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Interspecific-Competition Strongly Constrains Species-Richness and Species-Abundance Evenness in a Tropical Marine Molluscan Community Inhabiting *Caulerpa* Beds, as Compared to Coral-Reefs

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Author's contribution

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

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ABSTRACT

Increasing species-richness at the local scale (within species communities) is accommodated, first, by the diversification of the niches respectively associated to species. Yet, in case of excessive supply in colonizing species issued by dispersal from the regional pool, the corresponding increase in the number of solicited niches may lead to some "niche-overcrowding" resulting in significant niche-overlaps. Then, strong interspecific competition for shared resource can arise, triggered by the density in individuals among those species co-occurring at niche-overlaps. Accordingly, the accommodation of species-richness within a local community involves a balance between (i) the positive contribution of improved niche-diversification and (ii) the negative consequence of induced interspecific-competition at increasing niche-overlaps, once the number of colonizing species becomes too large. This balance can strongly differ according to the local ecological conditions, are expected to strongly influence the range of "overcrowding-free" diversification of niches. So that, concretely, each community requires a specific analysis, in order to disentangle and quantify the

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respective contributions to this balance of the niche-diversification and the intensity of interspecific-competition to this balance. And, in particular, their respective roles upon both the species-richness and the degree of unevenness of species abundance within community. Beyond its *speculative* interest, this deeper understanding of the process involved in the hierarchic-like organization of species within community also answers more *practical* concerns, in particular the stability of species-richness, partly dependent on the intensity of interspecific-competition.
In this perspective, we quantify and compare how species-richness accommodation proceeds in two major taxonomic groups: Bivalves and Gastropods respectively, both belonging to a same molluscan community inhabiting *Caulerpa* beds, in the intertidal-zone of Siquijor Island (Philippines). Then, after having compared these two different taxonomic groups, the influence of environmental conditions on species-richness accommodation is addressed, showing that "*Caulerpa*-beds" habitat features far-less rewarding to Gastropods communities than can be the classical "coral-reef" habitat.

Keywords: Accommodation; niche-diversification; niche-overlap; resource-allocation; interspecific-competition; unevenness.

1. INTRODUCTION

1.1 General Context of the Study

The internal organization of species within species assemblages – involving in particular the species-*richness* and the species-abundance *unevenness* – is a major topic of community ecology [1,2]. Addressing this issue makes particular sense because various combinations of species-richness and species-abundance unevenness directly result from various patterns of niches display and, in particular, from varying intensity of interspecific-competition at niche overlaps. With both the niche display and the competitive intensity being, in turn, dependent upon the local environmental conditions.

1.2 The Associated Methodological Approach and its Requirements

Conversely, the particular combination of species-richness and abundance-unevenness, straightforwardly observed in a given local community, allows to make predictions about those hardly detectable factors evoked above, in particular the type of niche display accommodating species-richness and the mean intensity of interspecific-competition for shared resource, triggered at niches overlaps according to the overall density of individuals.

This convenient method to disentangle and quantify the hardly detectable causes – on behalf of their far more easily observable and measurable consequences – requires, however, using specific mathematical tools. In particular:

(i) the implementation of a reliable procedure of numerical extrapolation of samplings when the latter prove remaining incomplete, as is most often the case in practice ([3-5], see also section 2.2) and

(ii) the relevant splitting of the measured species-abundance unevenness in terms of its two, *well separated* contributors, namely: the level of species-richness on the one hand and the intensity of interspecific-competition on the other hand. All the mathematical tools involved in these respects are now made available (briefly described if the following section). Thereby allowing accordingly the successful achievement of the approach, as already demonstrated in a recent series of applied studies [6-17].

1.3 The Specific Purpose of the Present Study

Among the diversity of subjects that can be addressed rationally according to this methodological approach, the – hardly straightforwardly observable – influence of environmental conditions upon the most prominent aspects of internal organization of species within community makes a particularly interesting topic of interpretative research, at both the *speculative* and the *practical* points of view.

Hereafter, I apply this approach to a marine mollusk community, comprising both Bivalves and Gastropods groups, inhabiting intertidal *Caulerpa* beds under tropical climate. This particular kind of habitat deserves specific attention, as it is in sharp contrast with the – far more often studied – *coral-reefs* environments. Accordingly, the main purpose of the present case study is to highlight, in quantitative terms,

the marked differences expected to occur between the internal organizations of those mollusk communities respectively established on these contrasted kinds of habitats – hopefully expecting, finally, to derive relevant interpretations of these highlighted differences.

2. MATERIALS AND METHODS

2.1 The Reported Field Data

The present study is based on the inventory, by WAGEY and coworkers, of a community of molluscs associated to *Caulerpa* beds, in the intertidal zone of Solong-on Bay, Siquijor Island (Philippines). All details regarding the precise location of the community and the sampling procedure are provided in the open-access reference [18] and need not being repeated here. The sampling of the Gastropods group revealed remaining slightly incomplete, as suggested by the subsistence of "singletons" (species recorded only once), so that, in this case, a numerical extrapolation of the species list and of the resulting Species Abundance Distribution have been implemented at first.

2.2 The Numerical Extrapolation Procedure Required for Incomplete Samplings

To avoid making strongly biased inferences regarding the main structural descriptors of ecological communities (i.e., total species-richness and abundance-unevenness), it is required to rely upon (sub-) exhaustive inventories [19-24]. Yet, as stated in reference [24]: "*virtually always, species richness cannot be observed but needs to be estimated because some species may be present but remain undetected. This fact is commonly ignored in ecology and management, although it will bias estimates of species richness and related parameters…*". This is all the more important that rare species (beyond their own intrinsic interest) may also disproportionately contribute to the functional structuring of communities, as has often been pointed out [25-35]: "*rare species are critical for bio-assessment*" as stated in [35].

