

# Analyzing the Role of Increasing Water Pollution on Species-Richness, Interspecific-Competition and Abundance-Unevenness in Reef-Associated Fish Communities, off Jakarta Bay (Indonesia)

Jean Béguinot<sup>1\*</sup>

<sup>1</sup>Université Bourgogne, 6, Boulevard Gabriel, 21000 Dijon, France.

## Author's contribution

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

## Article Information

DOI: 10.9734/IJECC/2021/v11i630420

### Editor(s):

(1) Dr. Daniele De Wrachien, State University of Milan, Italy.

### Reviewers:

(1) Farah Bani Affan, Koya University, Iraq.

(2) Santosh Kumar Abujam, Rajiv Gandhi University, India.

(3) V. C. Wokem, University of Port Harcourt, Nigeria.

Complete Peer review History: <https://www.sdiarticle4.com/review-history/70817>

Original Research Article

Received 10 May 2021

Accepted 16 July 2021

Published 23 July 2021

## ABSTRACT

Not far from the exceptionally rich 'Coral Triangle' on the one hand but, on the other hand, exposed to strongly varying degree of anthropogenic environmental stresses, the reef-associated fish assemblages all along 'Seribu Islands' (off Jakarta Bay) are, thus, confronted to both positive and negative ecological influences. As such, these fish assemblages offer especially interesting opportunities to analyze these opposite ecological influences, at both the descriptive and the functional points of views. The *least-biased* numerical extrapolation of a series of recently reported – yet incomplete – samplings has allowed a sub-exhaustive account of both the estimated *total* species-richness and the *completed* distribution of species abundances – including the set of those rarer species which had remained unrecorded. Thanks to this numerically completed information, it became possible to tackle some important issues – which otherwise would have remained difficult to address properly. First, a remarkably good correlation was highlighted between the distance of fish assemblages to Jakarta Bay (distance considered as a reliable surrogate to the improvement of environmental conditions for fish assemblages) and a theoretically derived index characterizing the accommodation capacity of sites for fish assemblages. This good correlation suggests that this index offer a way to reliably accounts for the "environmental quality" of marine waters, as

\*Corresponding author: E-mail: jean-beguino@orange.fr;

appreciated by fish communities. In quite another respect, comparing primary and secondary-feeding guilds, provides still further empirical support to a seemingly *common trend* according to which the guild of secondary-feeders features usually more species-rich, while exhibiting less interspecific competition intensity at niche overlaps, than does the primary-feeders guild.

*Keywords: Numerical extrapolation; sampling completeness; distribution evenness; feeding guild; anthropogenic environmental stresses.*

## 1. INTRODUCTION

Tropical marine ecosystems in shallow waters are of major interest, being considered as embodying remarkably high levels of diversity and biological complexity [1-5]. Also, these ecosystems are of major concerns to ecologists and conservationists, as they are considered as one of the first kind of ecosystems to suffer significantly from anthropogenic environmental stresses, in particular increasing marine waters pollution issued from large and busy mega-cities.

Reef-associated *fish communities* are, most often, important components of these tropical ecosystems. Accordingly, reef-associated fish communities are among the more significant biota to be considered, when addressing the fundamental question of how various environmental stresses, and especially water pollution, can more or less affect the level of species-richness and the intensity of interspecific-competition, as well as their combined outcomes in terms of the degree of unevenness of species-abundances and, more generally, in term of the hierarchic organization of species distribution within communities.

Madduppa et al. [6] recently reported on a series of reef-fish communities, sampled all across the archipelago of “Seribu Islands”, encompassing as such a large range of various distances from Jakarta City, considered as a major source of marine water pollution. Hereafter, I expand the analysis from this reported data base, by considering in particular how (i) the density in individuals, (ii) the species-richness and (iii) the species-abundance unevenness respectively responds to gradually decreasing levels of pollution with increasing distances from Jakarta. Being emphasized – from a methodological point of view – that these three *descriptive* parameters are, at first, *reliably extrapolated numerically* in order to reduce, if not cancel, the bias due to unavoidable sampling incompleteness [7].

Moreover, beyond these three *descriptive* parameters, I disentangle the fundamental

structuring role and the significant contribution of a fourth – this time *functional* – parameter, namely the average *intensity of interspecific-competition* within community. This factor, very hard to straightforwardly appreciate – and still more difficult to quantify directly – fortunately reveals being open to reliable *indirect* derivation, thanks to considering a specifically defined metric of abundance unevenness.

As a whole, and beyond merely descriptive aspects, this refined approach allows for a deeper understanding of how fish communities can react, in terms of structural and functional responses, to increasing levels of water pollution. In line with this perspective, a high degree of positive correlation is highlighted between the distance to the pollution source and a newly designed index defined as proportional to both individuals’ density and true species richness and inversely proportional to competition intensity. Besides, and in quite another perspective, a seemingly general rule according to which “the species-richness is lower and the competitive-intensity is stronger” among primary feeders than among secondary feeders – proves remaining rather robust, independently of the severity of pollution stresses.

Thus, hereafter, the following issues are successively addressed:

- which are the *quantitative responses* of reef-fish communities to *decreasing water pollution*, in terms of (i) the overall density of individuals, (ii) the true species-richness (i.e.: duly extrapolated as far as necessary), (iii) the average intensity of interspecific-competition and (iv) an appropriate combination of these three parameters, intended to synthetically highlight the improved “accommodation-performance” of communities, as expected from decreasing level of water pollution;

- how far the seemingly general rule evoked above – which opposes the species structuration of primary feeders to the species structuration of secondary feeders – actually proves remaining

robust regardless of the level of water pollution stresses.

## 2. MATERIALS AND METHODS

### 2.1 The Reported Field Data

The present study is based on the survey, by Madduppa et al. [6], of a series of five reef-associated fish communities located along the Seribu Islands archipelago, at *progressively increasing distances* from the highly polluted inshore water of Jakarta Bay, towards the progressively less polluted offshore waters of the outer islands of the Seribu archipelago. Thus acquired along a strong gradient of anthropogenic pressure – in particular water pollution – the field data reported in [6] thereby offer a good opportunity *to test the influence of environmental quality* on those (potentially) exceptionally rich fish communities, in a region very close to the “Coral Triangle” hotspot. All additional details regarding the precise location of the communities and the sampling procedure are provided in the open-access reference [6], so that these points are no longer reported here.

Importantly, all five samplings remain more or less incomplete, as revealed by the subsistence of “singletons” (species recorded only once during sampling), so that implementing numerical extrapolations of the five samplings is required – and realized at first – in order to estimate, for each community, both the *true (total) species-richness* and the *completed distribution of species abundances, including those species remained unrecorded*.

### 2.2 The Numerical Extrapolation Procedure, as Required for Incomplete Samplings

To avoid making biased inferences regarding the main structural descriptors of ecological communities (i.e.: total species richness and species-abundance unevenness), it is required to rely upon (sub-) exhaustive inventories [7-12]. Yet, as stated in reference [7]: “*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 disproportionately

contribute to the functional structuring of communities, as has often been pointed out [13-23]: “*rare species are critical for bio-assessment*” as quoted in [23].

Now, fortunately, when only incomplete samplings are available, some reliable procedures of *numerical extrapolation* can serve as an efficient surrogate [7]. Newly developed numerical extrapolation procedures [24-26] 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 [10]), the distribution of species abundances can provide synthetic data, in both *qualitative* and *quantitative* terms, regarding the underlying process that drives the hierarchical structuring of species abundances within community [27-31].

\* **Estimation of 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 [24,25] 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.

\* **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 [26,32], 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 [26], briefly summarized in Appendix 2 and concretely exemplified in details in reference [33]. 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  $a_{S_t}$  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 [34,35], it is the degree of *unevenness* – rather than evenness itself – that should be preferred to address the hierarchical structuring of species abundances in communities. 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 [36]. That is:

$$\begin{aligned} U &= [\log_{10}(a_1) - \log_{10}(a_{S_t})]/(S_t - 1) \\ U &= [\log_{10}(a_1/a_{S_t})]/(S_t - 1) \end{aligned} \quad (1)$$

with  $a_1$  and  $a_{S_t}$  standing for the highest and the lowest 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 [37]. 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 [37].

Now conventional (un-)evenness metrics – including the present expression  $U$  of abundance-unevenness – suffers from serious limitations regarding both their “descriptive” and their “interpretative” capacities. At the *descriptive* point of view, many authors [27,30,37-48] 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 [27,30,37-48]. Indeed, as duly required in reference [37] “*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, in the literature, of any associated interpretation of this kind: 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 [33,47,49-50], positively addressing both kinds of limitations evoked above. By 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 the major limitations pointed out above [50]. 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, in term of the explicit contributive outcome of competition intensity to the uneven distribution of species-abundances.

This double success being the direct consequence 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 [51]. Further information upon both the argumentation and the practical implementation of this newly designed unevenness index are extensively detailed in reference [50].

