Influence of coral architecture on species richness and the hierarchical structuration of species abundances in reef fish communities: a case study in the Eastern tropical Pacific

Original Research article

Abstract

The role of coral reef architecture on species richness and the structuration of the associated fish communities has already been addressed several times. The reported results, however, usually remain controversial, possibly because they are based upon incomplete field data issued from partial inventories. Indeed, incomplete samplings are almost unavoidable in practice with such species-rich communities having very uneven distribution of abundances. In this context, the *numerical extrapolation* of incompletely sampled communities may serve as a reliable surrogate. Accordingly, numerical extrapolations were implemented, here, to compare two fish-communities respectively associated to coral reefs that sharply differ by their topographic architectures. Both a higher total species richness and a sharper unevenness of species abundances were found to characterize the fish community associated to the more tormented reef habitat exhibiting the more complex architecture. Yet, paradoxically, the true intensity of the underlying process of hierarchical structuring of abundances proves being insensitive to the architecture of coral habitats. This apparent opposition between the unevenness *pattern* and the underlying structuring *process* results, in fact, from the additional negative dependence of abundance unevenness to species richness between compared communities.

Key-words : species diversity, ranked abundance distribution, evenness, incomplete sampling, numerical extrapolation, Gorgona island, Colombia

1. Introduction

Tropical marine ecosystems in shallow waters, especially those hosted by coral reefs, are of major interest, being considered as embodying remarkably high levels of diversity and biological complexity [1-6]. Reef fish communities are emblematic examples of highly rich and diverse assemblages of species co-occuring at a same location. This high diversity is still enhanced by tight relationships binding reef fishes and the surrounding coral settings [7, 8]. On the other hand, tropical marine ecosystems, especially those hosted by coral reefs, are particularly sensitive to environmental stresses in general and climate change in particular. This, in turn, urges to monitor the progressive alteration of these ecosystems, especially focusing on reduction in species richness and sharper unevenness of species abundance distribution.

Now, monitoring is one thing, rationally interpreting the causes of recorded observations is another one. Indeed, the structure of animal communities are not only affected by detrimental anthropogenic activities but are dependent also upon a series of *other* ecological and environmental determinants. Thus, to disentangle the contribution of anthropogenic degradation of environment from the consequences of other “natural” causes, it is necessary, first, to improve our knowledge regarding the influence of different kinds of “natural” factors (such as, for example here, the type of architecture of the coral setting).

The influence of coral setting architecture in general and the degree of "reefscape" rugosity in particular, have already motivated a series of studies devoted to this topic [7-13].

Now, to avoid making seriously biased inferences regarding the main structural descriptors of reef fish communities (such as total species richness and abundance unevenness), it is imperatively required to rely upon (sub-) exhaustive inventories [14–17]. 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* [18] that can provide estimates with minimized bias regarding the number of the still unrecorded species and 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: [19-28] and [29] 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 bioassessment" [29].

Fortunately, a recently developed procedure of numerical extrapolation takes into account these needs. In particular, this new extrapolating tool invites to revisit the already available reported data based upon non-extrapolated partial inventories and to critically reconsider the interpretations supported by these incomplete inventories. The purpose being to tentatively establish more relevant interpretations, based on *numerically completed* samplings. More specifically, once properly numerically completed (and *only* when it is so [16]), 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 [30-34].

Hereafter, I question how the main descriptors of reef fish communities respond to two substantially distinct kinds of architectures among coral-reefs: (i) a formation composed of *large massive coral colonies* that made a heterogeneous, high-relief "reefscape" and (ii) a formation dominated by *branching coral colonies* forming a monotonous framework of low relief.

2. MATERIALS AND METHODS

2.1 – The reported field data

The present study is based on two partial samplings of reef fish communities conducted along the shore of Gorgona island, off the Pacific coast of Colombia (2°58'27"N - 78°11'13"W) and reported by Maria del Mar Palacios and Fernando Zapata in reference [35]. All details regarding the precise locations of compared habitats and the sampling procedure are provided in the open-access reference above and need not being repeated here. The most 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 required because the relatively high proportion (around 10%) of species recorded only once ("singletons") suggests that reported samplings are substantially 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.

Two types of coral-reef fish communities were sampled:

- a "*massive coral*" fish community (labelled "MCC") in a coral setting composed of large massive coral colonies that made a heterogeneous, high-relief "reefscape", holding coral species such as *Gardineroseris planulata* (Dana 1846), *Pavona clavus* (Dana 1846), *Pavona varians* Verrill

1864, *Pavona frondifera* Lamarck 1816, *Porites lobata* Dana 1846, which can reach large sizes approaching two meters high and up to three meters in diameter;

- a "*branching coral*" fish community (labelled "BCC") in a coral setting composed of a dense and continuous, rather homogeneous stand of *Pocillopora* sp. plur. colonies.

Illustration of *Gardineroseris planulata* (Dana 1846)
typical of the habitat of the community "MCC" © Eva DiDonato

Illustration of *Pavona varians* Verrill 1864
typical of the habitat of the community "MCC" © Ryan McMinds

Illustration of *Porites lobata* Dana 1846
typical of the habitat of the community "MCC" © Picasa

Illustration of *Pocillopora* sp.
typical of the habitat of the community "BCC" © Eva DiDonato

2.2 - The Numerical Extrapolation procedure and its exploitation

2.2.1 - *implementation of the procedure of numerical extrapolation*

* *Total species richness*: the least-biased estimation of the number of still undetected species during partial sampling and the resulting estimation of the total species richness of the partially sampled community are derived according to the procedure defined in [36-37] 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 of 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 [38,

39], 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 [39], briefly summarized in Appendix 2 and concretely exemplified in details in [40]. 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 apparent 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 [41]. In turn, the "S.A.D." can be synthetically summarized in two of its major features: the *total species richness* 'S_t' and the *degree* 'U' *of unevenness* of the abundances distribution. Indeed, following [42], 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 [43], that is:

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

2.2.3. - *the underlying process of species abundance structuration*

Beyond the unevenness pattern U, the underlying process of hierarchical structuration of abundances is worth being considered, in terms of both (i) the kind of *mechanism* involved and (ii) the genuine *intensity* of this structuring process.

