Progressive Recovery of a Marine Gastropod Community Following Atmospheric Nuclear Tests in French- Polynesia: A Socio-ecological Interpretation

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Author's contribution

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

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ABSTRACT

Aims: The way species-richness is accommodated and how species-abundance distribution is organized in a hierarchic pattern is central to community ecology. Yet, the process by which species-richness and species-abundances are progressively accommodated can hardly be monitored, in practice, at a sufficiently large spatial scale. Fortunately, the progressive recovery of marine communities, after their complete destruction by atmospheric nuclear tests, yet offered *unique opportunity* to monitor the full process of accommodation of increasing species-richness and the associated, transient development of strong interspecific competition, all along the process of recovery.

Methods: Taking full advantage of such monitoring yet requires, first, to relevantly overcome two important practical issues: 1) achieving reliable numerical extrapolations of the usually unavoidably incomplete samplings in order to accurately estimate both the *true* species-richness and the *completed* distribution of species-abundances, including the *abundance* of undetected species and 2) disentangling (i) the *positive* contribution of improved *niche-diversification* to species-richness and species-abundance evenness from (ii) the *negative* contribution of increasing *interspecific-competition*, all along the recovery progress. This, indeed, is a rather tricky challenge, yet relevantly solved by using the newly developed “standardized unevenness index”, conceptually based upon MacArthur approach to interspecific-contest at niche overlaps.

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Results: Applying both tools above to the monitored recovery of a reef-associated Gastropod community, entirely wiped-out previously by severe nuclear blasts, had allowed a deeper understanding of the dynamic interplay between *species-recruitment*, *niche-diversification* and *interspecific-competition* in the regeneration of the community. In particular, along the recovery process, a transient, *metastable* phase – involving *severe interspecific-competition* at niche-overlaps – precedes a *gradual return to dynamic stability*, with the virtual extinction of interspecific competition

Keywords: *Resilience; species-richness; evenness; niche-diversification; resource-partitioning; niche-overlap; interspecific competition, Fangatau atoll.*

1. INTRODUCTION

Understanding how species organization within natural species assemblages progressively arises and maintains is one of the major focal issues in community ecology [1-3]. And beyond species composition and the overall density of individuals, it is by considering and analyzing in detail the (*complete*) *distribution of species abundances* that it becomes possible to get deeper enlightenment on how proceeds the organization of species within communities [4]. In practice, two quantitative aspects of the distribution of species abundances are generally considered to synthesize the main features of this distribution of species abundances: the *total number of co-occurring species* and how *uneven* are their *abundances*. The abundance unevenness reflecting, synthetically, the outcome of the complex and intricate relationships that co-occurring species establish with (i) the local environment (*abiotic* constraints) and (ii) between them all (*biotic* relationships, especially *competitive* interactions). The (*total*) *species richness* and the degree of *unevenness* of species abundances thus feature as the two major quantitative guides which will aptly serve, not only as synthetic *descriptors* of species organization but, still more importantly, as convenient *tools to interpret* the origin of this organization and, in particular, to disentangle the *ecological drivers* involved therein.

Considering now the practical issues arising from this approach, the emphasis put, above, on the notions of “*total*” species richness and “*complete*” distribution of species abundances simply means that these two parameters, central for the description of species internal organization, should imperatively be derived from *exhaustive field data*, as far as possible. Exhaustivity being reached by either:

- (i) conducting sampling of the studied community in order to reach full completeness,

- (ii) or, if this reveal being impossible to achieve in practice – as is often the case for speciose communities – by implementing an appropriate *numerical extrapolation* of the incompletely achieved sampling, a procedure which now becomes easily practicable for estimating, not only the species richness but also the respective abundances of each of the undetected species [5-7].

Now, once species *richness* and *abundance unevenness* have been derived from exhaustive field data or reliable numerical extrapolation, a major objective of community ecology can be approached, namely: how these two fundamental factors are *accommodated* (i) at first, progressively during the natural establishment of a community and (ii) ultimately, when the community is expected to have reached some apparent or real equilibrium stage. In particular, two interrelated factors deserve special consideration:

- the improved *niche-diversification* thereby *favoring* both species-abundance evenness and species-richness accommodation (“*species packing*”);
- the increased degree of *niches (functional) overlaps*, which may arise from niches overcrowding resulting from niche-diversification being insufficient to accommodate efficiently the recruited species-richness, thereby *disfavoring* both species-abundance evenness and species-richness accommodation.

Thus, of prime importance is trying to uncover the balance between these two related aspects – *niche-diversification* and *niche-overlapping* – and their opposite influences (respectively positive and negative) on both species-*accommodation*, and abundance-*evenness*. And, finally, on the resulting *stability* of species-richness (as far as species-richness stability is an expected

outcome of improved species evenness). Since, it is likely, that this *subtle balance* may substantially differ among natural communities – even when communities happen to share the same level of species-richness. Hence the interest of multiplying case-studies in this respect.

The subject is, indeed, of both *speculative* and *practical* interests.

Speculative interest, since a deeper understanding of the processes involved in the accommodation of both species-richness and species-abundance unevenness will cast more light upon how species communities are internally structured, in particular in term of the establishment of the hierarchic distribution of abundances among co-occurring species.

Practical interest, because gaining a better knowledge upon all those factors which either can help stabilize or, on the contrary, contribute to destabilize the level of species-richness within communities is of obvious major concern, in particular for conservation biologists.

And, in this respect, it is important to disentangle the respective roles of (i) *internal* processes acting within the community (in particular, the role of interspecific competition, likely elicited when the number of recruited species markedly exceeds what may be ideally accommodated by niche-diversification) from (ii) the direct influence of *external* drivers (i.e. environmental factors, dispersal capacity, etc ...), since both can affect the level of accommodated species-richness and its expected long-term stability.

