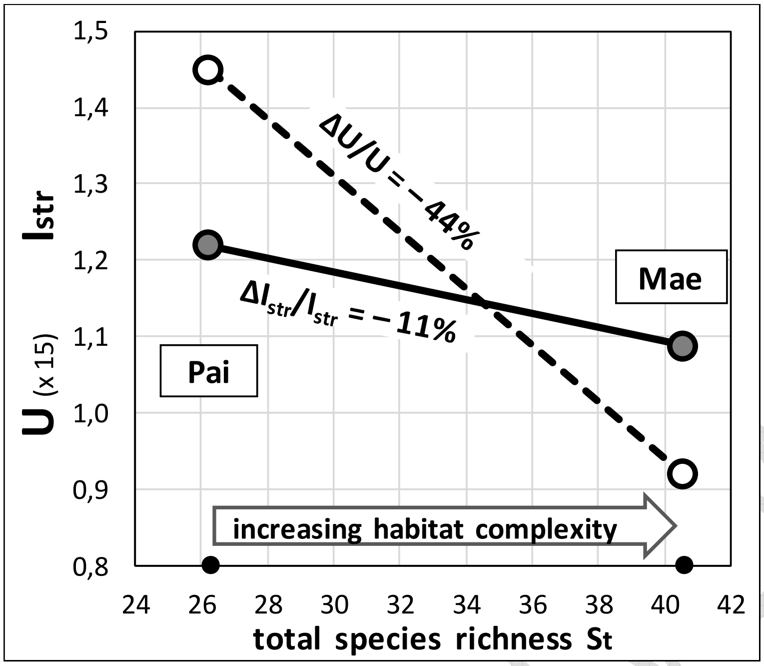


Figure 10 – The degree U of abundance unevenness (*dashed* line) and the intensity I_{str} of the underlying structuring process (*solid* line) plotted against the total species richness St, for the two studied communities at "Pai" and "Mae" Islands. The abundance unevenness U strongly decreases (by 44%) as the result of both (i) the tendential, negative direct influence of S_t upon U (contributing for 33%) and (ii) a complementary, "genuine" contribution highlighted by the 11% decrease of the standardized unevenness I_{str}. *Note that for commodity of graphical comparison between U and I_{str}, the values of U are uniformly multiplied by a same factor 15.*

As the degree of abundance unevenness accounts for the mean level of competitive intensity within community (*cf.* section 2.2.3), it follows that the complexification of the coral habitat at "Mae" is conducive to a reduction of the mean competitive intensity in the associated fish community attributable:

- for ¾ (= 33%/44%), to the direct tendential influence of the (43%) increase in species richness;

- for ¼ (= 11%/44%), to an additional, *genuine* contribution to the relaxation of the mean competitive intensity, specifically ("idiosyncratically") attached to the community at "Mae" (i.e. independently of the influence of its 43% higher species richness).

Figure 10 provides a graphical representation of these responses of S_t, U and I_{str} to the complexification of habitat at "Mae", as compared to "Pai".

4. DISCUSSION

It has been argued that fish assemblages associated to tropical coral reefs exhibit close *positive* relationships with the degree of habitat complexity [5, 16], resulting in particular from the morphology and the overall "rugosity" of the coral display [7-16, 60-63]. Coral species diversity has also been advocated has a determinant of richness and structuration of reef fish communities [60]. As a whole, a positive influence of habitat complexity on the species richness of reef fish communities has been highlighted.

Yet, in most case studies devoted to this subject, two important aspects, conditioning the relevance of the analysis, had been neglected and, therefore still needed to be addressed:

- the bias resulting from the (often unavoidable) *incompleteness* of available samplings [9, 10, 43, 64-67];
- beyond its role on species richness, the usually overlooked effect of habitat complexity on the distribution of species abundance, especially the degree of *abundance unevenness*.

Here, as in preceding reports dealing with coral reef-associated communities [9, 10, 43, 64-67], *numerical* extrapolations are implemented to compensate for the lack of exhaustive samplings, thus providing least-biased estimates of the number of unrecorded species and their respective abundances – using a dedicated procedure, recently made available [39, 42]. Thereby, the full-range of the Species Abundance Distribution is derived, including the set of species that had remained undetected. In particular, major traits of community organization – the true (total) species richness S_t, the degree of species abundance unevenness U and the standardized abundance unevenness I_{str} – are provided in Tables 1 & 2 and Figures 1 & 2.

4.1 - Effect of habitat complexity on the true species richness and the taxonomic composition of associated fish communities

A higher species richness in reef fish community is anticipated at "Mae" as compared to "Pai", answering a significantly more tormented coral habitat (10% higher rugosity); what was confirmed with a 43% higher estimated true species richness at "Mae".

The substantial taxonomic dissimilarity highlighted between the two fish communities (estimate of Jaccard similarity index comprised between 0.60 and 0.65) results from the community at "Pai" being essentially nested in the community at "Mae" (rather than from simple taxonomical turn-over). The community at "Pai" only keeps the subset of the most abundant species from "Mae", being deprived from the rarer species which, apparently, can only survive thanks to the more tormented coral habitat at "Mae": Figure 3. This fits the likely expected trend according to which depauperate ecological communities tend to lose their less abundant species first and, similarly, the trend according to which taxonomic turnover, if any, tends to preferentially target the less abundant species first [67].