Now, fortunately, when incomplete samplings only are available, some reliable procedures of *numerical extrapolation* can serve as an efficient surrogate [24]. Newly developed numerical extrapolation procedures [3-5] now allow to estimate not only the *number* of unrecorded species, but, still further, the *respective abundances* of each of these unrecorded species. And once having been properly numerically completed (and *only* when it is so [21], the distribution of species abundances can provide synthetic data, in both *qualitative* and *quantitative* terms, regarding the underlying processes that drive the hierarchical structuring of species-abundances within community [36-40].

2.3 Estimation of the Total Species Richness

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

2.4 Numerical Extrapolation of the Species Abundance Distribution

As mentioned above, the Species Abundance Distribution ("S.A.D.") is intended to provide the basic data necessary (i) to describe the *pattern* of structuration of species abundances within community and (ii) to qualify and quantify the underlying process that drives this structuration. Yet, to accurately exploit its full potential [5,41], the "S.A.D." requires (i) to be *corrected* for the bias resulting from drawing stochasticity during sampling of finite size and, still more importantly, (ii) to be *completed* by *numerical extrapolation*, to the extent that sampling is suspected to be incomplete, as revealed by the subsistence of singletons. The appropriate procedure of correction and least-biased numerical extrapolation of the as-recorded partial "S.A.D." is described in details in reference [5], briefly summarized in Appendix 2 and concretely exemplified in details in reference [6]**.** 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 their abundances (with, thus, a_1 and a_{St} respectively standing for the highest and the lowest abundances in a community of S_t species).

2.3 Abundance Unevenness, Niches Display and Interspecific Competition

Following [42-43], it is the degree of *unevenness* – rather than evenness itself – that should be preferred to address the hierarchical structuring of species abundances in communities. And, according to the usual mode of representation of "S.A.D.s", it goes natural to quantify the degree of abundance unevenness U as the average slope of the log-transformed species-abundance decrease, as already proposed in [44]. That is:

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

with a_1 and a_{St} standing for the highest and the lowest species-abundances in the studied community. Note that choosing this mode of definition of abundance unevenness preserves the *symmetric account* of *abundant* as well as *minor* species, that is, the *equitable account* of *all co-occurring species, independently of their respective abundances* – which may be admittedly considered as desirable: see, in particular, reference [45]. Thereby contrasting, in this respect, with many commonly used metrics of (un-) evenness which *conventionally* attribute different weight to co-occurring species, according to their commonness or rarity [45].

Now, conventional (un-)evenness metrics – including the present expression U of abundance-unevenness – suffers from other serious limitations regarding both their "descriptive" and their "interpretative" capacities. At the *descriptive* point of view, many authors [36,38,39,46-55] have already repeatedly emphasized the formal *non-independence* of conventional (un-) evenness metrics upon species-richness. This leading, in particular, to *unacceptable bias* when comparing communities differing by their respective species-richness, thus making these metrics *unreliable descriptors* in this respect [36,38,39,46-55]. In fact, as duly required in reference [45], "*to make sense, (un)evenness must be independent of species richness*".

And, on the other hand, as regards now the capacity to provide *relevant ecological interpretations*, the weakness of conventional (un-)evenness metrics of species abundances is readily highlighted by the usual absence of any associated interpretation of this kind in the literature – the implementation of conventional (un-)evenness metrics being, usually, restricted to a purely descriptive purpose only.

Accordingly, a *newly designed abundance-unevenness metric* – the "standardized abundance-unevenness" index – has been recently proposed [6,54,56], positively addressing both kinds of limitations evoked above. Thanks to standardizing a conventional measure of abundance-unevenness (such as the "crude" abundance-unevenness index U defined just above) to the corresponding measure, U', of the abundance-unevenness in the well-known *"broken-stick" model* (taken as an appropriate referential standard), the resulting "standardized unevenness" index (I_{str} = U/U') proves being able to overcome both major limitations pointed out above [56]. Indeed, this new index, I_{str}, benefits by being both:

(i) *formally independent* of species-richness, thereby allowing reliable, *unbiased* comparisons of abundance (un-)evenness between species-communities, *whatever* their difference in species-richness;
(ii) able to *relevantly quantify* the *mean intensity of interspecific-competition* within community, expressed in term of the explicit contributive outcome of competition intensity to the uneven distribution of species-abundances.

This double success being the direct consequences of the properties of the "broken-stick" distribution model, originally put-forth in a well-known, yet insufficiently thoroughly exploited paper by the regretted Robert MACARTHUR [57]. Further information upon both the argumentation and the practical implementation of this newly designed unevenness index are extensively detailed in reference [56].

The "standardized abundance-unevenness" index "I_{str}" is defined as:

I_{str} = U/U', that is:

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

and thus:

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

with a_1 and a_{St} standing for the highest and the lowest relative abundances in the studied community and a'_1 and a'_{St} standing for the

CONTRIBUTORS to ABUNDANCE → UNEVENNESS	* uneven niche rewards to their respectively associated species	* interspecific contest for shared resource at niches overlaps
$I_{str} < 1$	*only partial occupancy* of available niches and preferentially those niches providing *more similar* rewards to their respectively associated species → hence, low levels of abundance unevenness and this all the more than I_{str} is less than 1	*no* interspecific contest (no niche functional overlap, since niches are separate)
$I_{str} = 1$	*full occupancy* of available niches (i.e. "*contiguous*" non-overlapping niches) → hence, rewards of niches to their associated species are more uneven than they were above, thus leading to more uneven distribution of species abundances than above : $I_{str} = 1$	still *no* interspecific contest, since niches, being contiguous, there are still no functional-overlap between niches
$I_{str} > 1$	*full occupancy* of available niches (now partially intersecting) → hence, the same contribution, as above, to the uneven distribution of species abundances, *but* see now the new contrib. of intersp. contest	*interspecific contests* now adding supplementary *abundance unevenness* and all the more than $I_{str} > 1$ (answering the increase in functional-overlaps)