In practice, among those case studies, called above to fuel the analysis in this respect, the monitoring of the progressive recovery of a community, following its brutal destruction, features of major interest. In this perspective, nuclear experimental tests, conducted around the mid-twentieth century, directly above marine invertebrate communities, in some remote islets of the central Pacific Ocean, offer attractive opportunities to follow such a radical recovery after complete destruction.

Hereafter is proposed an ecological analysis of such a case study, based on the reported restoration of a reef-dwelling gastropod community after a drastically destructive series of atmospheric nuclear tests conducted on Fangataufa atoll (French Polynesia) [8,9].

2. GENERAL CONSIDERATIONS

It is largely admitted that the accommodation of species richness within community essentially proceeds by a sufficient “diversification” of niches, offering sufficient *resource partitioning* to the co-occurring species, in order to avoid excessive contest for shared resource among the latter [10-18], thus allowing improved species “packing” [3,19-21]. Quoting [18]: “in species-rich areas, biotic interactions drive species to specialize” thereby adapting to more finely diversified resource allocations (i.e. improved resource partitioning).

Yet, most often, “ideal” niche diversification is not actually reached, letting subsist more or less extended niche-overlaps – more precisely “functional” (i.e. inducing interspecific contests) overlaps between more or less intersecting niches: see Appendix 1. Thus, it is worth examining to what extent interspecific competition for partially shared resource subsists or, even, is promoted during the accommodation process of an increasing number of recruited species, thereby involving the occupation of increasingly numerous niches. And this, especially, if the overall *density* in individuals actually encourages interspecific contests for shared resources at niches overlaps.

Beyond speculative interest, the issue is also of practical concern because, admittedly, stronger interspecific competition would likely induce a severe decrease in the relative abundance of the rarest species. Which in turn, would put these rarest species at risk of local extinction, thereby *threatening the stability of species richness* itself. Indeed, rarest species are especially prone to being dislodged by other, more competitive species, either already present or new coming [22]. Moreover, would these rarer species escape competitive elimination, their substantially decreasing abundance may ultimately fall under the fatal threshold of “Allee effects”, leading to their local extinction [23,24].

3. MATERIALS AND METHODS

3.1 The Reported Field Data

The present study is based on the reported recovery of a reef-associated gastropod community on Fangataufa, a small atoll located in mid-Pacific Ocean (Tuamotu Archipelago, French Polynesia) subjected to atmospheric nuclear testing between the end of 1968 and

1970 [8,9]. The monitored community was more precisely located on the reef flat and edge at 'Terme-Sud' of the Fangataufa atoll [precise location: 22°16'30"S, 138°44'48"W]. All additional details regarding the precise location of the community and the sampling procedure are provided in the open-access references [8,9] and need not being further repeated here. Six samplings were conducted, the first one in 1968, before the first test, the five following samplings after the series of tests, in 1972, 1974, 1977, 1987, 1997. Apart from the first sampling, all other samplings, from 1972 to 1997, revealed being slightly (1972, 1987, 1997) to more strongly incomplete (1974, 1977), as will be shown below in Table 1.

As (sub-)exhaustive inventories are required to avoid making biased inferences regarding the main structural descriptors of ecological communities (in particular, the total species-richness and the abundance-unevenness) [25–30], an appropriate numerical extrapolation procedure to estimate the number of undetected species and the relative abundances of each of them, was implemented for each of the five incomplete samplings. These numerical extrapolations prove, retrospectively, being mandatory to avoid severe bias in the description and ecological interpretation of the recovery process, as will be shown later in section 4.3.

3.2 The Numerical Extrapolation Procedure and Its Exploitation

A recently developed extrapolation procedure allows a least-biased estimation of the number of undetected species and can even provide, in addition, estimates of the respective abundances of each of these undetected species, as detailed in section 3.2.1. Thus, once properly numerically completed (and *only* when it is so [27]), the distribution of species abundances provides synthetic data, in both *qualitative* and *quantitative* terms, about the underlying process that drives the hierarchical structuring of species abundances within community [31-35].

3.2.1 Implementation of the procedure of numerical extrapolation

* *Total species richness*: The least-biased estimation of the number of those species that remained unrecorded 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

references [5,6] and briefly summarized in Appendix 2, based on 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 2 for computation. In practice, this extrapolation allows to *forecast* the likely additional sampling efforts that would be required to obtain any desirable increment in sampling completeness.

* *Species Abundance Distribution*: As mentioned above, the Species Abundance Distribution ("S.A.D.") is intended to provide the basic data necessary (i) to *describe* the *pattern* of structuration of species abundances within community and (ii) to *qualify* and *quantify* the underlying *process that drives this structuration*. Yet, to accurately exploit its full potential [7,36], 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 (species only recorded once during sampling). The appropriate procedure of correction and of numerical extrapolation of the as-recorded partial "S.A.D." is described in details in reference [7], briefly summarized in Appendix 3 and concretely exemplified in details in reference [37]. 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 relative 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).

3.2.2 Abundance unevenness: The pattern of species abundance structuration

Once numerically completed, the "S.A.D." conveys all the relevant quantitative data required to address the internal organization among species within a local community [4]. In turn, the "S.A.D." can be synthetically summarized by two of its major features: the *total species richness* ' S_t ' and the *degree 'U' of unevenness* of the abundance distribution. Following [38,39], it is the degree of *unevenness* – rather than evenness itself – that should be

preferred to address the hierarchical structuring of species abundances in communities. According to the 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 abundance decrease, as already proposed by [40], that is:

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

That is:

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

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 species* as well as *minor species* and, thus, the *equitable account* of each of the co-occurring species, *independently of their respective abundances* – which is admittedly desirable [41]. Thereby contrasting in that, with many commonly used metrics of (un-)evenness which *conventionally* attribute *different weights* to co-occurring species, according to their relative commonness or rarity [41].