The “standardized abundance-unevenness” index “ $I_{str}$ ” is defined as:

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

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

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 highest and the lowest relative abundances in the corresponding “broken-stick” distribution, computed (according to [27,50,51]) for the same species richness  $S_t$ . The distribution of the relative abundances  $a_i$  for the broken-stick distribution as well as the corresponding abundance unevenness  $U'(S_t)$  are easily computed, for the same species richness  $S_t$ , according to references [27,50,51]. As already argued above, thus defined, the standardized abundance-unevenness index  $I_{str}$  not only complies with the formal *independence* upon species richness, as 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 [50], since it specifies by how much the species-abundance unevenness is *multiplied*, as the consequence of interspecific competition. Indeed, from equation (2), it comes:

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

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*” [52-55.] 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 [50], see also Box 1 in Appendix 3 for a schematic outline.

CONTRIBUTORS to ABUNDANCE → UNEVENNESS	* uneven niche rewards to their respectively associated species	* interspecific contest for shared resource at niches overlaps
$I_{str} < 1$	<i>only partial occupancy</i> of available niches and preferentially those niches providing <i>more similar</i> rewards to their respectively associated species → hence, low levels of abundance unevenness and this all the more than $I_{str}$ is less than 1	<u>no</u> interspecific contest (no niche functional overlap, since niches are separate)
$I_{str} = 1$	<i>full occupancy</i> of available niches (i.e. “ <i>contiguous</i> ” 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 <u>no</u> interspecific contest, since niches, being contiguous, there are still no functional-overlap between niches
$I_{str} > 1$	<i>full occupancy</i> of available niches (now partially intersecting) → hence, the same contribution, as above, to the uneven distribution of species abundances, <i>but</i> see now the new contrib. of intersp. contest	<i>interspecific contests</i> now adding supplementary <u>abundance unevenness</u> 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 [50])

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:

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

with  $a_1$  and  $a_{St}$  standing for the highest and the lowest abundances in the studied community. That is, from equations (1) & (2):

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

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 [50]. 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 a synthetic guide for a relevant *socio-ecological interpretation* of the value taken by the standardized abundance-unevenness  $I_{str}$ .

### 3. RESULTS

#### 3.1 Estimated Total Species Richness of Communities

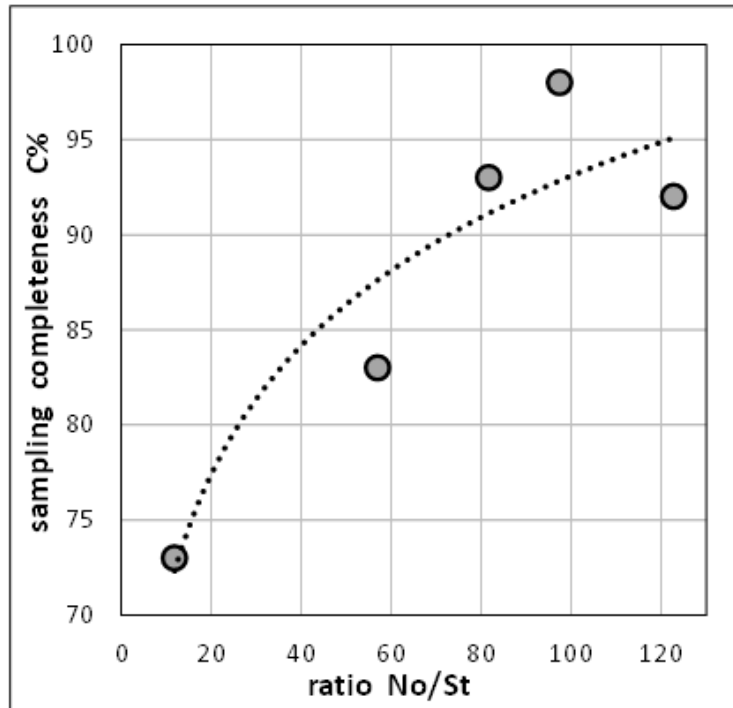
Five fish communities were considered along the Seribu Island archipelago, at progressively increasing distance from Jakarta center. These five communities are more precisely located at 'Pari', 'Tidung', 'Panggang', 'Kelapa' and 'Harapan' islands.

As mentioned above, due to the subsistence of significant proportions of singletons (species recorded only once during sampling), the samplings of all five surveyed fish communities were considered incomplete and therefore submitted to 'least-biased' numerical extrapolations (previous examples of application of this procedure are provided in references [33,56-67]). Table 1 provides, for each five communities, the reported sampling data and the corresponding *extrapolated numbers* of species remained undetected, from which is immediately derived the estimated total species richness.

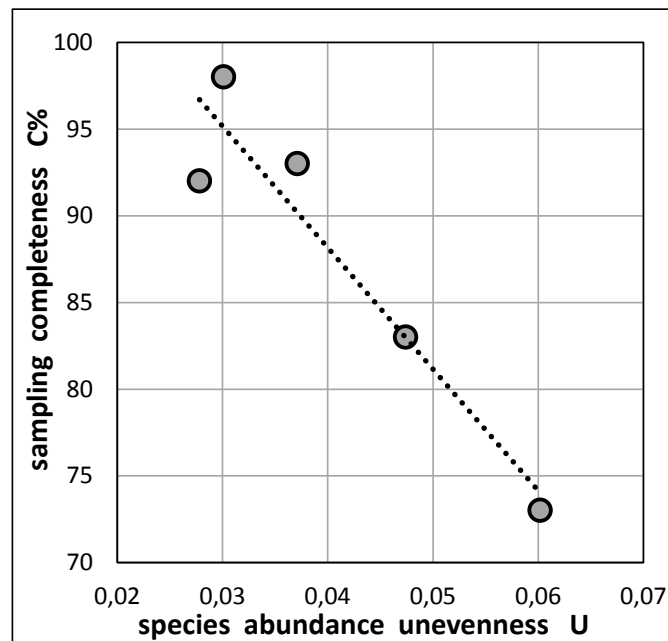
The degree of completeness  $C\%$  of samplings varies substantially, from 73% to 98% (Table 2) and it is interesting to address the causes of these variations. In this respect, it seems likely that sampling completeness should (i) increase with the ratio  $N_0/S_t$  between the number of recorded individuals  $N_0$  and the total species-richness  $S_t$  and (ii) decrease with increasing degree of unevenness  $U$  of species abundances (see Table 2), since the rarer is a species, the less likely it is expected to be encountered during

**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  $\Delta$  of unrecorded species, the resulting estimate of the "true" total species richness  $S_t (= R_0 + \Delta)$ , the resulting estimated level of sampling completeness  $R_0/S_t$ , the (extrapolated) overall density  $D$  of individuals per  $m^3$  of sampled water and the distance from Jakarta center. Pari: PAR., Tidung: TID., Panggang: PAN., Kelapa: KEL., Harapan: HAR**

Reef-fish communities	PAR.	TID.	PAN.	KEL.	HAR.
nb. collected individuals $N_0$	794	5412	10814	20018	9235
nb. recorded species $R_0 = R(N_0)$	49	79	109	150	105
selected least-biased estimator	JK-4	JK-3	JK-2	JK-3	JK-2
number unrecorded species $\Delta$	18	16	2	13	8
total species richness $S_t$	67	95	111	163	113
sample completeness $R_0/S_t$	73%	83%	98%	92%	93%
overall density of individuals ( $/m^3$ ) $D$	0.161	0.723	0.541	0.616	0.924
distance from Jakarta-center (km)	32	45	48	55	56



**Fig. 1.** The degree of sampling completeness C% plotted against the ratio  $N_0/S_t$  between the number of recorded individuals  $N_0$  and the total species-richness  $S_t$ .  
Logarithmic regression,  $r = 0.92$



**Fig. 2.** The degree of sampling completeness C% plotted against the degree of unevenness of species abundances  $U = [\log_{10}(a_1/a_{S_t})]/(S_t - 1)$ . Linear regression,  $r = 0.95$

sampling. Figs. 1 and 2 clearly support these expectations, with high levels of correlation coefficients ( $r = 0.92$  and  $0.95$ , respectively) suggesting statistical significance for both

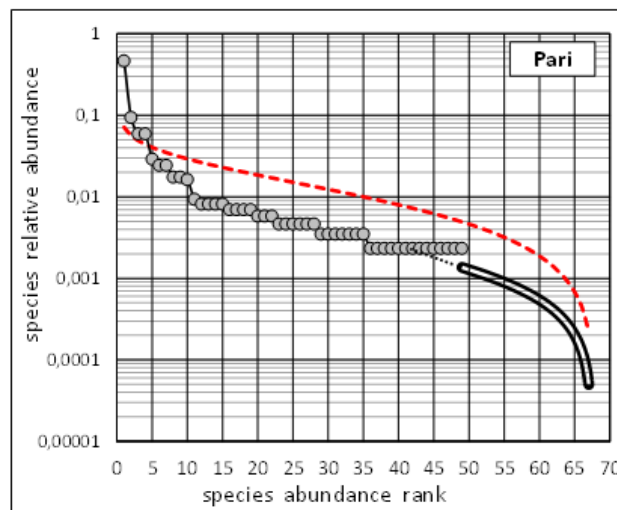
causes ( $p < 0.05$ ), in spite of the very low number (5) of considered samplings. Note that similar involvement of these two causes in the regulation of sampling completeness

has already been reported previously [65].