Image 1. A summarized guidance to the ecological interpretations attached to the "standardized abundance-unevenness index" I_{str} (after [56])

highest and the lowest relative abundances in the corresponding "broken-stick" distribution, computed (according to [36,56,57]) for the same species richness S_t. The distribution of the relative abundances a'_i for the broken-stick distribution and the corresponding abundance unevenness U'(St) are easily computed according to the same references [36,56,57]. As already argued above, thus defined, the standardized abundance unevenness I_{str} not only complies with the formal *independence* upon species richness required for making *reliable* comparisons between communities *whatever their difference in species richness*. But, *moreover*, the standardized unevenness I_{str} also proves being especially relevant as an *ecologically self-significant* metric of species-abundance unevenness [56], since it specifies by how much the species-abundance unevenness is *multiplied*, as the consequence of interspecific competition. Indeed, from equation (2), it comes:

$$U = [U'(S_t)].[I_{str}] \quad (3)$$

This equation thus highlights the essentially "*composite*" nature of species-abundance unevenness – regrettably ignored in conventional metrics of (un-)evenness. A composite nature which thus couples *multiplicatively*:

(i) a first contribution, equal to U' (i.e. the broken-stick unevenness), uniquely related to the *degree of niche-diversification* (which is the reason why U' is an univocal function $U'(S_t)$ of species-richness S_t). With the degree of niche-diversification (mirrored by 1/U') therefore accounting for the level of "species-packing" [2,58-60] allowing, in turn, the *accommodation* of the number (S_t) of co-occurring species;

(ii) a contribution I_{str} which quantifies the *mean intensity of interspecific competition* within community, expressed in the appropriate term of its proper contribution to the degree of species-abundance unevenness (with I_{str} involved as a *multiplicative factor* applying to what would be the abundance-unevenness (= U') in the absence of competition). Further details are available in reference [56], see also Box 1 in Appendix 3, for a schematic outline.

At last, in addition to the above three parameters S_t, U, I_{str}, a fourth useful descriptor of species structuration within community is the overall range, R_a, of species abundances which, in terms of conventionally log-transformed abundances, is defined as:
$R_a = [\log_{10}(a_1) - \log_{10}(a_{St})]$, that is:

$$R_a = [\log_{10}(a_1 / a_{St})] \quad (4)$$

with a_1 and a_{St} standing for the highest and the lowest abundances in the studied community. Then, from equations (1) and (2), it comes:

$$R_a = (S_t - 1).U = (S_t - 1).U'.I_{str} \quad (5)$$

Importantly, the variations of the overall range of species abundances R_a are mainly driven by the variations of the level of abundance a_{St} of the rarest species, while, on the contrary, a_1 varies comparatively very little: see both empirical evidence and theoretical support in [56]. Besides, it is the abundance a_{St} of the rarest species which is more decisive as regards the maintenance of species richness, since further decrease of the lowest abundance a_{St} likely increases the risk of dislodgement and subsequent local extinction of the rarest species. This makes two good reasons to devote particular attention, beyond R_a, to a_{St}. So that, in this respect, the lowest abundance a_{St} deserves being the third essential descriptor of natural species communities, after S_t and I_{str}.
Image 1 provides guidance to the *interpretation of the* standardized abundance unevenness I_{str}.

3. RESULTS

3.1 Estimated total Species Richness of the Bivalves and the Gastropods Groups

Within the *Bivalves* group, the recorded distribution of species abundances shows no singleton nor even doubleton, so that the Bivalves sampling, with its 6 recorded species, is estimated substantially exhaustive. As regards the *Gastropods* group, 26 species are recorded among which 2 singletons and 4 doubletons, thus suggesting a slight incompleteness of the Gastropods sampling. Numerical extrapolation is therefore required, not only to estimate the true, total species richness of the Gastropods group but also to provide the completed Species Abundance Distribution within this group. Numerical results for both groups are provided in Table 1 and Fig. 1.

3.2 Species Abundance Distributions Numerically Completed

The Species Abundance Distributions for Bivalves and Gastropods (as recorded for the former, numerically-extrapolated for the latter) are jointly provided in Fig. 1. The Species Abundance Distribution for the whole mollusk community (Bivalves and Gastropods together) is given in Fig. 2.

The corresponding "broken-stick" distributions (i.e., computed for the same levels of species-richness) are also plotted on the same Figures, allowing direct comparisons to this referential standard, which highlights what would be the corresponding situation in the "ideal" absence of interspecific-competition within community (see section 2.3). Bivalves and Gastropods groups, either examined separately or considered together, exhibit species abundance distributions clearly *more uneven* than are the corresponding broken-stick distributions, with, accordingly, the standardized unevenness index I_{str} largely in excess of unity: Table 2. *Strong levels of interspecific-competition* are therefore revealed within both groups, as will be further discussed later.

4. DISCUSSION

4.1 The Methodological and Ecological Issues Involved in the Study

In prolongation of the inventory of marine molluscan communities (*Bivalves* and *Gastropods*) on *Caulerpa* beds, carried out by WAGEY and coworkers [18] at Siquijor Island, the additional treatments of the reported field data, presented above, have allowed a more thorough understanding of the socio-ecological conditions characterizing these communities.

In particular, the numerical extrapolation of incomplete sampling (for the Gastropods group) has permitted to cancel out both the negative bias in the evaluation of species-richness and the artificial truncation of the species abundance distribution towards the rarer species, remained undetected. Then, following this improvement in the reliability and accuracy of input data, the refined analysis of the distribution of species-abundance, thanks to the newly designed "standardized" unevenness index I_{str} has allowed to open an enlightening window upon the underlying socio-ecological processes involved in the hierarchic-like organization of species-abundances within the studied community as a whole and its two member groups, Bivalves and Gastropods separately.

More specifically, it had become now possible to evaluate separately the respective contributions to the species-abundance unevenness of:

(i) what is related to the *diversification of niches* – typically ruled, mathematically speaking, by the "*broken-stick*" model, as a univocal function of species-richness – and
(ii) what is directly dependent upon the *intensity of interspecific-competition* (if any) *at niche-overlaps*, triggered by the density of individuals competing for shared resource at overlaps.