3.2.3 The “standardized” species abundance unevenness

For both descriptive purpose and functional interpretation, it is useful to derive from the “crude” abundance unevenness U (defined above) another, complementary expression of unevenness, the “*standardized unevenness index*” I_{str} , defined as the ratio U/U' between the crude unevenness U and the unevenness U' of a specific abundance distribution taken as a meaningful referential standard [42]. This standard being the well-known “*broken-stick*” distribution, originally proposed by MACARTHUR in his seminal paper [43]. The selection of the “broken-stick” distribution – as an especially appropriate and meaningful standard in the present context – is justified by two of its main characteristics, briefly argued below and further detailed in Discussion section and reference [42].

The “standardized unevenness index” $I_{str} = U/U'$, is thus defined as:

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

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

With a_1 and a_{St} standing for the highest and the lowest abundances in the studied community and a'_1 and a'_{St} standing for the highest and the lowest abundances in the corresponding “broken-stick” distribution for the same species richness S_t . The distribution of abundances for the “broken-stick” model and the corresponding abundance unevenness U' (with U' being a univocal function, $U'(S_t)$, of S_t) are computed according to [31,42,43], see also Appendix 4.

The standardization of the crude unevenness U to the corresponding “broken-stick” unevenness U' answers positively the two following points, which highlight the major interest of considering the “standardized unevenness” index “ I_{str} ”:

- From a *descriptive* point of view, the *crude* unevenness U has the major inconvenient of being partly dependent upon species-richness [4,31,34,41,44-52]. This makes it inappropriate (a serious source of bias) when comparing communities differing in species richness: indeed, as claimed in reference [41]: “*to make sense, (un)evenness must be independent of species richness*”. Now, being univocally dependent on species-richness [31,42], the “*broken-stick*” unevenness U' precisely conveys this very part of the crude unevenness U which is (negatively) dependent upon species-richness, as demonstrated in reference [42]. Accordingly, the “standardized” abundance unevenness, $I_{str} = U/U'$, is *formally independent* of species-richness, as duly required for making *reliable* comparisons between communities, *whatever* may be their difference in species-richness;
- As regards, now, the *functional* point of view, the standardization of the crude abundance unevenness by reference to the broken-stick distribution is also especially appropriate. Indeed, since the broken-stick distribution is functionally associated to the “contiguous, non-overlapping” niche pattern [43], this means that $I_{str} = 1$ refers to this particular non-overlapping niche pattern involving *no interspecific competition*. Conversely, *the more I_{str} is found to exceed unity, the stronger is the intensity of interspecific competition* among co-occurring species at niches overlaps (resulting from interspecific contests in the exploitation of shared resource at niche overlaps).

In short, the “*standardized abundance-unevenness*” I_{str} accounts for how much the niche-diversification (i.e. the degree of efficient resource partitioning among co-occurring species) is actually *restrained* within the considered species community. The account “currency” of this restriction in niche diversification being in term of *increased* abundance-unevenness, in other words of *steeper* average slope of the species abundance distribution).

In particular, I_{str} (when > 1) takes into account by how much is *multiplied* the abundance-unevenness (the average slope of the species abundance distribution), as a direct consequence of the intensity of interspecific competition at niche overlaps. That is, while unevenness U is equal to the corresponding “broken-stick” value, U' when niche display is efficiently diversified (i.e. contiguous non-overlapping niche display), it becomes $U = U' \cdot I_{str}$ as soon as *insufficient* niche diversification triggers the onset of interspecific competition for shared resource at niche overlaps, according to the level of density in competing individuals.

Conversely, $(1/I_{str})$ mirrors to what extent the niches display is efficiently diversified, that is how much *resource partitioning among co-occurring species is efficiently improved*.

Thus, the standardized unevenness index I_{str} features especially relevant at *both* the *descriptive* and the *interpretative* points of view [42].

At last, in addition to 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:

$$R_a = [\log_{10} (a_1 / a_{St})] \quad (3)$$

With a_1 and a_{St} standing for the highest and the lowest species-abundances in the studied community. That is, as well, from equations (1) & (2):

$$R_a = (S_t - 1) \cdot U = (S_t - 1) \cdot U' \cdot I_{str} \quad (4)$$

And for the corresponding “*broken-stick*” distribution:

$$R'_a = (S_t - 1) \cdot U' \quad (5)$$

It is important to emphasize that the variations of the overall range of species abundances R_a are mainly driven by the variations of the lowest abundance a_{St} , while, on the contrary, a_1 varies comparatively very little: see empirical evidence in [42] and theoretical argumentation in Appendix 5. Besides, it is the abundance a_{St} of the rarest species which is more decisive as regards the maintenance of species richness, since any further decrease of the lowest abundance a_{St} likely increases the risk of possible dislodgement and subsequent local extinction of the rarest species. This makes two good reasons to devote particular attention, beyond R_a , to the level of the lowest abundance a_{St} . So that, in this respect, a_{St} deserves also being considered as an *essential descriptor* of natural species communities, in addition to S_t , U and I_{str} .

3.2.4 Statistical testing

The statistical significance of the regression of the intensity of interspecific competition (mirrored by I_{str}) against species-richness and the overall density of individuals (implemented § 5.2) is estimated according to the conventional Student t-test procedure.