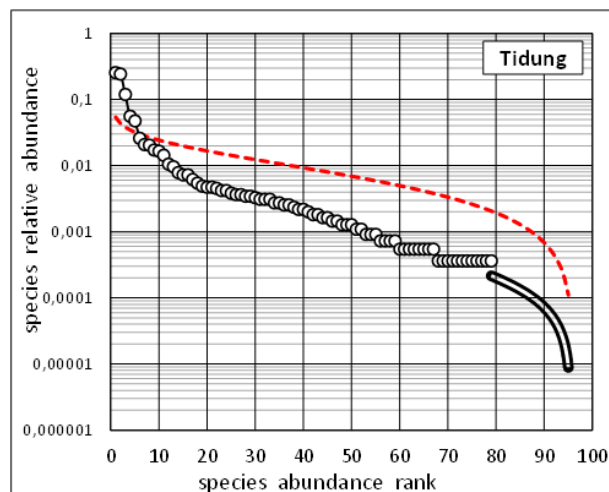
### 3.2 Species Abundance Distributions Numerically Completed

The bias-corrected and numerically extrapolated Species Abundance Distributions (S.A.D.s) are provided in Figs. 3 to 7. The corresponding “broken-stick” distributions (i.e.: computed for the same species richness) are also plotted on the same Figures, for the purpose of direct comparisons to this referential standard. In each of all five communities, the crude species

abundance unevenness  $U$  (i.e.: the average slope of the species-abundance distribution) is more or less stronger than is the crude unevenness  $U'(S_i)$  in the corresponding “broken-stick” distribution (i.e.:  $I_{str}$  always  $> 1$ ), thereby suggesting more or less intense interspecific competition at niches overlaps. The intensities of interspecific competition in the different fish communities are more precisely quantified in term of the standardized unevenness index  $I_{str} (= U/U'(S_i))$ , as shown in Table 2, which also provides complementary information relative to species abundances.



**Fig. 3.** The corrected and numerically completed Species Abundance Distribution of the fish community at site “Pari” (*grey discs*: recorded species, *double line*: numerically extrapolated part of the S.A.D.). For comparison, the “broken-stick” (*dashed line*)



**Fig. 4.** The corrected and numerically completed Species Abundance Distribution of the fish community at site “Tidung” (*grey discs*: recorded species, *double line*: numerically extrapolated part of the S.A.D.). For comparison, the “broken-stick” (*dashed line*)



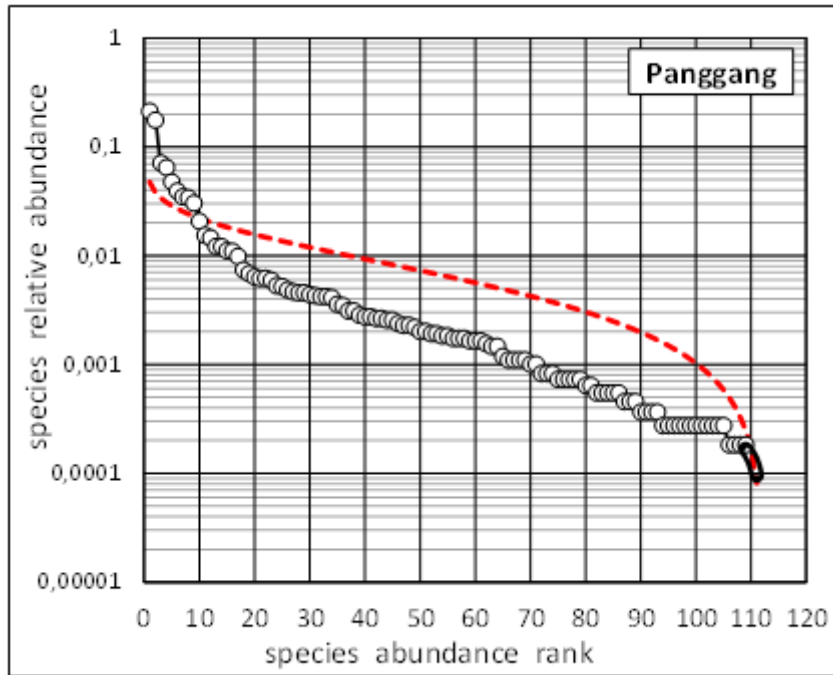


Fig. 5. The corrected and numerically completed Species Abundance Distribution of the fish community at site “Panggang” (*grey discs*: recorded species, *double line*: numerically extrapolated part of the S.A.D.). For comparison, the “broken-stick” (*dashed line*)

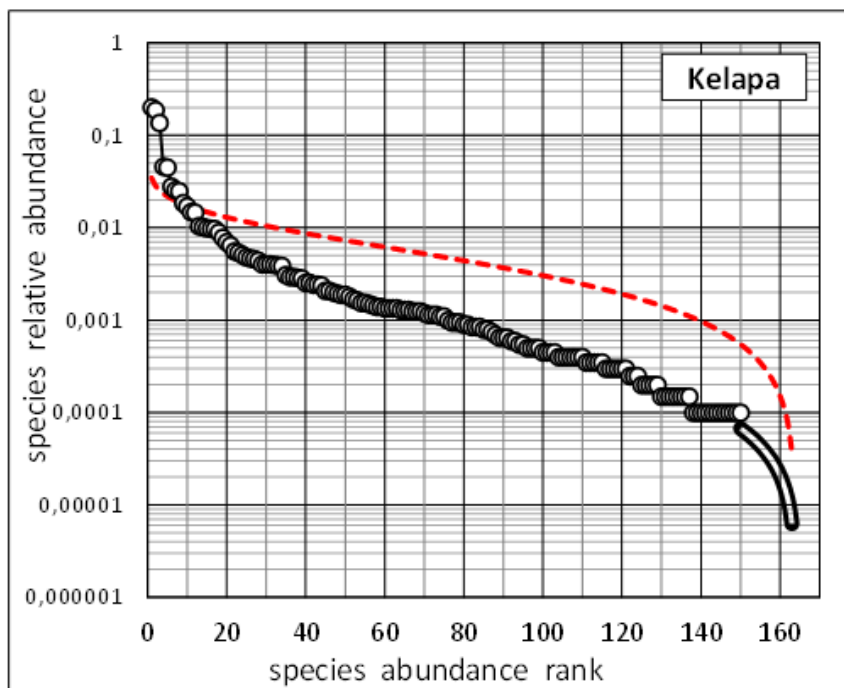


Fig. 6. The corrected and numerically completed Species Abundance Distribution of the fish community at site “Kelapa” (*grey discs*: recorded species, *double line*: numerically extrapolated part of the S.A.D.). For comparison, the “broken-stick” (*dashed line*)

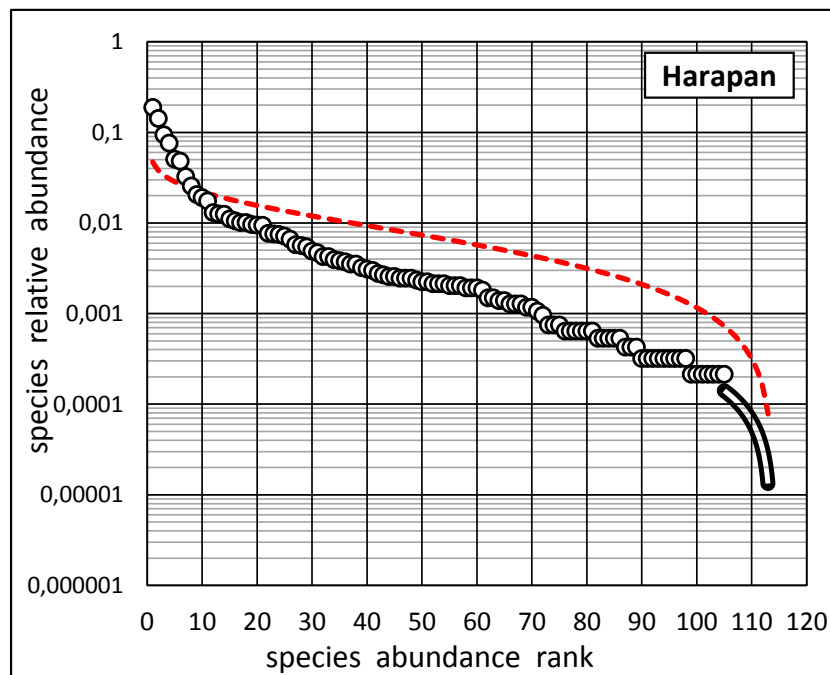


Fig. 7. The corrected and numerically completed Species Abundance Distribution of the fish community at site “Harapan” (grey discs: recorded species, double line: numerically extrapolated part of the S.A.D.). For comparison, the “broken-stick” (dashed line)