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

***Conus* community**	**Bivalves**	**Gastropods**	**Both**
nb. collected individuals N_0	264	3420	3684
nb. recorded species $R_0 = R(N_0)$	6	26	32
selected least-biased estimator	/	JK-2	JK2
number unrecorded species Δ	0	2	2
total species richness S_t	6	28	34
sample completeness R_0/S_t	100%	93%	94%

Table 2. A synthetic summary of the main quantitative features of the hierarchical organization of species abundances within community: (i) the total species richness S_t of the community ; (ii) the relative abundances a_1 and a_{St} of the most and the least abundant species (i.e. species of ranks 1 and S_t) ; (iii) the same, a'_1 and a'_{St}, for the "broken-stick" distribution, (iv) the abundance unevenness $U = \log_{10}(a_1/a_{St})/(S_t\text{-}1)$; (v) the abundance unevenness in the corresponding "broken-stick" distribution: $U' = \log_{10}(a'_1/a'_{St})/(S_t\text{-}1)$; (vi) the "standardized" unevenness index $I_{str} = U/U'$; (vii) the overall range of species abundances R_a

community	S_t	a_1	a_{St}	a_1/a_{St}	a'_1	a'_{St}	U	U'	I_{str}	R_a
Bivalves	6	.060	.00134	45	.0293	.00199	0.330	0.233	1.42	1.65
Gastropods	28	.292	.00010	2860	.1300	.00118	0.128	0.0756	1.69	3.46
Together	34	.292	.00010	2860	.1210	.00087	0.105	0.0650	1.62	3.46

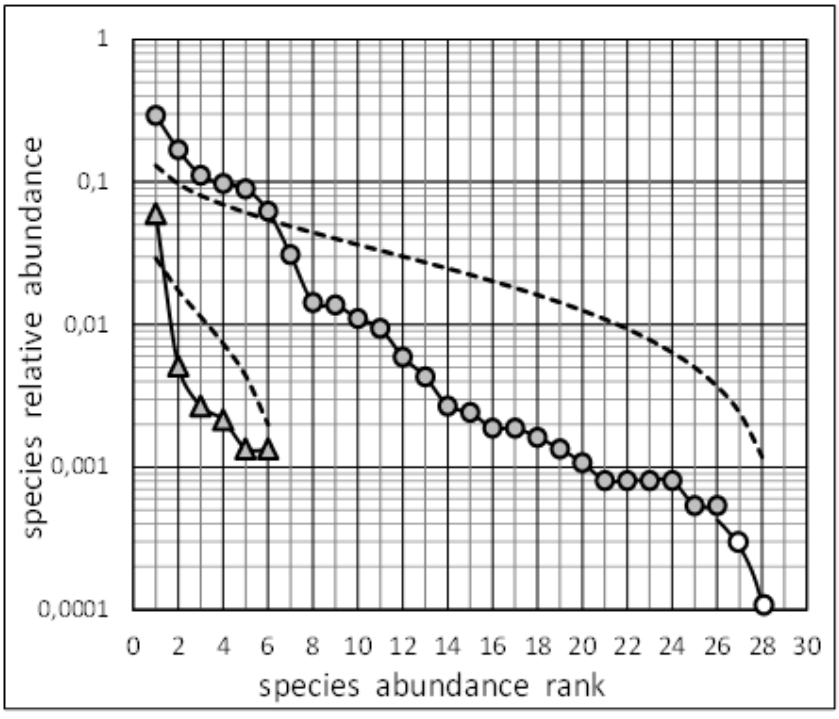

Fig. 1. The Species Abundance Distributions – as recorded for the Bivalves group (*triangles*) and numerically extrapolated for the Gastropods group (*discs*) – in the studied molluscan community at "Siquijor Island". As recorded data: *grey figures*; numerically extrapolated part: *white figures*. The corresponding broken-stick distributions of species abundances are plotted as *dashed lines*

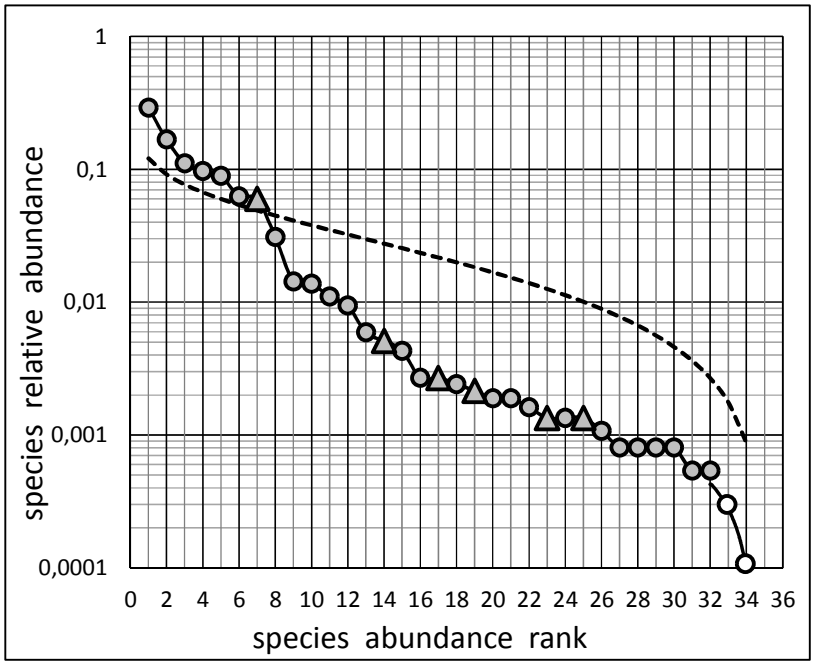

Fig. 2. The numerically extrapolated Species Abundance Distribution of the whole molluscan community at "Siquijor Island": Bivalves as *triangles* and Gastropods as *discs*. As recorded data: *grey figures*; numerically extrapolated part: *white figures*. The corresponding broken-stick distribution of abundances is plotted as *dashed line*

More precisely:

(i) The *diversification of niches* directly contributes to the number of species that can co-occur successfully within the community. That is the number of species which have been able, at first, to reach the community-site, then, to cope successfully with local environmental conditions as a whole (*abiotic* factors) and, finally, to find, there, a particular niche, allowing its own appropriate subsistence to each species respectively. While having to cope, in addition, with interspecific-competition at niche-overlap if any (*biotic* interactions). Thus, improved niche-diversification allows the accommodation of a higher species-richness, thanks to denser allowed "species-packing".