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 [30, 44-47].

As regards the *intensity* of the process of hierarchical structuration, it should be first emphasized that this intensity is by no means reliably mirrored by the degree of unevenness U, since the latter is *also* mathematically dependent (negatively) upon the species richness S_t [8, 48, 49]; see also Appendix 3. Thus, the unevenness *pattern* U cannot relevantly account for the *genuine* – i.e. biologically significant – intensity of the structuring *process* itself [32, 33, 50]. To get rid of this mathematical influence of species richness, the genuine intensity of the structuring process is appropriately quantified by standardizing the average slope, U, of the "S.A.D." to the slope U' of the so-called "broken-stick" distribution [30, 51], computed for the same species richness S_t [52-55]. This standardization is effective precisely because the average slope U' of the "broken-stick" distribution exactly represents the mathematical influence of species richness [30, 53]. Accordingly, the genuine intensity, "I_{str}", of the hierarchical structuring process is relevantly defined by the ratio U/U':

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

that is:

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

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.

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

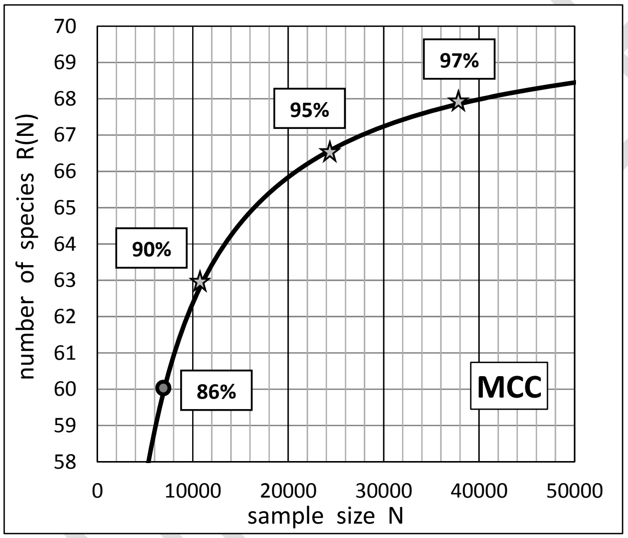
3. RESULTS

3.1 Estimated total species richness of each community

The two studied fish communities differs in *recorded* species richness [35], with the "massive coral" community ("MCC") and the "branching coral" community ("BCC") having respectively 60 and 52 *recorded* species (Table 1).

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

coral habitat	**MCC**	**BCC**
nb. collected individuals N_0	6997	14251
nb. recorded species $R_0 = R(N_0)$	60	52
selected least-biased estimator	JK-4	JK-1
number unrecorded species Δ	10	4
total species richness S_t	**70**	**56**
sample completeness R_0/S_t	86%	93%



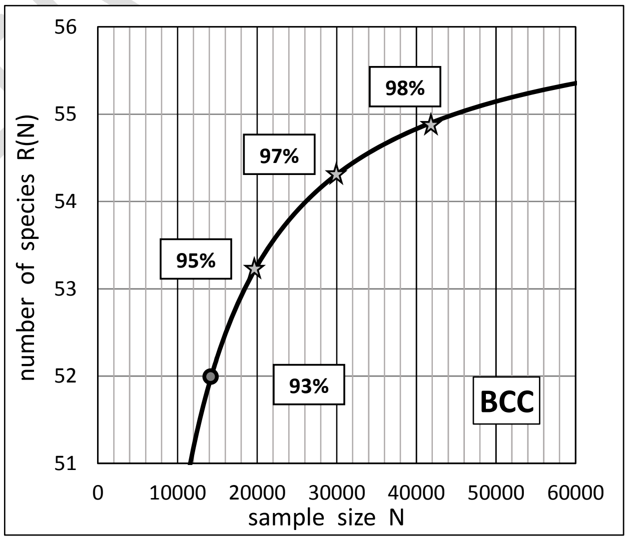


Figure 1 – Extrapolated part of the Species Accumulation Curve for the fish community "MCC" in "massive coral" habitat. This numerical extrapolation highlights the increase in the number of detected species R(N) as a function of growing sample size N, beyond the actually achieved sampling (N_0 = 6997, $R_0 = R(N_0)$ = 60, sampling completeness 86%). The expected additional sampling effort required to reach higher levels of sampling completeness, say for example 90%, 95% and 97% completeness, are around N = 11000, 24000, 38000 respectively.

Figure 2 – Extrapolated part of the Species Accumulation Curve for the fish community "BCC" in "branching coral" habitat. This numerical extrapolation highlights the increase in the number of detected species R(N) as a function of growing sample size N, beyond the actually achieved sampling (N_0 = 14251, $R_0 = R(N_0)$ = 52, sampling completeness 93%). The expected additional sampling effort required to reach higher levels of sampling

completeness , say for example 95%, 97% and 98% completeness, are around N = 20000, 30000, 42000 respectively.

Now, the numerical extrapolation provides the estimated numbers of unrecorded species: 10 species for “MCC” and 4 species for “BCC”. Accordingly, the estimated true (total) species richness amounts to 70 and 56 species for “MCC” and “BCC” respectively (Table 1).

It might be considered of interest to improve the completeness of inventories by further pursuing samplings. The extrapolation of the species accumulation curve beyond the actual sampling size allows to predict the additional sampling effort required to obtain any desired increment in sampling completeness and thus helps to make a rationnaly based decision as to whether it seems reasonable or not to pursue samplings any further: Figures 1 and 2.