Table 2. A synthetic summary of the main quantitative features of the hierarchical organization of species abundances within community, as derived from numerically completed “S.A.D.s” : (i) the total species richness  $S_t$  of the community ; (ii) the relative abundances  $a_1$  and  $a_{S_t}$  of the most and least abundant species (species rank 1 and  $S_t$ ) ; (iii) the mean relative variation of abundance, (iv) the average of the relative variation of abundance between two successive species along the S.A.D.,  $\Delta a_i/a_i = (a_i/a_{i+1}) - 1$ , (v) the unevenness of abundances in the community:  $U = \log(a_1/a_{S_t})/(S_t-1)$ ; (vi) the unevenness of abundances in the corresponding “broken-stick” distribution:  $U' = \log(a'_1/a'_{S_t})/(S_t-1)$ , (vii) the standardized unevenness index  $I_{str} = U/U'$ . Pari: PAR., Tidung: TID., Panggang: PAN., Kelapa: KEL., Harapan: HAR

community	$S_t$	$a_1$	$a_{S_t}$	mean $\Delta a_i/a_i$	$U$	$U'$	$I_{str}$
PAR.	67	0.4680	0.000050	0.149	0.0602	0.0381	1.58
TID.	95	0.2549	0.000009	0.115	0.0474	0.0286	1.66
PAN.	111	0.2124	0.000105	0.072	0.0301	0.0253	1.19
KEL.	163	0.2011	0.000006	0.066	0.0278	0.0183	1.52
HAR.	113	0.1895	0.000013	0.089	0.0371	0.0249	1.49

### 3.3 The Answers of Species-richness, Individuals’ Density and Interspecific Competition to Increasing Distance from Pollution Sources

The localizations of the five surveyed fish-communities range from 32 to 56 km from the main sources of marine water pollution, mainly concentrated in Jakarta Bay [6] (Table 1). A decreasing gradient of anthropogenic pressure – and especially of water pollution – is recognized with increasing distance from Jakarta [6]. This

offers the opportunity to follow the answers of the three main quantitative descriptors of the surveyed fish communities to gradually improving water quality – namely, the overall density  $D$  of individuals, the total species-richness  $S_t$  and the standardized unevenness  $I_{str}$ , directly reflecting the intensity of interspecific competition. From data presented in Tables 1 and 2, a synthetic overview is provided in the diagram in Fig. 8. As could be expected, there is a trend for some improvement of both the species-richness  $S_t$  and the individuals’ density  $D$  with increasing

distances from the main source of deleterious anthropogenic influences (coefficient of determination  $r^2 = 0.69$  and  $0.74$  respectively). More precisely, the trend is, at first, shared by both species-richness and individuals' density. Then individuals' density tends to stabilize, while species-richness further keeps increasing. The variations of the intensity of interspecific competition, on the contrary, do not show any definite trend.

Moreover, as will be shown in Discussion section, a far stronger correlation with distance to pollution source is obtained by considering a – theoretically justified – compound-parameter, appropriately combining  $D$ ,  $S_t$  and  $I_{str}$ .

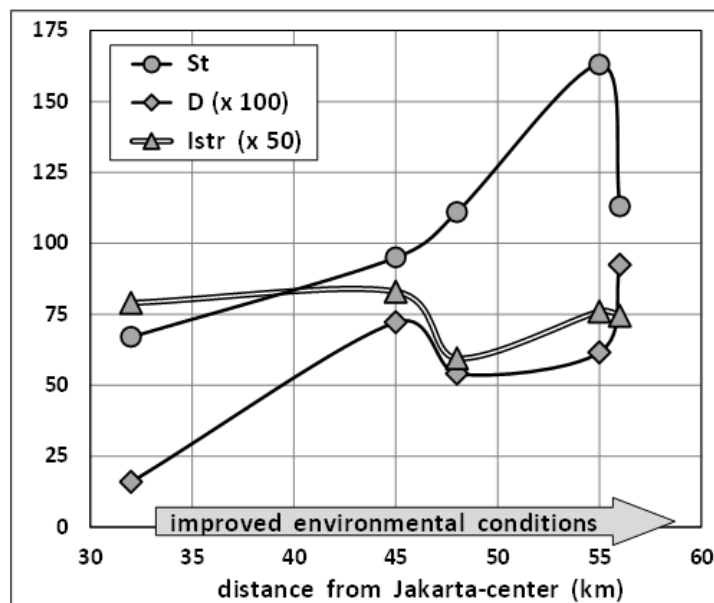
### 3.4 Comparing the Two Main Feeding Guilds as Regards their Species Richness and the Intensity of Interspecific Competition

It has been shown previously, in a series of marine communities, that there is a consistent trend for the guild of *secondary* consumers to be significantly *more species-rich* while being *less submitted to interspecific-competition* than it is the case for the guild of *primary* consumers [33,56,57,61]. This point is once again tested here. The communities from 'Pari' and from

'Kelapa' were selected for this study, as having respectively the lower and the higher level of species richness – this selection in order to control if species-richness might possibly influence the trend.

The numerical extrapolation procedure applied above to the entire communities (section 3.2) can be implemented *separately* for each of the two following feeding guilds: the *primary* feeders (considered here *sensu-lato*, including both herbivores and planktivores as well) and the *secondary* feeders (i.e.: strictly-speaking carnivores, while the omnivores of ambiguous status were discarded). The main results are provided in Table 3 and Fig. 9.

The guild of *secondary* consumers is *two to three times more species-rich* than is the guild of *primary* consumers, while the *average competition intensity* within guild – as reflected by the standardized unevenness  $I_{str}$  – is lower among *secondary* consumers than among *primary* consumers. Moreover, this trend remains the same for both communities at Pari and Kelapa – despite the large difference in species richness of these two communities. Thus, these results provide new empirical support to the trend already reported previously: Fig. 10.



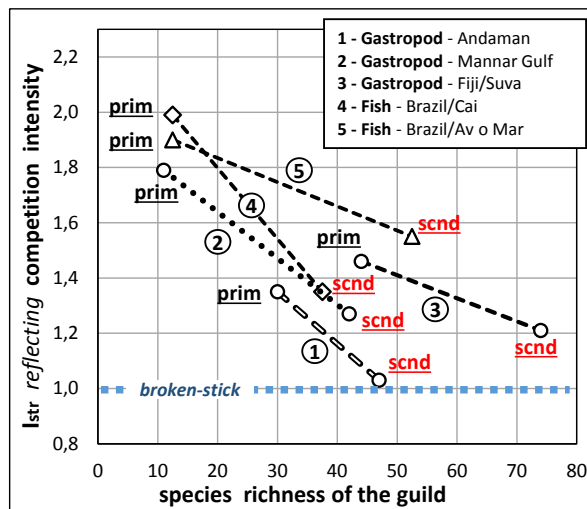
**Fig. 8.** The total species-richness  $S_t$ , the overall density  $D$  of individuals and the intensity of interspecific competition (mirrored by the standardized unevenness  $I_{str}$ ) plotted against increasing distances from pollution sources (from Tables 1 & 2). Coefficient of determination  $r^2 = 0.69$ ,  $0.74$  and  $0.07$  for  $S_t$ ,  $D$  and  $I_{str}$  respectively.  $D$  is multiplied by 100 and  $I_{str}$  by 50 to allow a common graphic representation

**Table 3. Species-richness  $S_t$  and interspecific-competition intensity (as mirrored by the standardized unevenness  $I_{str}$ ) compared between the guilds of primary and secondary feeders, in two fish communities located at Pari and Kelapa**

	PARI		KELAPA	
	Primary	Secondary	Primary	Secondary
Species-richness $S_t$	10	32	32	73
Standardized-unevenness $I_{str}$	2.21	1.43	1.69	1.38



**Fig. 9. The species-richness and the standardized abundance-unevenness  $I_{str}$  (that mirrors the intensity of interspecific competition) for each of the two main feeding guilds – primary feeders “prim” and secondary feeders “scnd”. Two fish communities are considered, located at Pari “P” and Kelapa “K”. The trend for the guild of primary consumers to have lower species richness while involving stronger competition intensity than the guild of secondary consumers is common to the two communities**



**Fig. 10. The species-richness and the standardized abundance-unevenness  $I_{str}$  (that mirrors the intensity of interspecific competition) for each of the two main feeding guilds – primary feeders “prim” and secondary feeders “scnd”. Five previously reported case studies: three marine gastropod communities from coral-reefs at (i) Andaman Islands (India) [33], (ii) Mannar Gulf (India) [56], (iii) Fiji Islands [57] and two marine fish communities from Brazilian coral-reefs [61]. The trend for primary consumers to have lower species richness while involving stronger competition intensity than secondary consumers is common to all five communities**

## 4. DISCUSSION

### 4.1 The Methodological and Ecological Issues Involved in the Study

In prolongation of the inventory of five fish communities, carried out by Madduppa et al. [6] at Seribu Islands archipelago, the additional treatments of the rough field data presented above have allowed a more thorough understanding of the socio-ecological conditions characterizing these communities.