(ii) The *intensity of interspecific-competition at niche-overlaps* accounts, in turn, for the difficulty to accommodate the achieved species-richness. The greater the difficulty, the more intense will be the interspecific-competition and, consequently, its (multiplicative) contribution, I_{str}, to the crude species-abundance unevenness U. So that, at a same level of species-richness, it is the *standardized unevenness index* I_{str} – as the direct outcome of interspecific-competition intensity – which *relevantly distinguishes each community idiosyncratically*, therefore contrasting it from any other communities that would share the same species-richness (i.e. that would benefit by an equivalent degree of niche-diversification).

Thus, all species-communities are facing, more or less, the following *"challenging balance"* between:

(i) *accommodating higher species-richness*, thanks to higher niche-diversification,

(ii) to the price, however, of a potentially *increased risk of niche-overcrowding*. With, consequently, resulting niche-overlaps, triggering in turn increasing interspecific-competition, according to the density of individuals competing for shared resource at niche-overlaps. Thereby potentially exposing to ultimate dislodgment and local extinction the "less-competitive" species – and *challenging*, accordingly, the accommodation of species-richness offered by niche-diversification.

In short, *higher species-richness* on the one hand and *stronger interspecific-competition* on the other hand can progressively come to a confronting balance, at least when the overall density of individuals exacerbates interspecific contests for shared resource (food, space, protective surrounding environment, etc…).

It is *important*, however, to emphasize that this "challenging balance" should be considered more readily effective *only when all other things remain equal*. Indeed, there is little doubt that significantly "more rewarding" sites, actually offering, for example, a larger diversity of feeding resource and/or protective shelters, will be able to host communities substantially richer in species without necessarily triggering a higher intensity of interspecific-competition. The "challenging balance" evoked above is, therefore, *not* intended to be of general validity. Indeed, no general applicability is supported empirically either: see reference [56].

Anyway however, beyond the niche-diversification (beneficial to species-richness), the intensity of interspecific-competition within community plays, as expected, a *focal role* in community ecology.

Hence the importance to *disentangle* – and *separately quantify* – the respective contributions of the *species-richness* and of the *interspecific-competition intensity* to their combined socio-ecological outcomes, in terms of the hierarchic-like distribution of species-abundances within community. And hence, therefore, the *pivotal role* played by the "*standardized" abundance-unevenness index* I_{str}, as a relevant tool to disentangle, and reliably gauge, the respective contributions of species-richness and interspecific-competition.

The present work (as a series of preceding case studies [6-17]) once again exemplifies the benefits from implementing this refined methodological approach. The latter, focused here on:

(i) comparing two co-occurring molluscan groups – Bivalves *versus* Gastropods – and
(ii) comparing the "*Caulerpa*-beds" habitat to the more classically studied "*coral-reef*" habitat, as regards their respectively hosted Gastropod communities.

4.2 Species-Richness and Competition-Intensity both distinguish and singularize these two Taxonomic Groups as well as these two Habitat-Types

Fig. 3, which synthetized the elaborated results above, provides suggestive comparisons, as regards both the species-richness (S_t) and the severity of interspecific competition, aptly quantified by the standardized abundance-unevenness index (I_{str}). With these comparisons being conducted:

(i) between the Gastropods and the Bivalves groups;
(ii) between the *Caulerpa*-beds and the coral-reef habitats, from the point of view of their hosted Gastropods communities.

4.2.1 Comparison between taxonomic groups: Gastropods and Bivalves

Fig. 3 calls for the following comments.

At first, both the Bivalves and the Gastropods member-groups of the molluscan community show substantial to even quite strong levels of interspecific-competition: I_{str} = 1.41 for Bivalves up to even I_{str} = 1.69 for Gastropods. With, also, the Gastropod group being more than four-times higher in species-richness than is the Bivalves group (S_t = 28 and 6 respectively). This parallel increase of both S_t and I_{str}, from Bivalves to Gastropods, fairly complies with expectation derived from the "competing-balance" between species-richness and interspecific-competition intensity argued above. Indeed, increased diversification of niches – if it turns out to result in niches overcrowding and increased niche-overlaps – can trigger stronger interspecific-competition.

While, on the other hand, the non-general validity of this "balance" complies well with the obvious absence of correlation between the intensity of interspecific-competition (reflected by I_{str} value) and the true species-richness S_t, considering Gastropod communities as a whole, as also highlighted in Fig. 3. Note also that, while enduring stronger intensity of interspecific-competition, the Gastropod group on *Caulerpa*-beds exhibits a higher degree of "species-packing" than does the Bivalves group – thanks to likely larger niche-diversification [2, 58-60]. From data in Table 2, the degree of species-packing (defined by (1/U')) is 3.08 times stronger in the Gastropod group than it is in the Bivalves

group (3.08 = (1 / 0.0756) / (1 / 0.233)). This, indeed, was logically expected, since the degree of species packing (1/U') is an increasing function of species-richness S_t (see section 2.3). This, also, could have been expected from the typically far more diversified life-traits within Gastropod group as compared to Bivalve group.

Coming back to species-richness, it should be emphasized that the more than four-times higher species-richness in the Gastropods group is achieved to the price of a substantially depressed abundance of the rarest species: a_{St} = 0.00010, to be compared to a_{St} = 0.00134 in Bivalves group (Table 2). This makes the rarer species in the Gastropods group more likely being subjected to possible future local extinctions as a consequence of so-called "Allee effects" [61,62]. Accordingly, as compared to the Bivalves group, a (yet minor) part of the considerably higher species-richness in the Gastropods group might be considered as being *potentially more unstable*.