3.2 Taxonomic dissimilarity between the two fish communities

3.2.1 Jaccard dissimilarity index

The fish communities “MCC” and “BCC” have respectively 60 and 52 detected species, among which 42 are shared in common [35]. Thus the recorded value of the Jaccard similarity index is only J = 0.60 (= 42/(60+52–42)). Yet, considering samplings incompleteness highlighted above, this inference remains somewhat *hypothetical* or, at least ill-defined, since either all, part or none of the undetected species in each community may be shared by the other community. Fortunately, although the taxonomic identities of the undetected species remain unknown, the numerical extrapolation can partially clear up the issue. Among the 10 undetected species in the community “MCC”, from none of them to all of them may possibly be shared with the community “BCC”. Thus, the total number of shared species between both communities – including the 42 shared species that were already detected – is comprised between 42 and 52 (= 42+10) species. The extrapolated value of the Jaccard similarity index is therefore comprised between J = 0.50 (= 42/(70+56–42)) and J = 0.70 (= 52/(70+56–52)). Thus, instead of the hypothetical estimation derived from incomplete samplings, we can now safely conclude that J = 0.60 ± 0.10. This relatively low value supports a significant role of coral architecture on the taxonomic composition of the associated fish communities.

3.2.2 Exclusive versus non-exclusive species according to recorded data

Based on recorded data, 18 species (= 60–42) are considered exclusive to “MCC” and listed in [35]. But in fact, as shown above (§3.2.1), the number of species exclusive to “MCC” is comprised between 14 (= 70–56) and 28 (= 18 + 10). Thus, it may be that up to 4 of the 18 species listed as exclusive to “MCC” indeed are not. And it may be that up to 10 additional exclusive species should be added to the list of 18.

As regards “BCC”, 10 species (= 52–42) are exclusive and listed in [35], on the basis of recorded data only. But in fact, as shown above (§3.2.1), the number of species exclusive to “BCC” is comprised between 0 (since it cannot be ruled out that these 10 exclusive are the 10 undetected species in “MCC”) and 10 (since it cannot be ruled out that none of these 10 exclusive are among the 10 undetected species in “MCC”). Thus, it may be that part, or even all the 10 species listed as exclusive to “BCC” indeed are not.

In another respect, considering feeding guilds, it should be noticed that both communities similarly show a weak contribution of herbivores, as compared to omnivores and carnivores: only 8% (“BCC”) to 13% (“MCC”) in term of species richness and no more than 1% only in number of individuals for both “BCC” and “MCC” (based on recorded species).

3.2.3 Species showing a relative preference for one of the two communities

Complementary to strict taxonomic distinctiveness, 26 species show highly significant difference in term of relative preference for one or the other type of coral habitat: χ^2 test (with Yates correction) > 10.83, $p < 0.001$.

Stegastes flavilatus © Laszlo Ilyes

Acanthurus xanthopterus © Bernard Dupont

Illustrations of fishes with preferences for "MCC" (*above*) or for "BCC" (*below*)

Ophioblennius steindachneri © Laszlo Ilyes

Thalassoma lucasanum © Laszlo Ilyes

Thus:

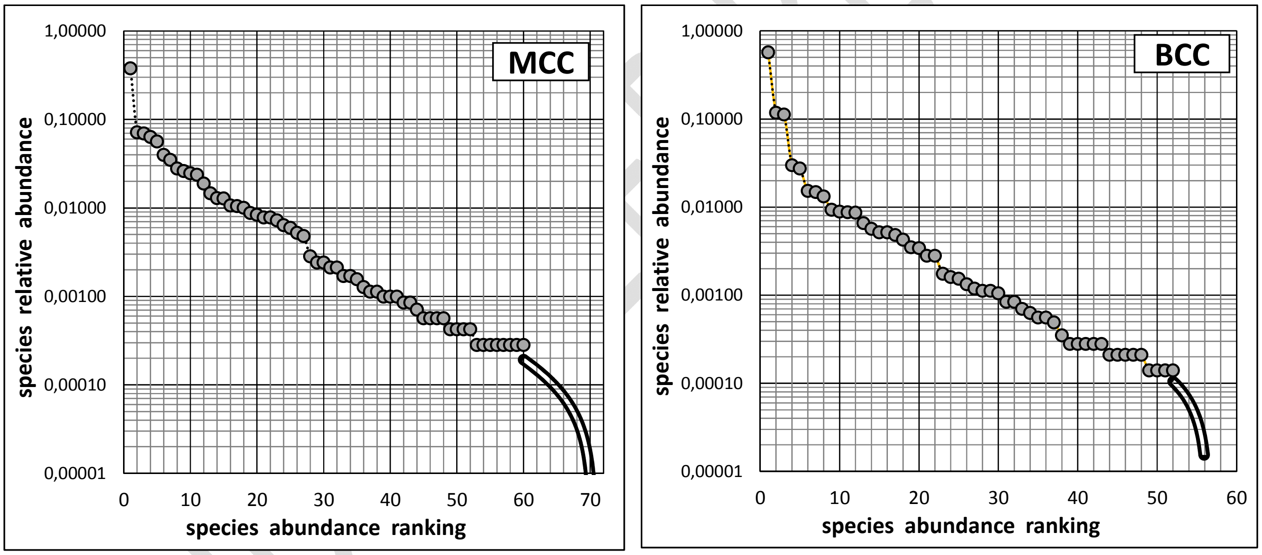
- among the 70 species in community "MCC", 20 species show a statistically significant preference for the "massive coral" habitat hosting "MCC" community. These species are: *Acanthurus xanthopterus* Valenciennes 1835, *Pseudobalistes naufragium* (Jordan & Starks, 1895), *Coryphopterus urospilus* Ginsburg 1938, *Haemulon flaviguttatum* Gill 1862, *Haemulon maculicauda* (Gill 1862), *Haemulon steindachneri* (Jordan & Gilbert 1882), *Bodianus diplotaenia* (Gill 1862), *Halichoeres dispilus* (Günther 1864), *Halichoeres melanotis* Gilbert 1890, *Halichoeres nicholsi* (Jordan & Gilbert 1882), *Halichoeres notospilus* (Günther 1864), *Lutjanus argentiventris* (Peters 1869), *Lutjanus guttatus* (Steindachner 1869), *Lutjanus inermis* (Peters 1869), *Mulloidichtys dentatus* Whitley 1929, *Abudefduf troschelii* (Gill 1862), *Stegastes flavilatus* (Gill 1862), *Odontoscion xanthops* Gilbert 1898, *Cephalopholis panamensis* (Steindachner 1877), *Canthigaster punctatissima* (Günther 1870). Note that among the 18 species considered by [35] as exclusive to "MCC" habitat (§3.2.2), no less than 11 species, however, do not reach the level of statistical significance chosen above for concluding to "MCC" preference; these are: *Caranx lugubris* (Poey 1860), *Gymnomuraena zebra* (Shaw 1797), *Hoplopagrus guentherii* Gill 1861, *Kyphosus analogus* (Gill 1862), *Kyphosus elegans* (Peters 1869), *Lutjanus novemfasciatus* Gill 1862, *Mycteroperca olfax*

(Jenyns 1843), *Mycteroperca xanarcha* (Jordan 1888), *Prionurus laticlavius* (Valenciennes 1846), *Scarus compressus* (Osburn & Nichols 1916), *Elacatinus* sp.