Namely, the numerical extrapolation of incomplete samplings has permitted to cancel both the negative bias in the evaluation of species richness and the artificial truncation of the species abundance distribution towards rarer, undetected species. Then, following this improvement in the reliability and accuracy of input data, the refined analysis of the distribution of species-abundance, profiting by 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 communities.

More specifically, it had become 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 statistically-derived “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.

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, here, a particular niche allowing its own subsistence for each species respectively.

And this, while having, in addition, to cope also with *biotic* interactions, that is, interspecific-competition at niche-overlaps (if any). *Improved* niche-diversification thereby allows the accommodation of *greater* species-richness, thanks to denser “species-packing”.

- (ii) in turn, the *intensity of interspecific-competition at niche-overlaps* accounts for the difficulty to accommodate the level of species-richness thus achieved. The greater this difficulty, the more intense will be the interspecific-competition and, thus, its (multiplicative) contribution,  $I_{str}$ , to the degree of unevenness of species abundance distribution. 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*. Hence contrasting it with any other communities sharing the same species-richness (i.e.: benefiting 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*, due to higher niche-diversification,
- (ii) *increasing, yet, the risk of niche overcrowding*. With, consequently, the resulting niche-overlaps triggering, in turn, an increasing level of interspecific-competition, according to the density of individuals competing for shared resource at these niche-overlaps. Thus 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. No general applicability is also supported empirically: see reference [50].

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 (i) the *species-richness* and (ii) 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 [33,56-67]) once again exemplifies the benefits from implementing this *refined methodological approach*.

#### 4.2 Numerical Restitution of Total Species-richness and Abundance Distribution, Including Those Rarer Species that Escape Sampling

As is practically unavoidable [7], the reported samplings of fish communities at Seribu Islands [6] reveal being more or less incomplete, with completeness ranging from 73% to 98%. And, as already emphasized in the introductory section, contrary to what is sometimes alleged, neglecting (the unrecorded) rare species may have, indeed, significant inconvenient. Neglecting the subset of rare species is not only a source of bias in the *description* of the true reality of the species community under study but, also, may potentially lead to more or less erroneous interpretations as regards the *functional* aspects of the internal organization of the community: “rare species are critical for bio-assessment” as quoted in [23].

Both Table 1 and Figs. 3 to 7 allow to compare the differences – and the resulting bias – between the *as recorded* data and the appropriately *numerically extrapolated* description of the communities, in terms of their true level of species-richness as well as their completed distribution of species abundances. Incidentally, the opportunity was taken to confirm empirically the expected factors making a community of species more or less sensitive to sampling incompleteness: that is, not only the insufficiency of the ratio  $N_0/S_t$  between the number of recorded individuals  $N_0$  and the total species-richness  $S_t$  (see Fig. 1), but also the level of species-abundance unevenness  $U$  (see Fig. 2). Thus, providing additional empirical support to previous investigation [65].

The estimative restitution of the quantitative descriptors for the five fish communities (i.e., as if the samplings had been performed exhaustively) are summarized in Table 2, which highlights in particular, the degree of *standardized abundance unevenness*,  $I_{str}$ , of each community, in a way that is *truly independent* of its total species-richness  $S_t$ . Thus, highlighting the possibility of reliably comparing, among different species communities, the *average intensity of interspecific competition at niches overlaps* – reliably *mirrored by* the value of  $I_{str}$  when in excess of unity. Thereby deciphering a *major descriptive and functional factor* governing the internal organization within species communities – which is, regrettably very generally overlooked, due to the huge practical difficulty to estimate otherwise the average degree of interspecific competition within each studied community.

#### 4.3 Species Richness and Interspecific Competition Intensity between the Primary and the Secondary Feeding Guilds

Results reported in Fig. 9 show that the guild of *secondary* consumers is *two to three times more species-rich* than is the guild of *primary* consumers, while the *average competition intensity* within guild – as reflected by the standardized unevenness  $I_{str}$  – is clearly lower among *secondary* consumers than it is among *primary* consumers. This was assessed for the *more* species-rich (‘Kelapa’) as well as for the *less* species-rich (‘Pari’), among the five studied communities. Thereby demonstrating that the *trend is robust* despite substantial differences in community richness. Moreover, the same trend proves also being robust encompassing a large

diversity of taxonomic and geographic ranges of marine communities [33,56,57,61], as is summarized in Fig. 10. It should also be noted that this trend has been argued on both theoretical and empirical point of view in [68].

#### 4.4 Answers of Species-richness, Individuals' Density and Interspecific Competition to Increasing Distance from Pollution Sources

As expected, the species-richness  $S_t$  and the overall individuals' density  $D$  both increase with growing distances from Jakarta, i.e., with reduced anthropogenic environmental stresses, while the standardized abundance unevenness (accounting for the intensity of interspecific competition) does not show any definite trend (Fig. 8). Note that a similar pattern of answers to improved environmental conditions, with an increase of species-richness and a substantially invariant intensity of interspecific competition, was already highlighted for marine gastropods communities at Fiji Islands [57].

#### 4.5 Improved Accommodation of Co-occurring Species with Progressively Better Environmental Conditions: A Quantitative Assessment

Increasing distance from Jakarta Bay is deemed to ensure better environmental conditions at the local scale, likely allowing, in turn, improved capacity of the site to accommodate *more numerous* co-occurring species. How to quantify this accommodation capacity? It is important to consider, first, those parameters of the species-community which could give relevant evidence of the improvement of environmental conditions. Obviously, the overall density in individuals  $D$  (all co-occurring species taken together) and the total species-richness  $S_t$  (both quantified in Table 1) – that is the “richness” of species community in *quantitative* (individuals' density) as well as *qualitative* (species taxonomic diversity) terms. Yet, another, third parameter ought to be considered: with progressively increasing level of species-richness, some niche overcrowding, generating partial niche overlaps, becomes more likely to occur. With, accordingly, interspecific-competition for shared resource likely to occur, all the more triggered by increasing density in individuals at niche overlaps. The *intensity of interspecific-competition at niche overlaps*, potentially favored by both species-richness  $S_t$  and individuals-density  $D$  [50,66], should thus be considered, *in complement to* parameters  $S_t$  and

$D$ : indeed, the accommodation capacity of the site will feature all the best that not only  $S_t$  and  $D$  can reach larger values, but *also* that these improvement of  $S_t$  and  $D$  will not trigger stronger interspecific competition. This is all the more relevant that the stronger the average level of interspecific competition, the greater the risk of local disappearance of the less favored species and, consequently, the fragility of the level of species-richness that has been reached. Thus, considering also the standardized abundance unevenness  $I_{str}$ , which relevantly mirrors the average intensity of interspecific competition within community, looks obvious. So that, finally, from a theoretical basis, a relevant metric “rAP” of the “*realized Accommodation Performance*” of a site can be appropriately defined as an increasing function of  $S_t$  and  $D$  and a decreasing function of  $I_{str}$ :

$$rAP = f(S_t, D, I_{str}) \quad (6)$$

with  $\partial f/\partial S_t > 0$ ,  $\partial f/\partial D > 0$  and  $\partial f/\partial I_{str} < 0$

One among simpler forms complying with the general relation above can be written as:

$$rAP = D \cdot (S_t)^a / (I_{str})^b \quad (7)$$

with ‘a’ and ‘b’ as adjustable, positive exponents.

Examining the possibility to reach a high level of correlation between this expression (7) of the accommodation capacity and the distance to Jakarta Bay (taken as a surrogate measure of environmental quality according to [6]), it turns out that an excellent correlation is obtained with the adjustable parameters ‘a’ and ‘b’ being both chosen equal to 1, thus inviting to adopt, here, for evaluating the accommodation capacity of sites, the very simple formulation:

$$rAP = D \cdot S_t / I_{str} \quad (8)$$

Fig. 11 shows the remarkably tight correlation that is obtained with  $rAP = D \cdot S_t / I_{str}$ . This excellent adequation thus provides additional *empirical* support to the soundness of the *theoretical* derivation of the accommodation capacity proposed above, at least in its more general and comprehensive expression, given by equation (6). So that, a metric of the accommodation capacity – provided it is defined in compliance with the general formulation of “realized Accommodation Performance” given by the comprehensive equation (6) – could serve as a convenient, practical way to derive a relevant appreciation of the global “ecological quality” of a site.