4. RESULTS

4.1 Estimated Total Species Richness of the Gastropod Community before Its Destruction and Along Its Progressive Recovery

As mentioned above, due to the subsistence of one or several singletons (species recorded only once during sampling), the samples reported for years 1972, 1974, 1977, 1987 and 1997 were considered incomplete and therefore submitted to ‘least-biased’ numerical extrapolations (previous examples of application of this procedure are provided in references [37,53-62]). Table 1 provides, at each date, the reported sampling data and the corresponding *extrapolated numbers* of those species that had remained undetected, from which is immediately derived the estimated *total* species richness.

4.2 Species Abundance Distributions Numerically Completed

The bias-corrected and numerically-extrapolated Species Abundance Distributions (S.A.D.s) are provided in Figs.1 to 6.

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. The crude species abundance unevenness U is either equal (in 1968), slightly larger (in 1972, 1987, 1997) or substantially larger (in 1974, 1977) than is the crude unevenness $U'(S_i)$ in the corresponding “broken-stick” distributions, computed for the same species-richness S_i . The differences 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.

4.3 Evolution of the Main Characteristics of the Distribution of species Abundances within Community along Thirty Years of Recovery Process

Due to their particular socio-ecological significance, four characteristics of the Species Abundance Distribution were especially followed during the course of recovery of the gastropod community after its complete destruction: the *species richness* S_i , the *crude abundance unevenness* U , the *standardized abundance unevenness* I_{str} and the *relative abundance* a_{Si} of the *rarest species*. The respective variations of these four parameters from 1968 (before destruction) up to 1997, when recovery seems having approach a new “equilibrium”, are provided in Figs. 7 to 10. These Figures also provide, for instructive comparison, the results that would have been derived if only *non-extrapolated* field data would have been considered. As is immediately evident, and although the degrees of sampling incompleteness were not excessive (all completeness levels > 75%), yet strikingly different, *strongly biased* results – and consequently *irrelevant associated ecological interpretations* – would have resulted from ignoring sampling incompleteness and neglecting the required numerical extrapolations of incomplete samplings. Of course, bias are all the more stronger than sampling completeness is lower, with bias being thus particularly severe for years 1974 and 1977 (completeness levels 80% and 76% only).

Complementary to these four descriptors of Species Abundance Distributions, the variations of the overall density D of individuals (all co-occurring species considered together) deserves consideration: Fig. 11. And this not only for descriptive purpose but also, as will be seen later, for the relevant interpretation of the

variations in interspecific competition intensity, because the density of individuals is part of the factors triggering interspecific contests at niches overlaps.

The socio-ecological interpretations that can be derived from the respective variations of all these major factors, contributing together to the species organization within community, are further analyzed in the Discussion section.

4.4 Rough Classification of Species, According to their Respective Answer during the Recovery Process of the Gastropod Community at Fangataufa

The overall 24 gastropod species identified on reef flat and edge at Terme-Sud of Fangataufa atoll, before and after nuclear tests, can be roughly distributed in four main types, according to their recovery status:

* A – species *originally present* and with *consistent* recovery answer:

Turbo setosus Gmelin 1791, *Tenguella granulata* (Duclos 1832), *Morula uva* Röding 1798, *Drupa ricinus* Linnaeus 1758, *Mitra litterata* Lamarck 1811, *Conus ebraeus* Linnaeus 1758, *Conus miliaris* Hwass in Bruguière 1792, *Conus nanus* Sowerby I 1833, *Conus sponsalis* Hwass in Bruguière 1792.

* B – species *originally present* and with *irregular* recovery answer:

Patella flexuosa Quoy & Gaimard 1834.

* C – species *originally absent* but with *seemingly well-established* recovery answer:

Nerita plicata Linnaeus 1758, *Monetaria moneta* Linnaeus 1758, *Imbricaria conovula* Quoy & Gaimard 1834.

* D – species *originally absent* with *transient or tardive* recovery answer:

Turbo argyrostomus Linnaeus 1758, *Cerithium echinatum* Lamarck 1822, *Cerithium nesioticum* Pilsbry & Vanatta 1906, *Cerithium* sp., *Tectarius grandinatus* Gmelin 1791, *Canarium maculatum* Sowerby II 1842, *Drupa grossularia* Röding 1798, *Drupa morum* Röding 1798, *Mancinella armigera* Link 1807, *Conus chaldeus* Röding 1798, *Conus rattus* Hwass in Bruguière 1792.

Figs. 1 to 6. The corrected and completed species abundance distributions of the studied reef-associated gastropod community before (1968) and after nuclear blasts, i.e. from 1972 to 1997. As recorded data: *grey discs*; numerically extrapolated part of the abundance distribution: *white discs*. For comparison, the abundance distribution of the corresponding “broken-stick” model, computed at the same species richness, is plotted as a *double line*.

Fig. 7. Variations of total species richness S_t along the recovery process

Fig. 8. Variations of crude abundance unevenness U along the recovery process

Fig. 9. Variations of the standardized unevenness I_{str} along the recovery process

Fig. 10. Variations of lowest species abundance a_{st} along the recovery process

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

Conus community	1968	1972	1974	1977	1987	1997
Number of collected individuals N_0	454	342	489	361	335	332
Number of recorded species $R(N_0)$	11	15	16	16	17	18
Selected least-biased estimator	/	JK-1	JK-5	JK-5	JK-1	JK-2
Number of unrecorded species Δ	0	0.5	4	5	1	1
Total species richness S_t	11	15.5	20	21	18	19
sample completeness R_0/S_t	100%	97%	80%	76%	94%	95%

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 crude abundance unevenness $U = \log(a_1/a_{St})/(S_t-1)$; (v) the abundance unevenness in the corresponding “broken-stick” distribution: $U' = \log(a'_1/a'_{St})/(S_t-1)$; (vi) the “standardized” unevenness index $I_{str} = U/U'$; (vii) the overall range of species abundances R_a

	S_t	a_1	a_{St}	a_1/a_{St}	a'_1	a'_{St}	U	$U'(S_t)$	I_{str}	R_a
1968	11	.275	.0086	32	.275	.0083	.151	.153	0.99	1.51
1972	15.5	.235	.00279	84	.218	.0042	.133	.119	1.12	1.93
1974	20	.295	.00027	1092	.178	.0025	.159	.097	1.64	3.04
1977	21	.289	.00028	1032	.171	.0022	.148	.093	1.59	3.01
1987	18	.232	.00218	106	.196	.0031	.120	.106	1.13	2.03
1997	19	.244	.00174	140	.187	.0028	.119	.102	1.17	2.15

Fig. 11. The overall density D of individuals per unit area (number of individuals per m^2 - all species being taken together) before and along the recovery process.
No reported data was made available for year 1997

Half of these species, belonging to one or the other among the four types above, are illustrated below.