- among the 56 species in community "BCC", 6 species show a statistically significant preference for the "branching coral" habitat hosting "BCC" community. These species are: *Ophioblennius steindachneri* Jordan & Evermann 1898, *Gnathanodon speciosus* (Forsskal 1775), *Cirrhitichtys oxycephalus* (Bleeker 1865), *Halichoeres chierchiae* (Di Caporiacco 1948), *Thalassoma lucasanum* (Gill 1862), *Chromis atrilobata* Gill 1862. Note that among the 10 species considered by [35] as exclusive to "BCC" habitat (§3.2.2), no less than 9 species, however, do not reach the level of statistical significance chosen above for concluding to "BCC" preference; these are: *Apogon atrodorsatus* Heller & Snodgrass 1903, *Caranx melampygus* Cuvier 1833, *Elagatis bipinnulata* (Quoy & Gaimard 1825), *Gymnothorax dovii* (Günther 1870), *Gymnothorax flavimarginatus* (Rüppell 1830), *Lutjanus viridis* (Valenciennes, 1846), *Myripristis berndti* Jordan & Evermann 1903, *Ostracion meleagris* Shaw 1796, *Rypticus bicolor* Valenciennes, 1846.

3.3 Completed Species Abundance Distribution for each community

The bias-corrected and numerically extrapolated Species Abundance Distributions ("S.A.D.") of the two studied communities are provided in Figures 3 & 4. 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.

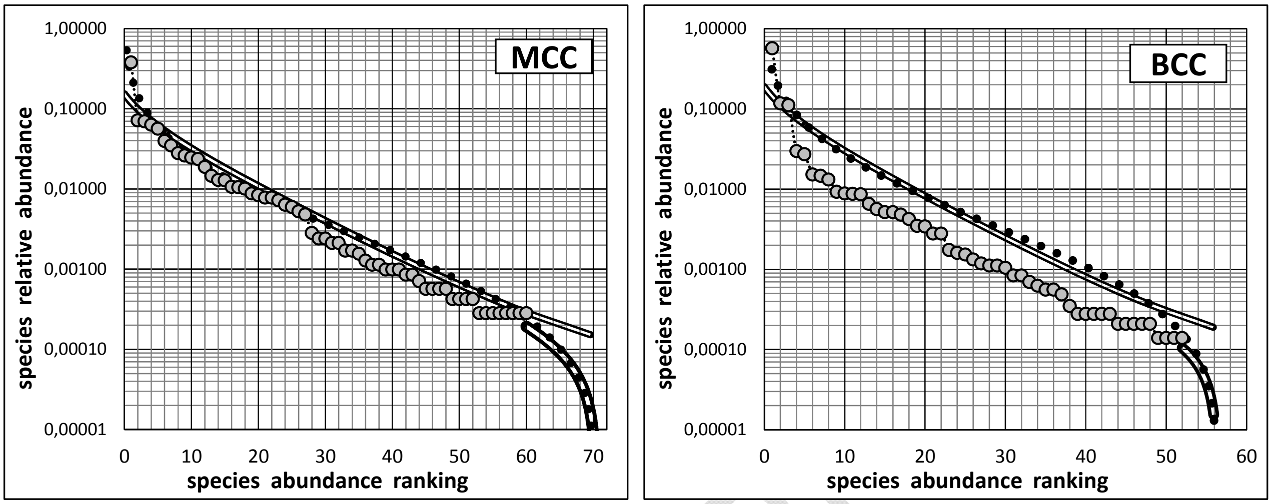


Figures 3 & 4 – The numerically completed Species Abundance Distributions ("S.A.D.") for the two studied fish communities. *Grey circles*: recorded part of the "S.A.D." after correction for bias. *Coarse double line*: least-biased extrapolation of the abundance distribution for the set of species remaining unrecorded. *Left*: community "MCC" in "massive coral" habitat (sampling completeness: 86%) ; *right*: community "BCC" in "branching coral" habitat (sampling completeness: 93%).

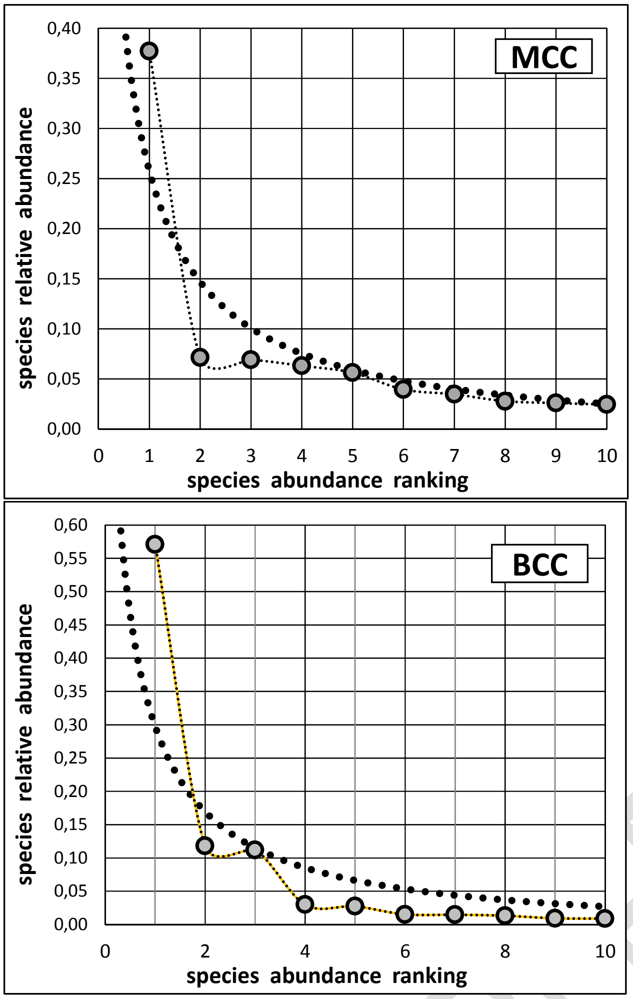
3.4 Testing for the type of process involved in the structuring of species abundances