4.2 - Type of process involved in the structuring of species abundances

The numerically-completed "S.A.D.s" of both fish communities clearly fit best the "log-normal" than the "log-series" models (Figures 4 and 5), thereby suggesting that the hierarchical structuring of species abundances is governed by the combined influence of many independent factors, rather than by one or very few dominant factor(s). Note that the conclusion would have remained less clear if only the recorded part of the "S.A.D.s" was available, thereby emphasizing, once again, the interest of numerical extrapolations of incomplete inventories. The conformity of both "S.A.D.s" to the "log-normal" model, is not surprising, being rather common in most species-rich communities, at least when they are not subjected to excessively harsh environmental stresses (pollutions, etc …) [47, 49, 50].

4.3 - Effect of coral habitat complexity on the mean competitive intensity and the species abundance unevenness within associated fish community

The lower habitat complexity at "Pai" is associated to a stronger level of rough abundance unevenness U (Table 2, Figure 10), reflecting in turn a substantial increase in mean competitive intensity resulting from the more uniform habitat at "Pai". The latter likely offers less varied feeding niches and fewer opportunities of protection against potential predation. Hence the increase in mean competitive intensity at “Pai” and the parallel decrease in species richness, already underlined above. Moreover, the increase of competitive intensity and abundance unevenness U slightly exceeds what is expected from the negative direct relationship between U and S_t (section 2.2.3): the standardized unevenness I_{str} (made freed from the direct influence of species richness) remains 11% larger at “Pai” than it is at “Mae” (Table 2, Figure 10). This clearly underlines the role of “physical” simplification in the coral habitat upon the degree of mean competitive intensity and the resulting severity in the hierarchical structuring of species abundances in associated fish community. Conversely, a higher physical complexity of the coral habitat likely allows an improved resource partitioning (*sensu latissimo*) among co-occurring fish species and, accordingly, leads to both an improved relaxation of mean competitive intensity (hence the decrease of both U and I_{str}) and the resulting opportunity to accommodate a larger number S_t of co-occurring species.

4.4 – Comparison with other case studies dealing with the same subject

The influence of coral habitat complexity on the *total species richness* S_t, the *rough abundance unevenness* U, the *standardized abundance unevenness* I_{str} and the *degree of taxonomic differentiation*, are compared between three reef fish communities respectively located at Bonaire (Dutch Caribbean) [9], Gorgona Island (Columbia) [10] and Itaipu (present study): Table 3.

1) total species richness S_t

The positive role of higher coral habitat complexity on the total species richness of the associated fish community was also reported at Gorgona Island, while (rather surprisingly) the studied site at Bonaire provides what seems a counterexample, with a slight decrease in species richness associated to an apparently stronger habitat complexity – which remains unexplained.

2) rough abundance unevenness U

Due to the prominent negative direct influence of species richness on abundance unevenness, the answer of rough abundance unevenness U to habitat complexity is systematically opposite to the answer of species richness. Accordingly, the rough unevenness decreases at Itaipu and Gorgona, but slightly increases at Bonaire.

3) standardized abundance unevenness I_{str}

The systematic decrease, in all three case studies, of the standardized unevenness I_{str} with higher habitat complexity is still more interesting, and ecologically significant, as this reflects the *likely systematic* contribution of higher habitat complexity to the reduction of the mean competitive intensity (beyond the general trend linking positively relaxed competition and species richness).

4) Taxonomic differentiation: Jaccard similarity index J

Jaccard similarity between the two compared communities at Itaipu is estimated in the range 0.62 ± 0.03, that is close to the estimated values of Jaccard index at Gorgona and Bonaire. Some consistency is thus highlighted also regarding the degree of taxonomic differentiation induced by increased habitat complexity, with Jaccard index remaining around J = 0.60 to 0.65.

Table 3 – The consequences of an increase in habitat complexity – compared in three sites (Brazil, Columbia, Dutch Caribbean) – in terms of: (i) variation $\Delta S_t/S_t$ of total species richness, (ii) variation

$\Delta U/U$ of rough abundance unevenness and its contributors, $\Delta U'/U'$ and $\Delta I_{str}/I_{str}$ (with $\Delta U/U = \Delta U'/U' + \Delta I_{str}/I_{str}$). Also mentioned is the estimated range for the Jaccard similarity index between compared communities.