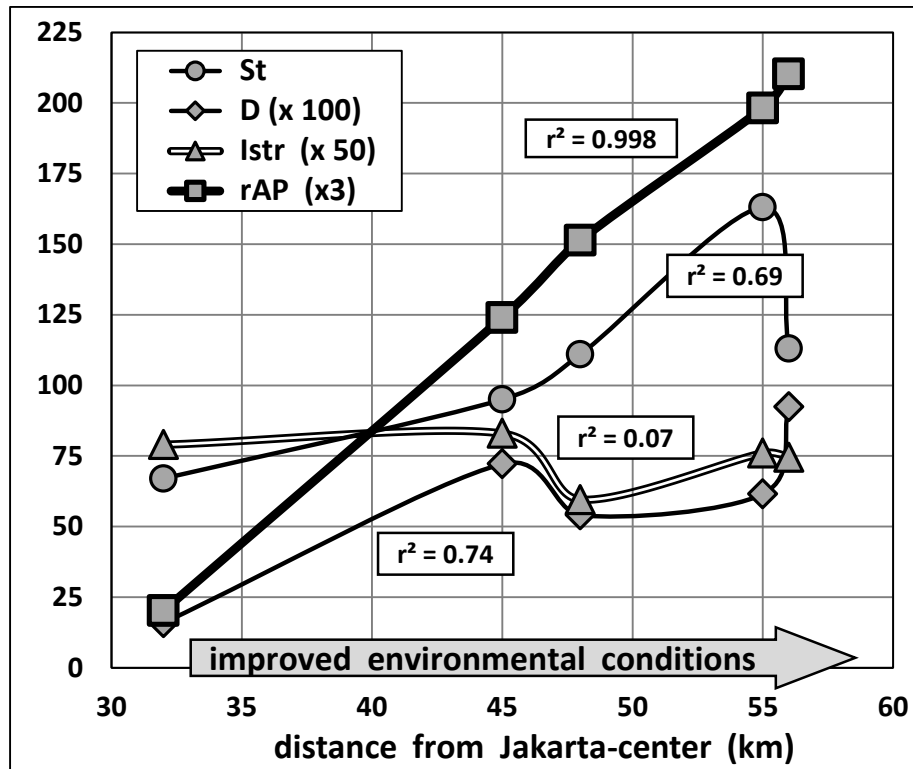


Fig. 11. Same as Fig. 8 with, in addition, the realized Accommodation Capacity rAP (here defined as  $= D \cdot S_t / I_{str}$ ) plotted against the distance from Jakarta-center, taken as a surrogate of the degree of improvement of environmental conditions. Note that the correlation of rAP ( $= D \cdot S_t / I_{str}$ ) with increasing distance from Jakarta is excellent and, by far, stronger ( $r^2 = 0.998$ ) than are the correlations obtained for each of its three components, considered separately: D ( $r^2 = 0.74$ ),  $S_t$  ( $r^2 = 0.69$ ) and  $I_{str}$  ( $r^2 = 0.07$ )



Plate 1. *Thalassoma lunare* (Linnaeus, 1758) © Leonard Low





**Plate 2. *Chaetodon octofasciatus* Bloch, 1787** © Bernard E. Picton



**Plate 3. *Amblyglyphidodon curacao* (Bloch, 1787)** © Dr. Dwayne Meadows





**Plate 4. Chlorurus sordidus (Forsskål, 1775)** © Tim Sheerman.Chase



**Plate 5. Scarus niger Forsskål, 1775** © Fernando Herranz Martin

## 5. CONCLUSION

Several important points – *descriptive* as well as *functional* – have been addressed, that complete the original report by Maddupa et al. [6] on fish assemblages along the Indonesian Seribu Islands Archipelago, off Jakarta. All these achievements required at first – and were only allowed by – the previous implementation of least-biased numerical extrapolations of the incomplete samplings reported in [6].

At first, the estimated *total* species-richness and the *completed* distribution of species abundances – *including the set of those rarer species remained unrecorded* – are provided, thereby improving the descriptive knowledge about these rich and interesting reef-associated fish assemblages, in the vicinity of Jakarta.

Then, focusing separately and comparatively upon the *primary* and the *secondary* feeding guilds, new empirical support is provided to what seems a rather frequent, if not general trend according to which the secondary-feeders guild reveals more species-rich, while exhibiting less interspecific competition intensity at niche overlaps, than does the primary-feeders guild.

At last, a remarkably good correlation is highlighted between the distance of fish assemblages from Jakarta Bay (distance considered as a reliable surrogate to the improvement of environmental conditions for fish assemblages) and a theoretically derived index 'rAP' ("*realized Accommodation Performance*") characterizing the accommodation capacity of sites for fish assemblages. Thus, arguably conferring to this index some reliable value to assess the "environmental quality" of marine waters, with respect to global fish exigences.

## ACKNOWLEDGEMENTS

I acknowledge the fruitful comments of three anonymous Referees.

## COMPETING INTERESTS

Author has declared that no competing interests exist.

## REFERENCES

1. Wells JW. Coral reefs: 609-632; in J.W. Hedspeth editor, Treatise on marine

- ecology and paleoecology. Geological Society of America. Mem. 1957;67.
2. Connell J. Diversity in tropical rain forests and coral reefs. Science. 1978;199:1302-1310.
3. Glynn PW. High complexity food webs in low-diversity eastern Pacific reef-coral communities. Ecosystems. 2004;7:358-367.
4. Graham NAJ, Wilson SK, Jennings S, Polunin NVC, Bijoux JP & Robinson J. Dynamic fragility of oceanic coral reef ecosystems. Proceedings of the National Academy of Sciences USA. 2006;103(22):8425-8429.
5. Ziegler M, Quéré G, Ghiglione J-F, Iwankow G, Barbe V, Boissin E, Wincker P, Planes S, Voolstra CR. Status of coral reefs of Upolu (Independent State of Samoa) in the South West Pacific and recommendations to promote resilience and recovery of coastal ecosystems. Marine Pollution Bulletin. 2018;129: 392-398.
6. Madduppa HH, Subhan B, Suparyani E, Siregar AM, Arafat D, Tarigan SA, et al. Dynamics of fish diversity across an environmental gradient in the Seribu Islands reefs off Jakarta. Biodiversitas. 2013;14(1):17-24.
7. Kery M & Royle JA. Inference about species richness and community structure using species-specific occupancy models in the National Swiss Breeding Bird survey MUB. Proceedings of the 2007 EURING Technical Meeting and Workshop, Dunedin, New Zealand ; 2007.
8. Bellier E, Grotan V, Engen S, Schartau AK, Diserud OH, Finstad AG. Combining counts and incidence data: an efficient approach for estimating the log-normal species abundance distribution and diversity indices. Oecologia ; 2012. DOI: 10.1007/s00442-012-2311-2
9. Cam E, Nichols JD, Sauer JR, Hines JE. On the estimation of species richness based on the accumulation of previously unrecorded species. Ecography. 2002;25:102-108.
10. Rajakaruna H, Drake DAR, Chan FT & Bailey SA. Optimizing performance of nonparametric species richness estimators under constrained sampling. Ecology and Evolution. 2016;6:7311-7322.
11. Connolly SR, Hughes TP, Bellwood DR. A unified model explains commonness and