More generally, note that the question of knowing *whether or not a higher species-richness would (systematically) induce stronger average intensity of interspecific-competition* is one major issue to be considered in community ecology. And while, for the case studied here, the answer is positive, a lot of other case-studies suggest, however, that no systematic trend actually arises in this respect (see Fig. 10 in reference [56]).

4.2.2 Comparison between habitats: Caulerpa-beds versus coral reefs

As regards, now, the comparison between habitats – the *Caulerpa*-beds and the coral-reefs – from the point of view of their hosted Gastropods communities, it seems clear that the former habitat differs from the latter in both:

(i) the level of species richness which remains remarkably low in the *Caulerpa*-beds, especially referring to what would be expected from the position of Siquijor island within the "Coral-Triangle hotspot" and

(ii) the stronger severity of interspecific-competition in the *Caulerpa*-beds habitat.

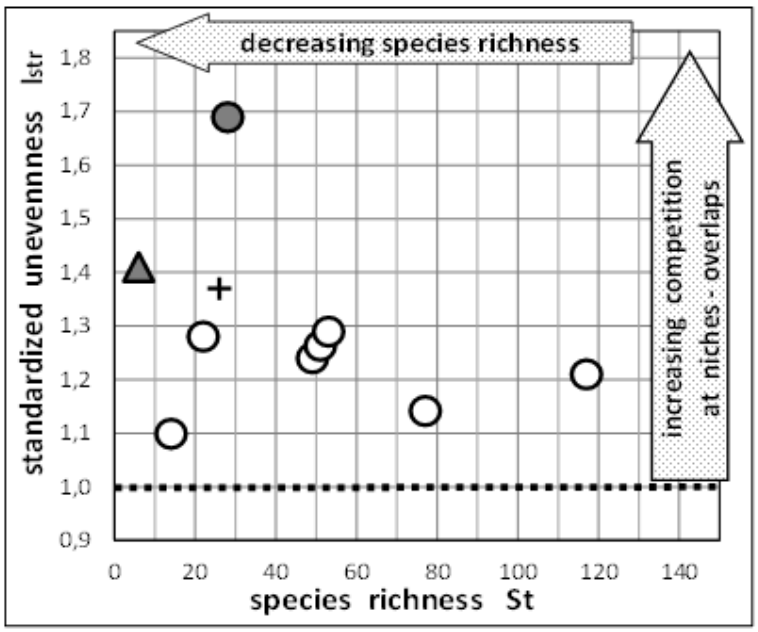

Fig. 3. True (total) species richness S_t and the standardized species-abundance unevenness I_{str} for the Bivalves and the Gastropods communities on *Caulerpa* beds at Siquijor Island, compared to seven other tropical reef-associated Gastropod communities, after [6-8]. *Grey figures*: Siquijor Islands, *white figures*: the seven reef-associated Gastropod communities taken for comparison. *Discs* are for Gastropod communities, the *triangle* for the Bivalve community. The *cross* label shows how *strongly biased* would be the evaluation of the intensity of the interspecific-competition within the Gastropod group at Siquijor if the numerical extrapolation of the incomplete sampling had been unduly neglected.

Pic. 1. *Mactra violacea* (Gmelin, 1791) © Jan Delsing

Pic. 2. *Anadara scapha* (Gmelin, 1791) © P. Bourjon

Pic. 3 Conus sulcatus Hwass in Bruguière,1792 © Eddie Hardy

Pic. 4. *Canarium urceus* (Linnaeus, 1758) © G&P Poppe

Pic. 5. *Epitonium scalare* (Linnaeus, 1758) © forum coquillages

Pic. 6.*Terebralia sulcate* (Born, 1778) © Femorale

It seems therefore likely that the *Caulerpa*-beds habitat offers significantly lower possibilities of niche-diversification (i.e. the number of available niches) and, moreover, a weaker degree of real differentiation between these less-numerous niches, triggering more interspecific-competition – as compared to the coral-reef habitats.

At last, in quite another vein, note that *neglecting the implementation of the numerical extrapolation* of incomplete sampling of Gastropod community would have introduce a *considerable bias* in the evaluation of the degree of interspecific competition, with I_{str} falling down from the actual value I_{str} = 1.69 to only 1.37 with non-extrapolated sampling data. Leading, thus, to an interpretative conclusion *totally different* from the one relevantly stated above. Hence, once more, the mandatory requirement of implementing numerical-extrapolations of incomplete samplings.

4.3 Discussing the Reason Why Severe Interspecific-Competition within Community can durably persist

Interspecific-competition undoubtedly strongly participates to the process of natural-selection at the local scale, favoring those "more locally competitive" species at the expense of the less locally well-adapted ones. It therefore seems to make sense, at first examination, that the ultimate outcome of interspecific-competition would be to reach a kind of stable equilibrium at the end of which the local resource is shared in a non-competitive way among the remaining (and therefore durably subsisting) species (despite the unavoidable uneven sharing). In this stable stage, interspecific-competition would have thus disappeared. This stable, "competition-free" ideal situation is thus intended to play the role of something like a kind of an "attractor", with interspecific-competition being the active – but only transient – way towards ultimate non-competitive stability [63-67]. Indeed, empirical support has been provided, in some circumstances, to this theoretical argumentation in favor of the *only-transient* character of interspecific-competition at the community level, finally leading to the cancellation of interspecific-competition. In particular, during the recovery of previously destroyed or strongly perturbed communities [17]. And, also, following a more global approach, empirical evidence has been provided in favor an appreciable proportion of communities closely approaching, or even reaching the quasi cancellation of competition – that is, say, I_{str} falling down to ≈ 1.0 ± 0.1: see for example the survey of 38 tropical marine communities distributed worldwide (Fig. 10 in reference [56]).