The numerically completed "S.A.D.s" of both studied communities clearly fit the "log-normal" model best than the "log-series" model (Figures 5 & 6).

Now, by focusing more specifically upon the set of the more abundant species (say, ranks less than i = 10), a significant discrepancy from the "log-normal" model is highlighted (Figures 7 and 8), especially for the most abundant species (rank i = 1), namely *Chromis atrilobata* for both communities. Indeed, the relative abundance of this species far exceeds what is predicted by the "log-normal" model, at the expense of the abundances of the following species (ranks i $\geq$ 2). For both communities the excess in relative abundance of *Chromis atrilobata*, as compared to what is expected from the “log-normal” model, is statistically very highly significant (χ^2 test with Yates correction, “MCC”: χ^2 = 238, p << 0.0001; “BCC”: χ^2 = 2132, p << 0.0001). This suggest a strong, positive density-dependence playing in favor of *Chromis atrilobata*, at the expense of the following species. For both communities, this density-dependence adds to the main multifactorial driver of hierarchical structuration. The cause of this density-dependence yet remains to be explained.



Figures 5 & 6 – 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. Community “MCC” in “massive coral” habitat and community “BCC” in “branching coral” habitat. Best fit is with the “log-normal” distribution for both communities.

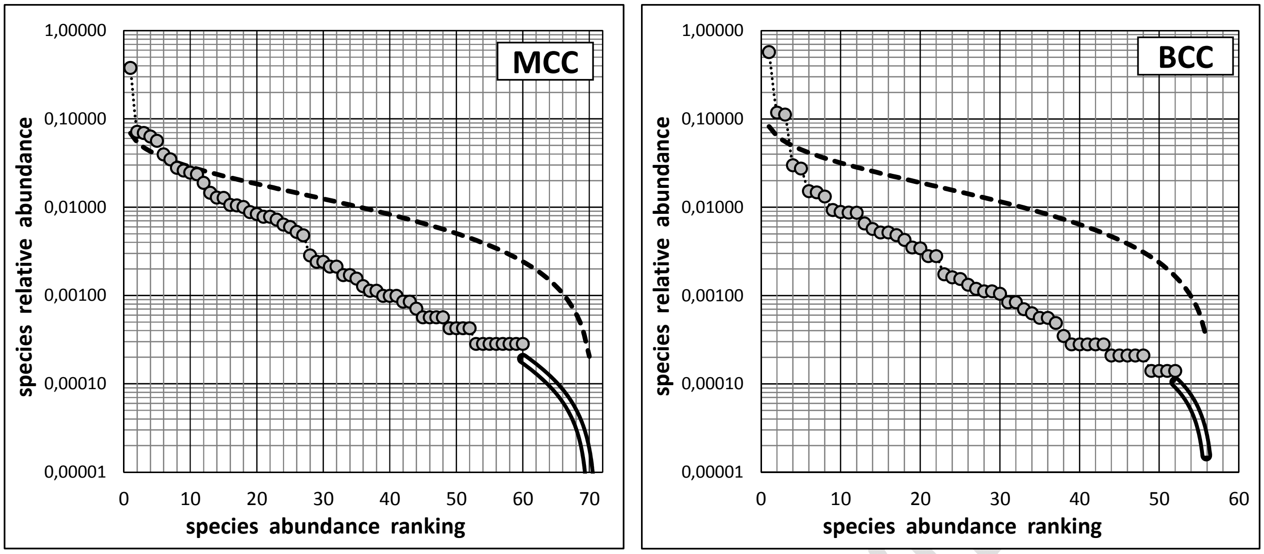


Figures 7 & **8** – Detail of the comparison between the Species Abundance Distributions of the two studied fish communities ("MCC" and "BCC") and the "log-normal" model (coarse dotted line); ordinate with *arithmetic* scale to make the comparison easier. Highlighted is the strong positive density-dependence in favor of the most abundant species (rank 1) at the expense of the following species.

3.5 Beyond the apparent unevenness of species abundances, the genuine intensity of the hierarchical structuring process

Figures 9 and 10, 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)).

The main results derived from this comparison are summarized synthetically in Table 2 which highlights in particular the variations of (i) the true total species richness S_t, (ii) the ratio a_1/a_{St} between the abundances of the commonest and the rarest species, (iii) the degree of unevenness U of species abundances and, finally, (iv) the genuine intensity I_{str} of the process driving the hierarchical structuration of species abundances.



Figures 9 & 10 – The Species Abundance Distribution for each studied community compared to the corresponding "broken-stick" model (dashed line): "MCC" in "massive coral" habitat and "BCC" in "branching coral" habitat.

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 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 genuine intensity of the structuring process $I_{str} = U/U'$.

Habitat types	S_t	a_1	a_{St}	a_1/a_{St}	a'_1	a'_{St}	U	U'	I_{str}
comm."MCC"	70	0.3774	0.0000086	43884	.0690	.000204	0.0673	0.0366	1.84
comm. "BCC"	56	0.5708	0.0000154	37062	.0823	.000319	0.0831	0.0439	1.89
"BCC"/ "MCC"	*0.80*	*1.51*	*1.79*	*0.845*	*1.19*	*1.56*	*1.234*	*1.199*	*1.027*

The numerically completed Species Abundance Distributions of both fish communities are plotted together in Figure 11 to allow more easy direct comparison of the respective influences of the two different coral architectures on the structuration of the associated fish communities.