- rarity on coral reefs. *Ecology Letters*. 2017;20:477-486.
12. Chen Y, Shen TJ. Rarefaction and extrapolation of species richness using an area-based Fisher's logseries. *Ecology and Evolution*. 2017;7:10066-10078.
  13. Rumohr H, Karakassis I, Jensen JN. Estimating species richness, abundance and diversity with 70 macrobenthic replicates in the Western Baltic Sea. *Marine Ecology Progress Series*. 2001;214:103-110.
  14. Fontaine B, Bouchet P. et al. The European union's 2010 target: Putting rare species in focus. *Biodiversity and Conservation*. 2007;139:167-185.
  15. Flöder S, Jaschinski S, Wells G, Burns CW. Dominance and compensatory growth in phytoplankton communities under salinity stress. *Journal of Experimental Marine Biology and Ecology*. 2010;395:223-231.
  16. Bracken M, Low N. Realistic losses of rare species disproportionately impact higher trophic levels. *Ecology Letters*. 2012 ;15:461-467.
  17. Mouillot D, Bellwood DR, Baraloto C, Chave J, Galzin R, Harmelin-Vivien M, Kulbicki M, Lavergne S, Lavorel S, Mouquet N, Paine CET, Renaud J, Thuiller W. Rare species support vulnerable functions in high-diversity ecosystems. *PLoS Biol*. 2013;11(5):e1001569.
  18. Jain M, Flynn DFB, Prager CM, Hart GM, DeVan CM, Ahrestani FS, Palmer MI, Bunker DE, Knops JHM, Jouseau CF, Naeem S. The importance of rare species: A trait-based assessment of rare species contribution to functional diversity and possible ecosystem function in tall-grass prairies. *Ecology and Evolution*. 2014;4(1):104-112.
  19. Ignatiades L, Gotsis-Skretas O. The contribution of rare species to coastal phytoplankton assemblages. *Marine Ecology*. 2014;35:132-145.
  20. Low-Decarie E, Kolber M, Homme P, Lofano A, Dumbrell A, Gonzalez A, Bell G. Community rescue in experimental communities. *Proceedings of the National Academy of Sciences USA*. 2015 ;112(46):14307-14312.
  21. Leitao RP, Zuanon J, Villéger S, Williams SE, Baraloto C, Fortunel C, Mendonça FP, Mouillot D. Rare species contribute disproportionately to the functional structure of species assemblages. *Proceedings of The Royal Society B*. 2016;283:e0084.  
DOI: 10.1098/rspb.2016.0084
  22. Violle C, Thuillier W, Mouquet N, Munoz F, Kraft NJB, Cadotte MW, Livingstone SW, Mouillot D. Functional rarity: The ecology of outliers. *Trends in Ecology ; 2017*.  
DOI: 10.1016/j.tree.2017.02.002
  23. Cao Y, Williams DD, Williams NE. How important are rare species in aquatic community ecology and bioassessment? *Limnology and Oceanography*. 1998 ;43(7):1403-1409.
  24. Béguinot J. Theoretical derivation of a bias-reduced expression for the extrapolation of the Species Accumulation Curve and the associated estimation of total species richness. *Advances in Research*. 2016;7(3):1-16.  
DOI:10.9734/AIR/2016/26387; <hal-01367803>
  25. Béguinot J. Extrapolation of the species accumulation curve associated to "Chao" estimator of the number of unrecorded species: A mathematically consistent derivation. *Annual Research & Review in Biology*. 2016;11(4):1-19.  
DOI: 10.9734/ARRB/2016/30522; <hal 01477263 >
  26. Béguinot J. How to extrapolate species abundance distributions with minimum bias when dealing with incomplete species inventories. *Advances in Research*. 2018;13(4):1-24.  
DOI: 10.9734/AIR/2018/39002
  27. May RM. Patterns of species abundance and diversity. In Cody M.L. & Diamond J.M. 1975 *Ecology and Evolution of Communities*. The Belknap Press of Harvard University. 81-120.
  28. McGill BJ, Etienne RS, Gray JS et al. Species abundance distributions: Moving beyond single prediction theories to integration within an ecological framework. *Ecology Letters*. 2007;10:995-1015.
  29. Ulrich W, Ollik M, Ugland KI. A meta-analysis of species-abundance distributions. *Oikos*. 2010;119:1149-1155.
  30. Komonen A, Elo M. Ecological response hides behind the species abundance distribution: community response to low-intensity disturbance in managed grasslands. *Ecology and Evolution*. 2017;7:8558-8566.
  31. Wang X, Ellwood F, Al D, Zhang R, Wang G. Species abundance distributions as a

- proxy for the niche-neutrality continuum. *Journal of Plant Ecology*. 2017;rtx 013.
32. Chao A, Hsieh T, Chazdon RL, Colwell RK, Gotelli NJ. Unveiling the species-rank abundance distribution by generalizing the Good-Turing sample coverage theory. *Ecology*. 2015;96(5):1189-1201.
  33. Béguinot J. Numerical extrapolation of the species abundance distribution unveils the true species richness and the hierarchical structuring of a partially sampled marine gastropod community in the Andaman Islands (India). *Asian Journal of Environment and Ecology*. 2018;6(4):1–23. DOI:10.9734/AJEE/2018/41293 <hal-01807454>
  34. Strong WL. Assessing species abundance unevenness within and between plant communities. *Community Ecology*. 2002 ;3(2):237-246. DOI: 10.1556/COME.C.3.2002.2.9
  35. Magurran AE. The commonness and rarity of species. in *Measuring Biological Diversity*. Blackwell Publishing Ltd ; 2004.
  36. Grzès IM. Ant species richness and evenness increase along a metal pollution gradient in the Boleslaw zinc smelter area. *Pedobiologia*. 2009;53:65-73.
  37. Smith B, Wilson JB. A consumer's guide to evenness indices. *Oikos*. 1996;76:70-82.
  38. Johnson MP, Raven PH. Natural regulation of plant species diversity. *Evolutionary Biology*. 1970;4:127-162.
  39. Berger WH, Parker FL. Diversity of planktonic foraminifera in deep sea sediments. *Science*. 1970;168:1345-1347.
  40. DeBenedictis PA. On the correlations between certain diversity indices. *The American Naturalist*. 1973;107:295-302.
  41. Heip CHR, Herman PMJ, Soetaert K. Indices of diversity and evenness. *Océanis*. 1998;24(4):61-87.
  42. Stirling G, Wilsey B. Empirical relationships between species richness, evenness and proportional diversity. *The American Naturalist*. 2001;158(3):286-299.
  43. Buzas MA, Hayek LAC. On richness and evenness within and between communities. *Paleobiology*. 2005 ;31(2):199-220.
  44. Jost L. The relation between evenness and diversity. *Diversity*. 2010;2:207-232.
  45. Loiseau N, Gaertner JC. Indices for assessing coral reef fish biodiversity: The need for a change in habits. *Ecology and Evolution*. 2015;5(18):4018-4027.
  46. Röpke CP, Amadio S, Zuanon J, Ferreira EJJ, Pereira de Deus C, Pires THS, Winemiller KO. Simultaneous abrupt shifts in hydrology and fish assemblage structure in a floodplain lake in the central Amazon. *Scientific Reports*. 2017;7:40170.
  47. Béguinot J. The hierarchical structuring of species abundances within communities: Disentangling the intensity of the underlying structuring process behind the apparent unevenness pattern. *Advances in Research*. 2018;16(1):1-12. DOI: 10.9734/AIR/2018/43918
  48. Su Q. A relationship between species richness and evenness that depends on specific relative abundance distribution. *Peer J*. 2018;6:e4951.
  49. Béguinot J. Disentangling and quantifying the functional determinants of species abundance unevenness in ecological communities. *Advances in Research*. 2019;19(1):1-14. DOI: 10.9734/AIR/2019/v19i130114
  50. Béguinot J. A new, ecologically self-significant metric of species-abundance unevenness, reliably highlighting the intensity of interspecific competition. *Annual Research & Review in Biology*. 2021;36(4):48-71. DOI: 10.9734/ARRB/2021/v36i430363
  51. MacArthur RH. On the relative abundance of bird species. *Proceedings of the National Academy of Sciences U.S.A.* 1957;43:293-295.
  52. Schoener TW. Resource partitioning in ecological communities. *Science*. 1974;185:27-39.
  53. Heck KL. Some critical considerations of the theory of species packing. *Evolution Theory*. 1976;1:247-258.
  54. Pigot AL, Trisos CH, Tobias JA. Functional traits reveal the expansion and packing of ecological niche space underlying an elevational diversity gradient in passerine birds. *Proceedings of the Royal society B*. 2015;283:20152013.
  55. Van de Perre F, Willig MR, Presley SJ, Mukinzi JC, et al. Functional volumes, niche packing and species richness: biogeographic legacies in the Congo Basin. *Royal Society Open Science*. 2020;7:191582.
  56. Béguinot J. The full hierarchical structuration of species abundances reliably inferred from the numerical extrapolation of still partial samplings: A case study with marine snail communities