The twelve species attributed to types “A” and “C” obviously endure positively the strongly competitive transient phase, during 1974 – 1977 (see Discussion, section 5.1) although, the three species attributed to type “C” had failed to subsist in the period preceding nuclear tests.

The twelve other species, attributed to types “B” and “D”, seem encountering more or less strong difficulty to (re-) establish, probably due to the harsh interspecific competition, either at the transient strongest competitive phase (1974 – 1977) or even later, when competition reduced but still remained somewhat higher than before nuclear tests (see Discussion, section 5.1).

5. DISCUSSION

Nuclear experiments performed on Pacific atolls during the second half of the last century had offered exceptional opportunities to monitor the recovery of completely destroyed marine communities, and this at a *far larger scale* than what could be practically implemented in the context of purely biological studies [4,5,63,64]. And, indeed, the effect of scale on recovery process is admittedly recognized as being of *major importance* [63].

The four main descriptors of the hierarchical organization of species within the monitored marine gastropod community – namely: *species-richness*, *crude* and *standardized abundance unevenness* and the *lowest level of species abundance* – all show remarkably strong variations along the progressive recovery of the monitored community. Analyzing these variations, both separately and conjointly, does reveal highly instructive, as regards both:

- *practical concern*: to which degree this marine community proves being *resilient* after its complete destruction and,
- *speculative considerations*, especially in favor of a better understanding of how proceeds (i) the accommodation of an increasing number of recruited species, (ii) the associated (transient) increase of competitive interactions and, finally, (iii) the resulting hierarchic organization of species-abundances, all along the recovery progress. And how the strongly competitive, highly unstable transient stage

of recovery finally gives up, opening the way to a less unstable situation.

5.1 Ecological Interpretations of the Variations of Species Richness, Abundance Unevenness and Lowest Abundance along the Community Recovery

**Species richness* S_t : as compared to the pre-destructing situation (1968), species richness, at first, strongly increases from zero, even rapidly generating a pronounced humpback at years 1974 and 1977, before, finally, tending to stabilization: Fig. 7. The transient, excessively high species richness – up to twice the original level – seems typical of a first stage of colonization (here, re-colonization). Indeed, at the beginning of this first stage, the species-richness is only constrained by abiotic filtering. It is later only that a second filtering process will contribute to dislodge the less competitive species, as a result of the transient severe interspecific-competition triggered by the excessive number of recruited species. So that, finally, the species-richness will strongly decrease – while yet remaining at a moderately higher level than before community destruction – and this for an unknown period. Interestingly, a similar, relatively long-standing improvement in species richness after the recovery following destruction by nuclear experiments was also reported for coral assemblages [64].

**Crude abundance unevenness* U : opposite to species richness, the crude unevenness shows a decreasing trend, as expected from its partially negative dependence upon species richness (see section 3.2.3, Appendix 1 and reference [42]). A decrease, yet, interrupted transitorily by a marked humpback at years 1974 and 1977 (Fig. 8), answering a sharp increase in interspecific competition intensity, as further analyzed below.

**Standardized abundance unevenness* I_{str} : starting from $I_{str} \approx 1$ before destruction (i.e. no significant functional overlaps among species-associated niches resulting in negligible interspecific competition), the standardized unevenness eventually return to almost the same low level ($I_{str} \approx 1.1 - 1.2$), but after a very pronounced humpback ($I_{str} \approx 1.59 - 1.64$), still more prominent than the one observed for species richness at the same period: Fig. 9. In compliance with the functional interpretation attached to standardized unevenness (see section 3.2.3, Appendix 1 and reference [42]),

Fig. 12. Ecological interpretation of the variations in the intensity of interspecific competition (mirrored by the standardized abundance unevenness I_{str} when > 1), driven by the severity of interspecific contests for shared resource at *functional overlaps* among partially intersecting niches. The degree of “functional overlap” depending on both (i) the extent of geometrical overlapping (promoted by *increasing species richness* and the corresponding, overcrowding number of associated niches) and (ii) the density of individuals sharing the same kind of resource at these niche overlaps

this mirrors the brutal onset of an intense interspecific-competition, expected to originate from severe interspecific contests for shared resource at niche overlaps during the period 1974 – 1977, due to the obviously excessive number of newly recruited species, following complete destruction (Fig. 12).

In turn, this severe competition for shared resource likely finds its origin in the concomitant combination of (i) the development of *substantial niche overlaps* between more numerous niches associated to an ever-increasing number of newly recruited species (Fig. 7) and (ii) a clear pic in the overall *density of individuals* at the same time (Fig. 11) which likely triggers harsher interspecific contests at those niche overlaps – which therefore become “strongly functional” overlaps. Additional quantitative support to this qualitative argumentation is provided in following section 5.2.