Yet, the same reference also shows at least as many cases where I_{str} values are substantially greater than 1.1, extending up to I_{str} = 2. Thus, indicating the subsistence of medium to high intensity of interspecific-competition. And thereby suggesting that the alleged transient-stage of interspecific-competition may, indeed, be quite longer than expected, if not even permanent!

Whatever it could be, it remains that, here, with fairly high values of I_{str} (= 1.41 and 1.69 respectively), both the Bivalves and the Gastropods groups are obviously still far from having approached the "attractive" stabilization stage, allowed by vanishing intensity of interspecific-competition.

In fact, the theoretical argumentation above would implicitly imply some strongly restrictive conditions to allow reaching a stable, competition-free ideal situation. Restrictive conditions which, indeed, may not so often be satisfied; in particular:

(i) communities should remain under substantially stable environmental conditions,
(ii) communities should remain isolated from the more or less prolix and sustained supply of colonizing species dispersed from the neighboring regional pool.

Non-satisfying the latter circumstance – due to the persistent supply of potentially colonizing species dispersed from the extremely species-rich regional pool – would provide an especially likely explanation for the severity of interspecific-competition highlighted for each of the two studied groups: namely, the position of Siquijor island, well within the exceptionnally species-rich "Coral-Triangle hotspot". Indeed the permanently renewed supply of species through dispersal from the plethoric regional pool in the "Coral-Triangle" is expected to iteratively reactivate the course of competitive process, even if the subsequent, more or less delayed but repeated elimination of under-competitive species is the unavoidable outcome, explaining the maintenance of the low level of species-richness, in conjonction with the high intensity of interspecific-competition.

4.4 Comparing the "Accommodation Capacity Index" of Caulerpa beds between Gastropods and Bivalves groups

The natural environment can be considered as being all the more "welcoming" for a community of species that it offers a resource

- *quantitatively* more *abundant* – thereby favoring higher level of overall density D of individuals;
- *qualitatively* more *diversified* – that is offering more niches allowing, in turn, the coexistence of more species, i.e. a higher level of species-richness S_t ;
- while *reducing* as much as possible the *intensity of interspecific competition* (mirrored by the standardized abundance unevenness I_{str}) likely to appear at niches overlaps and triggered by both a high species-richness S_t and a high level of individuals density D.

In this perspective a *realized* "Accommodation performance Index", labelled 'rA.P.', may be conceived as:

- an increasing function of species-richness S_t and the overall density D in individuals and
- a decreasing function of the standardized abundance unevenness I_{str} which aptly quantify the intensity of interspecific competition at niches overlaps:

rAP = f (D, S_t, I_{str}) with following constraints:

$$\partial f/\partial D > 0,\ \partial f/\partial St > 0,\ \partial f/\partial I_{str} < 0 \quad (6)$$

In particular, 'ACI' may be conventionally defined very simply as:

$$rAP = (D.S_t)/I_{str} \quad (7)$$

The log-transformed expression of rAP index being especially appropriate for disentangling the respective relative contributions of D, S_t and I_{str} to the observed difference in values taken by rAP when comparing different situations.

This index rAP (which has the same dimension than D, i.e. a surface or volumetric density) would conventionally account for the "accommodation capacity" of (i) a given local environment (for example, here, *Caulerpa* beds at Siquijor Island) for (ii) a particular kind of species community (here either Gastropods or Bivalves assemblages) and considering (iii) a given metapopulation context, conditioning the surrounding pool of species likely able to disperse and colonize the site (here the rich regional pool of species of the "Coral Triangle").

More generally, the rAP can serve either (i) to compare the accommodation capacities of different local environments for a given kind of community or, conversely, (ii) to compare the accommodation capacities of a given type of local environment for different kinds of communities.

The second possibility can be exploited, here, with a same environment (*Caulerpa* beds) and two different kinds of communities in this same environment (Gastropods and Bivalves groups).

The values of S_t and I_{str} are provided in Table 2 and the density D is quantified by the value of the number of collected individuals N_0 referred to the 8.4 m^2 of sampling area, that is D = 407 and D = 31 individuals/m2 for Gastropods and Bivalves respectively [see Table 1, slightly extrapolated to account also for non-detected species in Gastropods]. It comes accordingly: rAP = 407x28/1.69 = 6745 and rAP = 31x6/1.42 =131 for the Gastropods and the Bivalves assemblages respectively. That is no less than a fifty times higher hosting capacity of *Caulerpa* beds at Siquijor Island for Gastropods than for Bivalves.

5. CONCLUSIONS

Both *species-richness* accomodation and the resulting, more or less *uneven distribution of species abundances* – are *key factors*, essential to cast additional light upon the functional organization among species co-occuring within natural communities. Accordingly, a deeper understanding of this organization requires to readily focus upon a *reliable quantitative* evaluation of these two key factors. In this respect, the *total* species-richness (S_t) (*duly extrapolated once necessary*) and the "*standardized* species-abundance unevenness" (I_{str}) prove being the appropriate parameters – which suffice to characterize the *functional heart* of the internal organization among species within community. In particular the standardized abundance unevenness (I_{str}) allows to disentangle and measure the specific contribution of interspecific-competition intensity to the degree of unevenness of species abundance distribution. And, thereby, to uncover

a *reliable appreciation of the mean intensity of interspecific-competition* within community.

Besides, and now from a purely *descriptive* point of view, these two parameters, (S_t) and (I_{str}), also prove being adequate as well, thanks to their *mutual independence*. So that, at both the *interpretative* and the *descriptive* points of view, the implementation of the newly defined standardized unevenness (I_{str}) *clearly outstands* the conventional (un)eveness indices [56].

In the particular case of the investigated marine molluscan community on *Caulerpa* beds at Siquijor Island, the implementation of these appropriately designed tools – the numerical extrapolation of incomplete sampling and the standardized unevenness index – has allowed a deeper approach, on a rational basis, of the species-richness accommodation process involved in the Bivalves and the Gastropods groups respectively.