investigated sites **(each of them including two communities differing by their degree of habitat complexity)**	**species richness S_t**	**rough mean competitive intensity U**	**tendential influence from S_t**	**additional genuine contribution**	**level of taxonomic proximity**
	$\Delta S_t/S_t$	**$\Delta U/U$**	**$\Delta U'/U'$**	**$\Delta I_{str}/I_{str}$**	**Jaccard** index
Brazil – Itaipu Isld.	**+ 43 %**	**– 44 %**	**– 33 %**	**– 11 %**	0.62 ± 0.03
Columbia – Gorgona Isld.	**+ 22 %**	**– 21 %**	**– 18 %**	**– 3 %**	0.65 ± 0.15
Caribbean – Bonaire Isld.	**– 14 %**	**+ 7 %**	**+ 10 %**	**– 3 %**	0.61 ± 0.24
average trend	***+ 17 %***	***– 19 %***	***– 13 %***	***– 6 %***	*0.63*

5) synthetic view

The four main descriptors of the internal structuring in a community (S_t, U, U', I_{str}) are linked by two relationships: equation (2) above, which relies U, U', I_{str} and the mathematical dependence of broken-stick unevenness U' upon St (equation (2) in [56]). Accordingly, two descriptors only, among the four, can be chosen as mutually independent – and, therefore, two descriptors are sufficient to summarize the information conveyed by the all four descriptors. Here, *total species richness* S_t and *standardized unevenness* I_{str} are selected as the two independent descriptors. Figure 11 provides a synthetic view of how increased coral-habitat complexity affects these two descriptors, within each of the three reef fish communities considered above.

In particular, the systematic decrease of I_{str} highlights the "genuine", idiosyncratic contribution of higher habitat complexity to the relaxation of the mean competitive intensity, in complement to its indirect contribution to relaxation, *via* species richness.

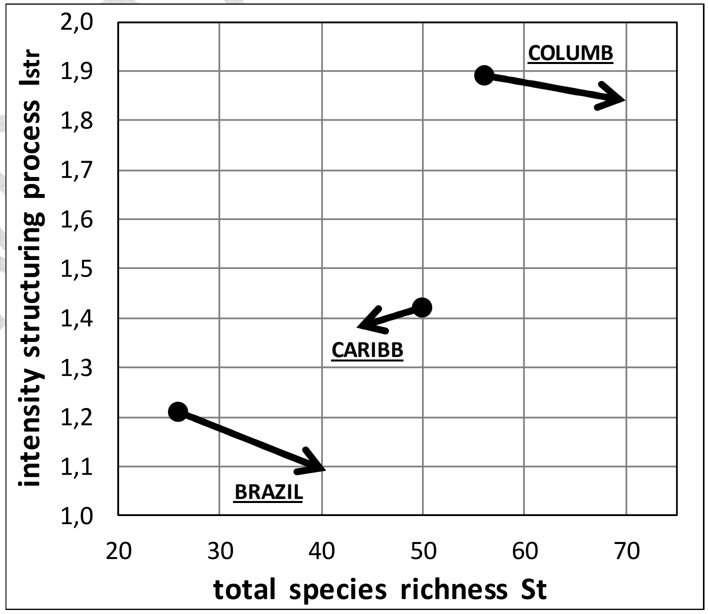


Figure 11 – The consequence of higher habitat complexity on (i) the total species richness S_t and (ii) the standardized unevenness I_{str}, at three sites (Brazil, Columbia, Dutch Caribbean).

5. CONCLUSION

Relevant data remains scarce regarding the influence of coral habitat complexity on the internal structuring of associated reef fish communities, as this requires first:

- dealing with either exhaustive or duly numerically completed samplings of fish communities,
- considering not only the influence of habitat complexity on total species richness but also species abundance unevenness in associated fish communities.

To my knowledge, only three such case studies, summarized in Table 3 (including the present report), are presently available, which, obviously, makes it rather difficult to draw well-founded conclusions. Accordingly, the following proposals are only forward-looking suggestions that require additional empirical confirmations, although they seem fairly consistent with reasonable expectations.

Increased physical complexity of coral habitat (often associated to, or resulting from higher taxonomic diversity within coral settings) is expected to offer more diversified feeding niches as well as more diversified protective shelters against predators. In short, more opportunities to improve "resource partitioning" among co-occurring fish species. This improved partitioning of the available resource is expected to allow for a larger number of species to share the same habitat, thus resulting in a substantial relaxation of mean competitive intensity and, consequently, a reduction in the level of abundance unevenness. Indeed, this parallel tendency for both a relaxed competitive intensity (reflected in the substantial decrease of rough abundance unevenness) and a growing total species richness is supported by the presently available data, at least as an average trend. Moreover, an additional, genuine contribution to the relaxation of the mean competitive intensity (reflected by the decrease of the standardized unevenness index I_{str}) is systematically highlighted.

Once again subjected to further confirmation, these results provide new empirical support regarding the benefits that reef fish communities can derive from more complex coral habitat: higher species richness and improved stability, favored by further relaxation of the mean competitive intensity.

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 [39, 68, 69]:

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

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 [39]:

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

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

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:

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

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

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

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

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

N.B. 1: As indicated above (and demonstrated in details in [39]), 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 [19, 21, 70-72]. Also, this shows that the approach initially proposed by [73] – 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 [40].

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 [42].

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:

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

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 $i > R_0$):

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

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.

COMPETING INTERESTS

Author has declared that no competing interests exist.

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