* *Lowest species abundance a_{st}* : the variations in the relative abundance of the rarest species show an almost perfect mirror symmetry to the trend standing for the standardized unevenness I_{str} described above. This is no surprise since, as already mentioned, the variations of the overall range of species abundance R_a (that is variations in unevenness at a same given species richness, highlighted by I_{str}) are mainly accommodated by a_{st} (rather than a_1): see Appendix 5. From an ecological point of view, the deep trough in the relative abundance of the rarest species, during the period 1974 – 1977, had likely put the subsistence of these rarest species at greater risk, due to their stronger exposure to local dislodgement, arguably resulting from either weaker positioning in the interspecific competitive challenge and/or sensitivity to ‘Allee’ effects. And, indeed, this likely contribute to explain the clear decrease in species richness following year 1977, that is, from 1987 onwards: Fig. 7.

5.2 Disentangling the Respective Contributions to Interspecific Competition of Both the Degree of Niche-Overlap and the Density of Individuals

As already emphasized, the interspecific competition, mirrored by the level of standardized unevenness I_{str} , is expected to increase with both: (i) the degree of geometrical niche-overlap, arguably expected to grow monotonically with the number S_t of co-occurring species and (ii) the average density of individuals at these niche-overlaps, itself mirrored by the overall density D of individuals per unit of area (m^2).

Based on the observed values of I_{str} , S_t and D , a linear regression of I_{str} against S_t and D yields:

$$I_{str} = 0.0794 S_t + 0.1987 D - 0.740 \quad (6)$$

This linear regression not only fairly well complies with *qualitative* expectations regarding the respective, positive, roles of species richness and individuals' density in promoting interspecific competition within community. It further exhibits a fairly good *quantitative* fit with the observed data: Fig. 13. This provides additional *empirical*

support – in now precise *quantitative* terms – to the *rationally expected positive answer* of standardized unevenness I_{str} (accounting for the *intensity of interspecific competition*) upon both:

* the true species richness S_t , as far as species richness is arguably expected to enhance the *degree of geometrical overlap* among increasingly numerous associated niches: *t-test*, $df = 2$, $t = 10.0$, $p = 0.01$ and

* the overall density D of individuals per area unit (m^2), expected to mirror the density of individuals at niche overlaps, triggering stronger interspecific contests therein: *t-test*, $df = 2$, $t = 4.6$, $p = 0.04$.

In other words, this result provides complementary *convincing support* in favor of the *niche-pattern* appraisal of species organization within communities (as opposed, for example, to the readily and purely stochastic view advocated in the so-called "Neutral Theory", at least when the latter theory is considered *stricto-sensu*). But – still more precisely – the result above clearly *complies fairly well* with the conception developed by MACARTHUR, in his seminal paper on the subject [43] (as briefly summarized in section 2 and Appendix 1).

Fig. 13. Comparison between *observed* and *computed* (according to equation (6)) variations of the intensity of interspecific competition (reflected here by the variations of the resulting standardized abundance unevenness I_{str}) as a function of its assumed main drivers: (i) the species richness S_t , promoting niche geometrical overlapping and (ii) the density of individuals D , triggering harsher interspecific contest for shared resource at niche overlaps.

5.3 Resulting Interpretative Overview of the Recovery Process of the Marine Gastropod Community at Fangataufa Atoll

The recovery process following complete destruction had involved a re-colonization of the site (recruitment of a new set of species from the neighboring regional pool) which turned out to aggregate significantly more numerous species than before destruction. With, as a result, an expected increase in the degree of niche-overlaps, triggering in turn, harsh interspecific contests for shared resource at niches overlaps and, consequently, intense interspecific competition, mirrored by the sharp increase of the standardized abundance unevenness I_{str} , reaching values largely in excess of unity.

In 1972, the species richness had already significantly exceeded its original level (Fig. 7), but the intensity of competition (as mirrored by I_{str}) had not much increased yet (Fig. 9). This is because the recovery of individuals' density remained still weak by 1972, well below its original value (Fig. 11) and, therefore, still does not generate significant contest for shared resource at, yet, already important niche geometrical overlaps.

However, two years later, in 1974, the density of individuals had now markedly increased, almost reaching its original value (Fig. 11), so that a high level of interspecific contest for shared resource is now expected to occur within niche overlaps, thereby causing a sharp increase in interspecific competition, as suggested by I_{str} now strongly exceeding unity: I_{str} reaching 1.64 by 1974 (Fig. 9).

Three years later, in 1977, species richness had still slightly increased (Fig. 7), as is likely the case for the associated degree of niche-overlap. But individuals' density had markedly fallen down, presumably due to the onset of the severe interspecific competition as soon as 1974 (Fig. 11). Accordingly, the intensity of interspecific competition had begun to (still very slightly) decrease, yet remaining at a still high level ($I_{str} = 1.59$ by 1977: Fig. 9).

This rather strong interspecific competition intensity, during the period 1974 – 1977, should subsequently lead both (i) to a further decrease in the density of individuals and, thereby also (ii) to an increasing exposure of the rarest species to progressively higher risks of disappearance. So

that the resulting expected decrease of species richness S_t , and the additional decrease of individuals' density D , now both contribute to the strong decrease of competition intensity. A decrease indeed highlighted by the standardized unevenness I_{str} falling down spectacularly from 1.59 to 1.13, ten years later, in 1987 (Fig. 9). So that, by 1987, 17 years after the last nuclear testing, the interspecific competition at niche overlaps had seriously weakened, almost returning back to the original situation, before nuclear experiments. But with species richness (partly inherited from the active recruitment at the first stage of recolonization) still remaining substantially higher than it was originally, in 1968 (Fig. 7).