The major informations arising from this comparison are that, here:

* the *improved diversification* of occupied niches in the Gastropods group, as compared to the Bivalves group, has not only allowed the accommodation of a correspondingly quite larger species-richness but has, also, led to some over-crowding among niches, resulting in significant *niche-overlapping* and the following onset of a more severe *competion* for shared resource among Gastropod species co-occurring at these niche-overlaps. This being clearly quantified by the comparison of the corresponding values taken by the *standardized* unevenness I_{str}.

* as compared to coral-reefs, the *Caulerpa* beds habitat at Siquijor Island appears being quite less rewarding to molluscan hosts, as highlighted by both the considerably lower levels of species-richness and, also, the stronger intensity of interspecific-competition. With the latter considered not to be only transient (as expected to be so in some circonstances [17]) but probably intrinsically durable.

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COMPETING INTERESTS

Author has declared that no competing interests exist.

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APPENDIX 1

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

Consider the survey of an assemblage of species of size N_0 (with sampling effort N_0 typically identified either to the number of recorded individuals or to the number of sampled sites, according to the inventory being in terms of either species abundances or species incidences), including $R(N_0)$ species among which f_1, f_2, f_3, f_4, f_5, of them are recorded 1, 2, 3, 4, 5 times respectively. The following procedure, designed to select the less-biased solution, results from a general mathematical relationship that constrains the theoretical expression of *any* theoretical Species Accumulation Curves R(N)(see [3, 4, 68-71]):

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

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 [3]:

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

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

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

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

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

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:

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

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

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

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

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

N.B. 1: As indicated above (and demonstrated in details in [3]), this series of inequalities define the ranges that are best appropriate, respectively, to the use of each of the five estimators, JK-1 to JK-5. That is the respective ranges within which each estimator will benefit of minimal bias for the predicted number of missing species.

Besides, it is easy to verify that another consequence of these preferred ranges is that the selected estimator will *always* provide the highest estimate, as compared to the other estimators. Interestingly, this mathematical consequence, of general relevance, is in line with the already admitted opinion that *all non-parametric estimators* provide more or less pronounced *under*-estimates of the true number of missing species [21,23,72-76]. Also, this shows that the approach initially proposed in [77] – 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*. Namely: the best estimate of the number of species remaining unrecorded after incomplete sampling is provided by the *non-parametric estimator providing the highest value, among the Chao and the series of Jackknife estimators*. And this is not only a likely admissible point of view, as suggested in [21,23,72-76], but, now, *a rationally established affirmation*.

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

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

APPENDIX 2

Correction and extrapolation (when required) of the as-recorded S.A.D

N.B.: details regarding the derivation of the following expressions are provided in [5].

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

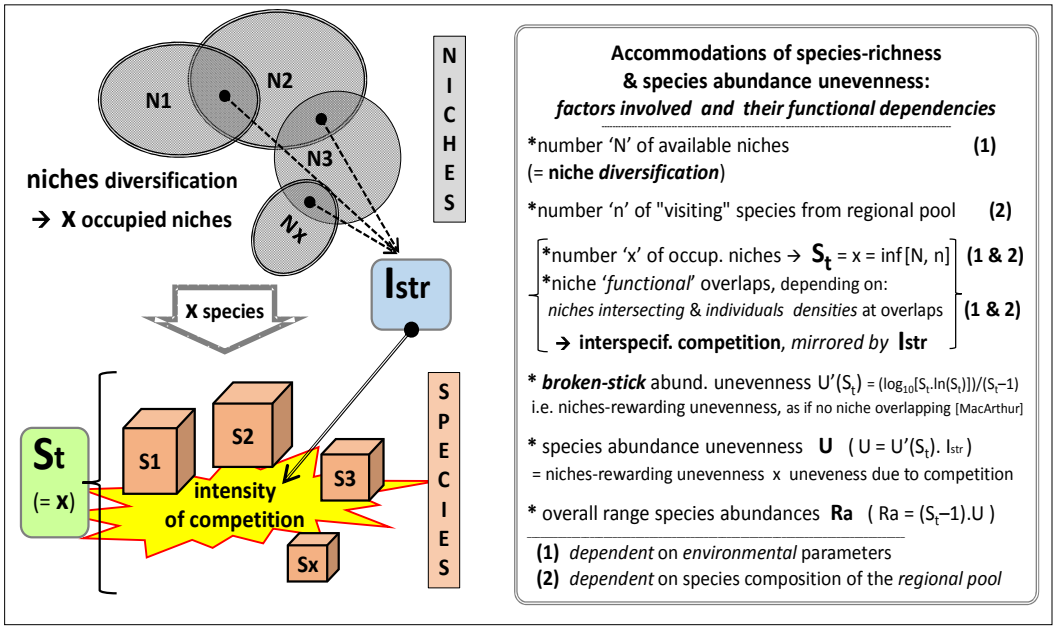
The following expression stands for the estimated abundance, a_i, of the unrecorded species of rank i (thus for $i > R_0$):

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

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



BOX 1 – Schematic representation of how the *accommodations* of both *species-richness* and *species abundance unevenness* are partially (i) *inter*-dependent and (ii)dependent on (ii.a) the *environmental* parameters and (ii.b) the *composition of the regional pool* of species. Species richness '$\mathbf{S_t}$' and the standardized unevenness '$\mathbf{I_{str}}$' are the two *main (and mutually independent) descriptive and functional factors* which, by themselves alone, suffice to characterize important quantitative aspects ruling the internal organization of species within communities. Two additional, subordinate factors, the crude abundance unevenness U and the overall rage of species abundances R_a are, for their own, entirely dependent upon the formers, S_t and I_{str}. The *broken-stick* abundance unevenness U'(S_t) – due to its meaningful linkage with the "non-overlapping niches display" [MacArthur, 1957] – thereby plays the role of a sort of "compass" supporting relevant functional interpretation of the "hierarchical" organization among co-occurring species within community.

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