The main trends derived from this comparison are graphically highlighted in Figure 12, where both the apparent unevenness U and the genuine intensity of the structuring process I_{str} are plotted together against the species richness S_t. While the intensity I_{str} of the structuring process remains sub-constant (only slightly decreasing by less than 3%) along the range of variation of species richness S_t, the degree of unevenness U, on the contrary, strongly decreases by 23%. This discrepancy between the unevenness *pattern* (quantified by U) and the intensity I_{str} of the underlying structuring *process*, although looking paradoxical at first sight, is entirely due to the already underlined negative mathematical dependence of U upon the species richness S_t (§2.2.3).

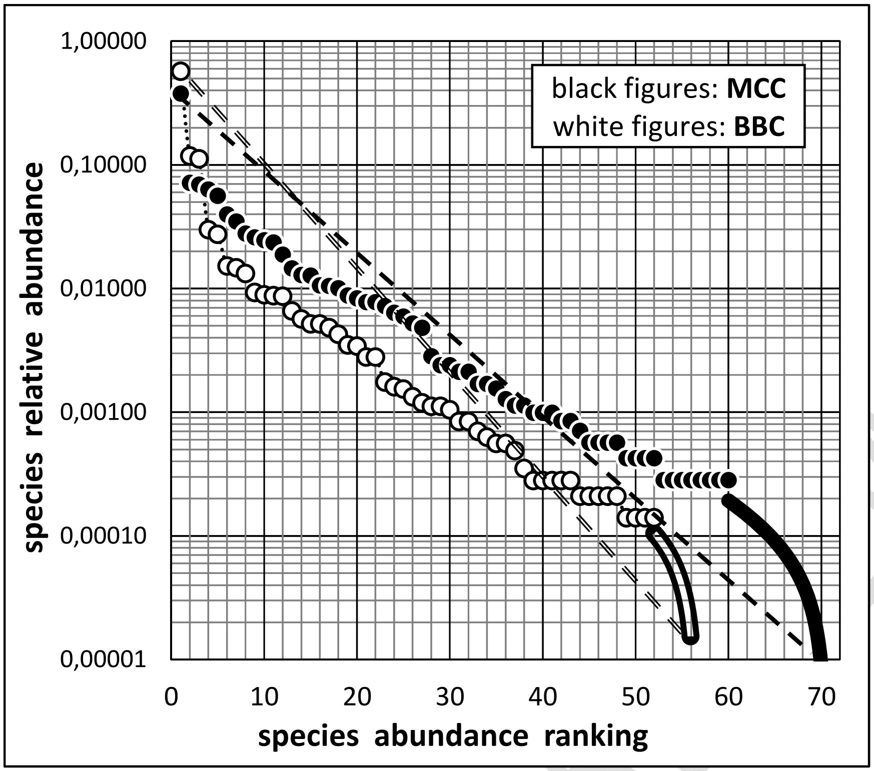


Figure 11 – The Species Abundance Distributions of both fish communities plotted together to allow direct comparison of the respective influences of the two different coral-reef architectures: “massive coral” (“MCC”) and “branching coral” (“BCC”).

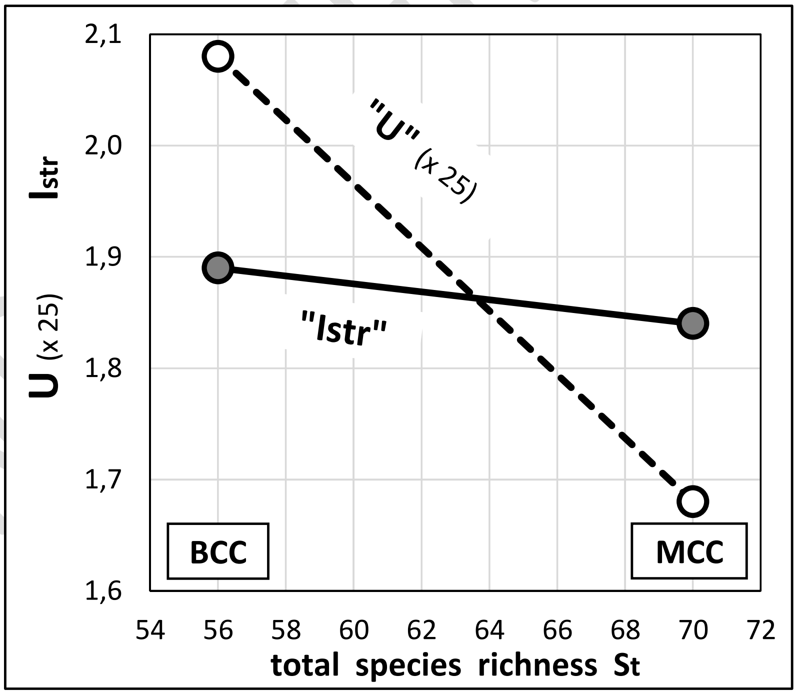


Figure 12 – The degree U of abundance unevenness (*dashed* line) and the intensity I_{str} of the underlying structuring process (*solid* line) plotted against the total species richness St, for the two studied communities. While unevenness U strongly decreases (by 23%) with increasing species richness, the intensity of the underlying structuring process I_{str} remains almost non-affected (slightly decreases by less than 3%): comments in text as concerns this apparent paradox. *Note that for commodity of graphical comparison between U and I_{str}, the values of U are uniformly multiplied by a same factor 25.*

4. DISCUSSION

It has been argued that fish assemblages associated to tropical coral reefs exhibit close relationships with the overall "rugosity" of the coral display [7-13, 56, 57]. Coral species diversity has also been advocated has a determinant of richness and structuration of reef fish communities [58]. The notion of "architecture" of the coral habitat may synthetize both parameters above, that is: the overall topography of the coral display and the diversity among particular coral shapes according to species, as reported by [35]. One *provisional* conclusion of this particular study is that the very diversified architecture of "massive coral" habitat (bringing together a large diversity of coral shapes and sizes) attracts a richer and more even fish community than does the "branching coral" habitat, with its more uniform overall architecture. Yet, these results were derived from *incomplete* inventories of the studied fish communities and sampling incompleteness may be a *sever source of bias*, as the evaluations of the species richness and the degree of unevenness of species abundances are both critically dependent upon the availability of the *whole range* of the Species Abundance Distributions ("S.A.D."). A point, indeed, clearly confirmed by the present work and other recent studies as well [8, 40, 54, 55].