Thus, although competition intensity had finally cancelled down (almost recovering its original sub-null value, after having reach transient very high levels during the first ten years following the full destruction of the community), the new situation, from 1987 onwards, still markedly differs from the original one. Part of the numerous newly recruited species had finally escaped the elimination by the harsh, transient interspecific competition during the 1974-1977 period and thus could subsequently subsist in the following period, thanks to the vanishing of competitive contest mainly due to still decreasing level of overall density of individuals, which remains now substantially weaker than it was before the destruction of the community (Fig. 11).

A new kind of *pseudo-equilibrium*, from 1987 onwards, thus seems to replace the original one, established before nuclear tests. While both (pseudo-) equilibria (before tests and after 1987) are likely maintained by a reduced (if not nil) level of interspecific competition ($I_{str} \approx 1$), these two kinds of equilibria significantly differ from each other as regards the way this reduced competitive intensity is obtained. Prior to destruction, it is the relatively *low species richness* which likely prevents niches intersections and geometrical overlaps, thereby avoiding any source of contest among co-occurring species, in spite of a relatively high density of individuals. On the contrary, after the transient period of recovery 1974-1977, it is now the relatively *low density of individuals* which reduces, if not avoids, interspecific contest among co-occurring species, in spite of possibly subsisting niches overlaps due to species richness remaining significantly higher than originally. These potentially subsisting geometrical-overlaps thus becoming "non-

functional", due to the now low density of individuals.

However, it may seem that rendering niche overlaps 'non-functional' in this way (by reducing the density of individuals rather than by suppressing niche overlaps themselves, as originally, before destruction of the community), could lead to a less stable situation than the one prevailing before nuclear tests. Indeed, comparing species lists between 1987 and 1997 shows an *important turn-over* in species composition during this time interval, with most of rarest species in 1987 (viz *Strombus maculatus*, *Imbricaria conovula* and *Cypraea moneta*) having still more or less further decline, or even disappear by 1997, likely due to their very low absolute densities. While another species, *Patella flexuosa*, still rare in 1987, had yet strongly increased in 1997, possibly being in process of restoring its dominant, likely more stable, original position in 1968.

6. CONCLUSION

The reported accounts, by LANCTÔT, LEGENDRE & SALVAT [4,5] of the recovery of a reef-associated gastropod community after a series of drastically destructive nuclear tests, had cast important light on the process of natural recolonization of the impacted site. Yet some important additional enlightenements have been provided, here, thanks to:

- (i) considering *numerically extrapolated* samplings – rather than basing only of the incomplete available samplings – which has highlighted to what extent considering numerically completed data (in terms of not only true species richness but also completed species abundance distribution including undetected species) can deeply modify the appraisal of the process of recovery, thereby leading to more representative description and, especially, more sound and relevant interpretations;
- (ii) making use of the notion of "*standardized*" *abundance unevenness*, rather than traditionally considering crude unevenness only. *Standardized unevenness* allows a more relevant appreciation of the *socio-ecological significance of the uneven distribution of species abundances* within community and, here also, favors more relevant interpretations of how increasing species is accommodated and how the hierarchic organization of species within

community actually proceeds – dealing first with *abiotic constraints* only and, subsequently, with additional *biotic mutual interactions* eliciting more or less transient interspecific competition. Disentangling from each other these two main kinds of contributions to the uneven distribution of species abundances within species assemblages highlights the considerable advantage of *partitionning* the crude abundance unevenness in terms of its two complementary multiplicative contributions: (i) the *species richness-related part* on the one hand (relevantly conveyed by the corresponding broken-stick unevenness U') and (ii) the *standardized unevenness* " I_{str} ", thus made formally independent of species-richness, on the other hand.

At last, as a highly significant by-product of this approach, *strong empirical support* (see Figs. 12, 13 & Fig. A.1) has been provided to the MACARTHUR *original conceptions*, regarding the source and the ecological explanation of species-abundance unevenness within communities, as being directly related to the patterns of the niche-associated display. With the *broken-stick* model – characterising (sub-) nul competitive intensity – no more serving as *the* universal model for species abundance distributions (as originally wrongly thought by MACARTHUR) but, quite more relevantly, offering a *useful benchmark*, against which to compare crude abundance unevenness – thereby offering a new, convenient approach for the estimation of the intensity of interspecific competition for shared resource at niche overlaps.

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COMPETING INTERESTS

Author has declared that no competing interests exist.

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APPENDIX 1

About the relevance of the ecological interpretation, by MACARTHUR, of niches-display patterns and the associated species-abundance distribution

The role of the “broken-stick” distribution as a model apt to be almost universally fitted by most (if not all) empirical Species Abundance Distributions – as originally suggested by MACARTHUR [43] (1957) has been largely refuted subsequently and its inadequacy in this particular respect has been recognized later on by MACARTHUR himself [65]. Some doubt has also been cast by a few authors as regards the association of the “broken-stick” model to the “contiguous non-overlapping niches” pattern, stated by MACARTHUR [43]. The issue is, admittedly, a complex matter, not so easy to decide from a purely theoretical point of view. Yet, growing *empirical evidence* now accumulates to support the “broken-stick” distribution as being *clearly central*, when considering how co-occurring species do structure their relative abundances within natural communities.

A first aspect of this growing empirical evidence is presented in Fig. A.1, established using data from 37 tropical, marine communities (the present study and data from references [37, 53-62]). Although not being a full demonstration, this piece of evidence looks rather convincing, when considering both:

- (i) the remarkable parallelism between the broken-stick unevenness $U'(S_t)$ and the overall trend for decrease of the crude unevenness U with species richness S_t and
- (ii) more precisely, the position of $U'(S_t)$ as a “baseline” for the distribution of crude unevenness values U for the 37 marine communities – a basal position which fairly well complies with the conception of the ‘broken-stick’ distribution as resulting from the “contiguous, non-overlapping niches” pattern, proposed by MACARTHUR [43]. This indeed provides strong support to the functional significance of the broken-stick distribution [66] and, accordingly, gives credit to the relevance of considering the broken-stick abundance unevenness $U'(S_t)$ and the related standardized unevenness index I_{str} , as appropriate tools to provide functional, ecologically sound, interpretations of the Species Abundance Distribution within natural communities.