- in Mannar Gulf (India). Asian Journal of Environment and Ecology. 2018;7(3):1-27. DOI: 10.9734/AJEE/2018/36831
57. Béguinot J. Analyzing the role of environmental stresses on species richness and the process of hierarchical structuring of species abundances in marine Gastropods communities at Suva (Fiji Islands). International Journal of Environment and Climate Change. 2018;8(3):200-233.
  58. Béguinot J. Inferring total species richness and the exhaustive hierarchical structuring of species abundances in tropical Sea-Stars communities (Asteroidea), using numerical extrapolation of partial inventories. Asian Journal of Environment and Ecology. 2018;8(2):1-25. DOI: 10.9734/AJEE/2018/46272
  59. Béguinot J. Comparing the complete hierarchical structuration of species abundances in reef fish communities according to coral morphology, using the numerical extrapolation of only incomplete inventories. Asian Journal of Environment and Ecology. 2018;8(1):1-20. DOI: 10.9734/AJEE/2018/45402
  60. Béguinot J. 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. Asian Journal of Environment and Ecology. 2018;8(3),1-21. Available:<https://doi.org/10.9734/ajee/2018/v8i330075>
  61. Béguinot J. Influence of fishing activity on the total species richness and the abundance unevenness in reef fish communities: a case study in a Brazilian tropical coral complex. International Journal of Environment and Climate Change. 2019;9(1):58-76.
  62. Béguinot J. Influence of coral complexity on species richness and the hierarchical structuration of species abundances in reef fish communities: A case study in south-east Brazil. Asian Journal of Environment and Ecology. 2019;9(3):1-20. DOI: 10.9734/AJEE/2019/v9i330098
  63. Béguinot J. Influence of environmental heterogeneity on the species composition, species richness and species abundances unevenness in reef-associated *Conus* communities (Neogastropoda) from Papua New-Guinea. Asian Journal of Environment & Ecology. 2019;10(3): 1-21. DOI: 10.9734/AJEE/2019/v10i330116
  64. Béguinot J. Variations in total species richness and the unevenness of species abundance distribution between two distant *Conus* communities (Neogastropoda): A case study in Mannar Gulf (India). Asian Journal of Environment & Ecology. 2019;9(4):1-18. DOI: 10.9734/AJEE/2019/v9i430102
  65. Béguinot J. Inferring true species richness and complete abundance distribution in six reef-fish communities from Red-Sea, using the numerical extrapolation of incomplete samplings. Asian Journal of Environment & Ecology. 2019;11(3):1-21. DOI: 10.9734/AJEE/2019/v11i330136
  66. Béguinot J. Progressive recovery of a marine Gastropod community following atmospheric nuclear tests in French-Polynesia: a socio-ecological interpretation. Annual Research & Review in Biology. 2021;36(1):77-110. DOI: 10.9734/ARRB/2021/v36i130335
  67. Béguinot J. Interspecific-competition strongly constrains species-richness and species-abundance evenness in a tropical marine molluscan community inhabiting *Caulerpa* beds, as compared to coral-reefs. Asian Journal of Environment and Ecology. 2021;14(4):26-46. DOI: 10.9734/AJEE/2021/v14i430214
  68. Garcia-Callejas D. On the variability of species abundance distributions with trophic guild and community structure. bioRxiv ; 2018. DOI: 10.1101/289348
  69. Béguinot J. An algebraic derivation of Chao's estimator of the number of species in a community highlights the condition allowing Chao to deliver centered estimates. ISRN Ecology; 2014. article ID 847328 DOI:10.1155/2014/847328; <hal-01101415>
  70. Béguinot J. When reasonably stop sampling? How to estimate the gain in newly recorded species according to the degree of supplementary sampling effort. Annual Research & Review in Biology. 2015;7(5):300-308. DOI:10.9734/ARRB/2015/18809; <hal-01228695>
  71. Béguinot J. On general mathematical constraints applying to the kinetics of species discovery during progressive sampling: Consequences on the theoretical expression of the Species

- Accumulation Curve. *Advances in Research*. 2016;8(5):1-17.  
DOI: 10.9734/AIR/2016/31791. <hal-01516141>
72. Li CT, Li KH. Species abundance distribution and species accumulation curve: A general framework and results. *arXiv*; 2020. 2011.07270v1 [stat.AP].
73. Menegotto A, Rangel TF. Mapping knowledge gaps in marine diversity reveals a latitudinal gradient of missing species richness. *Nature communications*. 2018;9:4713.  
DOI: 10.1038/s41467-018-07217-7
74. O'Hara RB. Species richness estimators: How many species can dance on the head of a pin? *Journal of Animal Ecology*. 2005;74:375-386.
75. Gotelli NJ, Colwell RK. Estimating species richness. pp. 39-54 in: *Biological Diversity: Frontiers In Measurement And Assessment*. A.E. Magurran and B.J. McGill (eds.), Oxford University Press, Oxford. 2010;345.
76. Gotelli NJ, Chao A. Measuring and estimating species richness, species diversity, and biotic similarity from sampling data. In: Levin S.A. (ed.) *Encyclopedia of Biodiversity*, second edition; Waltham, MA: Academic Press. 2013;5:195-211.
77. Bevilacqua S, Ugland KI, Plicanti A, Scuderi D, Terlizzi A. An approach based on the total-species accumulation curve and higher taxon richness to estimate realistic upper limits in regional species richness. *Ecology and Evolution*. 2018;8:405-415.
78. Brose U, Martinez ND, Williams RJ. Estimating species richness: Sensitivity to sample coverage and insensitivity to spatial patterns. *Ecology*. 2003;84(9):2364-2377.

## 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 [24,25,69-72]):

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

Compliance with the mathematical constraint (equation (A.1)) warrants *reduced-bias* expression for the extrapolation of the Species Accumulation Curves  $R(N)$  (i.e. for  $N > N_0$ ). Below are provided, accordingly, the polynomial solutions  $R_x(N)$  that respectively satisfy the mathematical constraint (A1.1), considering increasing orders  $x$  of derivation  $\partial^x R_{(N)}/\partial N^x$ . Each solution  $R_x(N)$  is appropriate for a given range of values of  $f_1$  compared to the other numbers  $f_x$ , according to [24]:

$$* \text{ for } f_1 \text{ up to } f_2 \rightarrow R_1(N) = (R(N_0) + f_1) - f_1 \cdot N_0/N$$

$$* \text{ for larger } f_1 \text{ up to } 2f_2 - f_3 \rightarrow R_2(N) = (R(N_0) + 2f_1 - f_2) - (3f_1 - 2f_2) \cdot N_0/N - (f_2 - f_1) \cdot N_0^2/N^2$$

$$* \text{ for larger } f_1 \text{ up to } 3f_2 - 3f_3 + f_4 \rightarrow R_3(N) = (R(N_0) + 3f_1 - 3f_2 + f_3) - (6f_1 - 8f_2 + 3f_3) \cdot N_0/N - (-4f_1 + 7f_2 - 3f_3) \cdot N_0^2/N^2 - (f_1 - 2f_2 + f_3) \cdot N_0^3/N^3$$

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

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

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

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

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

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

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

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

**N.B. 1:** As indicated above (and demonstrated in details in [24]), 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 [10,12,73-77]. Also, this shows that the approach initially proposed in [78] – 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 [10,12,73-77], 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 smoothed: this may be obtained either by rarefaction processing or by regression of the as-recorded distribution of the  $f_x$  versus  $x$ .

**N.B. 3:** For  $f_1$  falling beneath  $0.6 \times f_2$  (that is when sampling completeness closely approaches exhaustivity), then Chao estimator may alternatively be selected: see reference [25].

## 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 [26].

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

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

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

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

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

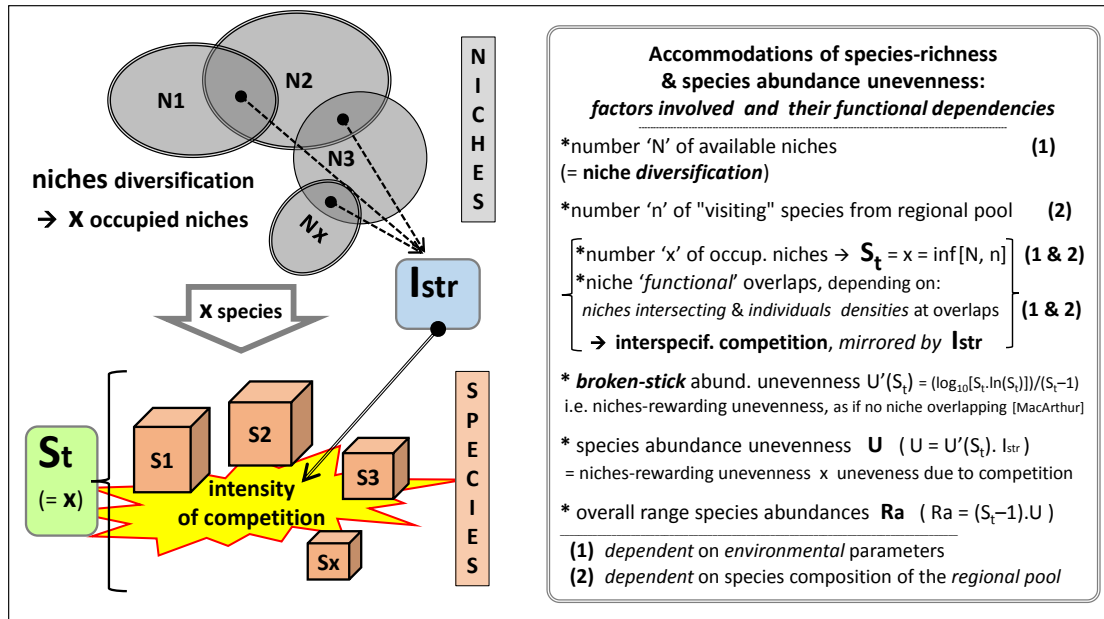
The following expression stands for the estimated abundance,  $a_i$ , of the unrecorded species of rank i (thus for  $i > R_0$ ):

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

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

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

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 ' $S_t$ ' and the standardized unevenness ' $I_{str}$ ' 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 range 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” as proposed by MacArthur [51] – thereby plays the role of a sort of “compass” supporting relevant functional interpretation of the “hierarchical” organization among co-occurring species within community

© 2021 Béguinot; This is an Open Access article distributed under the terms of the Creative Commons Attribution License (<http://creativecommons.org/licenses/by/4.0>), which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.

Peer-review history:  
 The peer review history for this paper can be accessed here:  
<https://www.sdiarticle4.com/review-history/70817>