To overcome these difficulties, the ideal solution would be continuing samplings until approaching full completeness but this would require exponentially growing additional efforts (as shown in Figures 1 and 2), hardly achievable in practice. Alternatively, the *numerical extrapolations* of (i) the number of unrecorded species and (ii) their respective abundances – deserve being considered and were implemented here, using a dedicated procedure, recently made available [36, 39]. 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 genuine intensity I_{str} of the hierarchical structuration of abundances – are thus made available: Figures 3 & 4 and Table 2.

4.1 - Effect of habitat type on the true species richness of fish communities

A higher species richness was anticipated for the fish community "MCC" associated to the "massive coral" habitat, with its tormented topography expected to offer far more refuges for fishes than the more regular "branching coral" habitat "BCC". This could have been already hypothesized from the as-recorded species richness (with 8 more fish species) but is definitely demonstrated after the numerical completion of inventories, with an estimated 14 more species in "MCC" as compared to "BCC" (Table 1).

4.2 - Taxonomic dissimilarity between the two fish communities

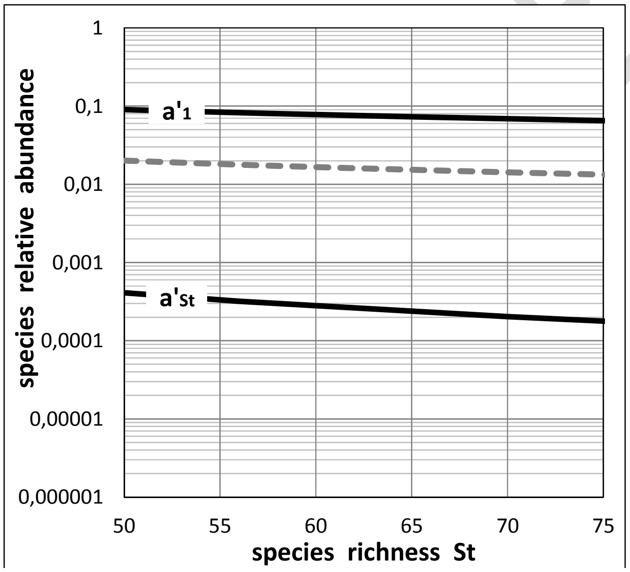
The level of taxonomic dissimilarity between the studied communities remained hypothetical as long as it relies only on incomplete samplings. Thanks to numerical extrapolation, an interval of confidence is specified for the Jaccard dissimilarity index: 0.50 – 0.70, thus highlighting a substantial effect of coral reef architecture on species composition, in addition to its influence on species richness, already mentioned above. In particular, no less than 26 species show statistically significant differences in their relative preference towards one or the other type of coral reef architecture.

4.3 - 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 5 and 6), 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 extrapolation 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 harsh environmental stresses (pollutions, etc …) [44, 46, 47]. Yet, in both communities, the most abundant species (rank i = 1) far exceeds the "log-normal" expectation. This highly statistically significant gap suggests the complementary involvement of a strong positive density-dependence phenomenon that adds to the main multifactorial driver of the distribution of species abundances and favors the most abundant species at the expense of the following species. The cause of this strong density-dependence, involving the same taxon, *Chromis atrilobata*, in both communities – remains conjectural.

4.4 - Effect of coral reef architecture on the fish abundance unevenness and the genuine intensity of the underlying structuring process

The degree U of abundance unevenness is stronger by 23% in the fish community associated to branching coral habitat "BCC" than in the fish community associated to massive coral habitat "MCC" (Table 2 and Figures 9, 10, 11). Yet, the apparent unevenness U does not depend uniquely on the intensity of the structuring process *itself*, but is also mathematically dependent (negatively) upon the species richness S_t of the community ([48, 49] see also Appendix 3). Thus, the apparent unevenness U does not reliably reflect the underlying structuring process itself [32, 33, 50], which intensity is best defined by the index I_{str}. Now, it turns out that I_{str} is practically the same for both fish communities "MCC" and "BCC" (Table 2, Figure 11), thus remaining virtually insensitive to coral architecture (the stronger unevenness in community "BCC" being entirely due to its lower species richness). Thus, differences in coral architecture should probably not significantly interfere with other environmental factors likely affecting the genuine intensity of the structuring process, as already reported [8].



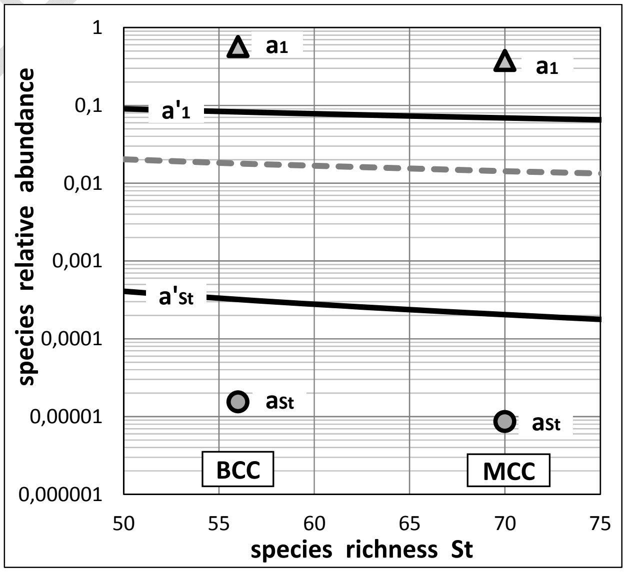


Figure 13 – The variations of the maximum and minimum abundances for the "broken-stick" model (a'_1 and a'_{St} : coarse lines) and for the perfectly "even" model (all abundances uniformly equal to $1/S_t$: dashed line) as a function of the species richness S_t of the community.