Fig. A1. Species abundance unevenness $U = \log_{10}(a_1/a_{St})/(S_t-1)$ in 37 marine communities (grey discs) – and for comparison the computed abundance unevenness $U'(S_t)$ for the ‘broken-stick’ distribution (double line) – both plotted against species richness S_t .

Fig. A2. The “broken-stick” distribution (here for species richness $St = 60$: *double line*) fits reasonably well the log-normal distribution computed, for the same species richness, with a particular standard deviation = 0.46 (*dotted curve*)

APPENDIX 2

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 [5,6,73-76]):

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

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 [5]:

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

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

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

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

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

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

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

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

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

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

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

N.B. 1: As indicated above (and demonstrated in details in [5]), 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 [27,29,77-81]. Also, this shows that the approach initially proposed in [82] – 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 [27,29,77-81], but, now, a *rationaly 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 $0.6 \times f_2$ (that is when sampling completeness closely approaches exhaustivity), then Chao estimator may alternatively be selected: see reference [6].

APPENDIX 3

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 [7].

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:

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

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 $i > R_0$):

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

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 2.

APPENDIX 4

Derivation of the expression of the abundance unevenness $U'(S_t)$ of the broken-stick distribution

The derivation of the expression for $U'(S_t)$ proceeds from reference [31] by MAY. In his Table 3, within reference [31], MAY defines the dominance 'd' in the broken-stick distribution as $d = \ln(S_t)/S_t$ (at least for S_t not too low, say > 10). As the dominance is defined as the higher relative abundance, namely a'_1 in the broken-stick, it comes:

$$a'_1 = \ln(S_t)/S_t$$

Then, 'J', the inverse of the lowest relative abundance a'_{S_t} (his equations (1.1)) is identified to S_t^2 (his equation (D.6)), so that:

$$a'_{S_t} = 1/S_t^2$$

And thus:

$$\begin{aligned} a'_1/a'_{S_t} &= [\ln(S_t)/S_t] / (1/S_t^2) = S_t \cdot \ln(S_t) \\ \text{Accordingly, from the definition of } U'(S_t): \\ U'(S_t) &= \log_{10}(a'_1/a'_{S_t}) / (S_t - 1) \\ \text{it comes finally:} \\ U'(S_t) &= (\log_{10}[S_t \cdot \ln(S_t)]) / (S_t - 1) \end{aligned}$$

APPENDIX 5

Demonstration that the overall range R_a of species abundances is strongly related to the level of the lowest abundance a_{St}

For the purpose of demonstration, let consider an assemblage of species with a species abundance distribution ideally fitting a geometric series with a constant ratio 'k' = a_i/a_{i+1} between two successive species, i and i+1, ranked by decreasing values of abundance. It comes, for the most and the least abundant species a_1 and a_{St} :

$$a_1 = (k^{St} - k^{St-1}) / (k^{St} - 1) \quad \text{and} \quad a_{St} = (k - 1) / (k^{St} - 1) \quad (A1)$$

Then:

$$\partial a_1 / \partial S_t = - (k - 1) \cdot k^{St-1} \cdot \ln(k) / (k^{St} - 1)^2 \quad (A2)$$

$$\partial a_{St} / \partial S_t = - (k - 1) \cdot k^{St} \cdot \ln(k) / (k^{St} - 1)^2 \quad (A3)$$

And

$$\partial \ln(a_1) / \partial S_t = (1/a_1) \cdot \partial a_1 / \partial S_t = - \ln(k) / (k^{St} - 1) \quad (A4)$$

$$\partial \ln(a_{St}) / \partial S_t = (1/a_{St}) \cdot \partial a_{St} / \partial S_t = - k^{St} \cdot \ln(k) / (k^{St} - 1) \quad (A5)$$

Thus:

$$\partial \ln(a_{St}) / \partial S_t = k^{St} \cdot \partial \ln(a_1) / \partial S_t \quad (A6)$$

As soon as $k > 1$, k^{St} rapidly exceeds unity, considering usual values of species richness S_t . It follows that $\ln(a_{St})$ decreases *much faster* with species richness than does $\ln(a_1)$. In practice, as soon as $k > 1.07$, $\ln(a_1)$ remains substantially constant while $\ln(a_{St})$ steadily decreases rapidly with increasing species richness.

Picture 1. [A] -*Turbo setosus* Gmelin, 1791 © Ph. Bourjon

Picture 2. [A]. *Morula uva* Röding, 1798 © Femorale

Picture 3. [A]. *Mitra litterata* Lamarck, 1811 © Ph. Bourjon

Picture 4. [A] . *Conus sponsalis* Hwass in Bruguière 1792 © Alex Medvedev

Picture 5. [A] . *Conus miliaris* Hwass in Bruguière 1792 © Ph. Bourjon

Picture 6. [A]. *Drupa ricinus* Linnaeus, 1758 © David Lum

Picture 7. [B] . *Patella flexuosa* Quoy & Gaimard 1834 © Jan Delsing

Picture 8. [C] . *Nerita plicata* Linnaeus, 1758 © D. Massemin MNHN

Picture 9. [C]. *Monetaria moneta* Linnaeus 1758 © Phillip66

Picture 10. [D]. *Drupa morum* Röding, 1798 © Femorale

Picture 11. [D]. *Tectarius grandinatus* Gmelin, 1791 © Raymond Huet

Picture 12. [D]. *Cerithium echinatum* Lamarck, 1822 © Ph. Bourjon

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