Figure 14 – Same as Figure 13, with the maximum and minimum abundances, a_1 and a_{St}, plotted for each of the two studied fish communities: "MCC" with S_t = 70 and "BCC" with S_t = 56 (data from Table 2).

Note, at last, that in both communities, the intensity of the structuring process takes remarkably high values (I_{str} = 1.84 and 1.89), exceeding by far the structuring intensities usually encountered in many marine invertebrates [40, 54, 55]. Thus, the ratio $(a_1/a_{St})/(a'_1/a'_{St})$ between the abundance range (a_1/a_{St}) in the community and the abundance range (a'_1/a'_{St}) in the corresponding "broken-stick" model reaches very high values: no less than 130 for the community "MCC" and 143 for the community "BCC" (Table 2). And, as shown in Figures 9 and 10, these very strong intensities of the structuring process (as compared to the "broken-stick" model) are due to both (i) excessively high abundance values (a_1) for the most abundant species and excessively low abundance values (a_{St}) for the least abundant species. Thus, according to Table 2, $A_1 = (a_1/a'_1) = 5.5$ (6.9) and $1/A_{St} = 1/(a_{St}/a'_{St}) = 23.7$ (20.7), for community "MCC" (respectively "BCC"). This is graphically highlighted at Figures 13 and 14.

5. CONCLUSIONS

Contrasted coral reef architecture had been expected to affect some aspects of the organization of associated fish communities. Here, higher *total* species richness, lower *apparent* unevenness and substantial difference in taxonomical composition are highlighted for the fish community associated to the more tormented coral reef habitat "MCC", as compared to the more uniform habitat "BCC". Yet, the lower *apparent* unevenness is deprived of biological relevance, being only the mathematical consequence of the higher species richness in "MCC", while, in fact, the *genuine* intensity of the structuring process remains virtually *unchanged* between the fish communities "MCC" and "BCC". This quasi-invariance in the true intensity of the hierarchical structuring of abundance features all the more remarkable, when compared to the rather strong differences in terms of both total species richness and taxonomic composition. This suggests that a relatively high degree of interchangeability between species remains fully compatible with a fairly stable intensity of the process that hierarchically structure the species abundances. This may be considered as one particular aspect of the so-called "functional equivalence" hypothesis [59-62].

At last, on a methodological point of view, this case study demonstrates, once again, the usefulness of numerical extrapolations in order to escape the risk of deriving erroneous conclusions from incomplete species inventories. This deserves all the more being emphasized that partial inventories often become quasi-unavoidable when having to deal with species-rich communities, with strongly uneven distribution of species abundances, a very common situation indeed for invertebrates and even for some vertebrates groups, in particular under tropical climate.

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 [36, 63, 64]:

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

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 $R_{\mathbf{x}}(N)$ that respectively satisfy the mathematical constraint (A1.1), considering increasing orders x of derivation $\partial^x R_{(N)}/\partial N^x$. Each solution $R_{\mathbf{x}}(N)$ is appropriate for a given range of values of f_1 compared to the other numbers f_x, according to [36]:

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

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

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

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

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

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

* $\mathbf{f_1} \leq f_2 \rightarrow \Delta_{J1} = f_1$; $R_{\mathbf{1}}(N)$

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

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

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

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

N.B. 1: As indicated above (and demonstrated in details in [36]), 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 [15, 17, 65-67]. Also, this shows that the approach initially proposed by [68] – 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 [37].

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 [39].

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

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

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

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

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

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

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

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

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

Appendix 3

The trivial (“mechanistic”) contribution of the level of species richness to the degree of structuring of species abundances

All things equal otherwise, the larger the species richness, the weaker is the slope of the Species Abundance Distribution.

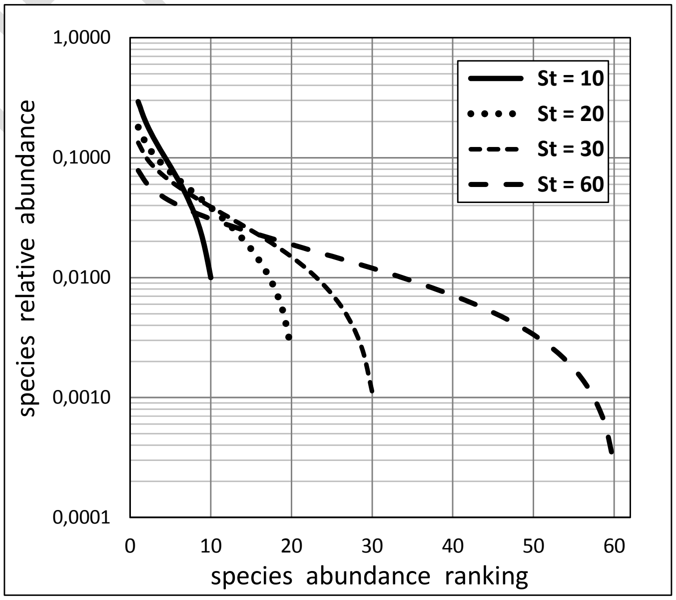


Figure A1 – The "broken-stick" distribution model applied to species communities with increasing species richness S_t = 10, 20, 30, 60. Although the theoretical structuring process involved in the "broken-stick" model remains unchanged (random apportionment of relative abundances among member species), the slope of the species abundance distribution strongly depends upon (and monotonously decreases with) the level of species richness S_t (the relative abundance of the species of rank 'i' is computed as: $(1/S_t).\Sigma_n (1/n)$, with the summation Σ_n on the integer n being extended from n = i to n = S_t, see reference [30, 39].

This can be easily exemplified and quantified, on a theoretical basis, by considering a theoretically constant structuring process - such as the random distribution of the relative abundances that characterizes the "broken-stick" distribution model. By applying this model successively to a series of communities with increasing species richness, a steadily decrease of the slope of abundance distributions is highlighted: Figure A3

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