1	On general mathematical constraints applying to the kinetics
2	of species discovery during progressive sampling: <mark>consequences</mark>
3	on the theoretical expression of the Species Accumulation Curve
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11	ABSTRACT
12	The "Species Accumulation Curve" accounts for the rate of increase of the number of
13	recorded species during progressive sampling of an assemblage of species. Due to the usual
14	incompleteness of samplings, the accurate extrapolation of the Species Accumulation Curve
15	has become an essential tool to estimate the total species richness of a sampled assemblage
16	and to predict the additional sampling effort required to obtain a given increase of sample
17	completeness. In this perspective, important efforts have been devoted to improve the
18	accuracy of the extrapolation of the Species Accumulation Curves. Substantial progressin
19	this respect was achieved recently by considering a general mathematical relationship that
20	constrainstne theoretical expression of any kind of Species Accumulation Curves. Moreover,
21	this general relationship proves having interesting corollaries applying specifically to the
22	detuiled process of species accumulation during progressive sampling.
23	together the variations of the numbers of energies respectively recorded 1, 2, 2, w
24 25	timesand their cumulative contributions to the Species Accumulation Curve. This in turn
25	provides suggestive insights regarding the remarkably regulated mechanism of species
20	discovery and accumulation during progressive sampling effort
27	uiscovery und decamatation <mark>daring</mark> progressive sampning effort.
29	Key-words: species discovery curve collector curve extrapolation estimation species
30	richness incomplete sampling regulation lackknife estimator
31	nemess, meemprete sampning, regulation, jaennine estimator
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34	1. INTRODUCTION
35	The process of continuous discovery of new species during progressive sampling of an
36	assemblage of species is expressed graphically in term of the so called "Species
37	Accumulation Curve", also formerly designed as "Discovery Curve" or "Collector Curve"
38	[1, 2]. The Species Accumulation Curve is the basic tool which is systematicallyreferred
39	to <mark>when dealing with</mark> inventories of biodiversity [<mark>2 to 8</mark>].
40	Species Accumulation Curves are quite polymorphic,apart from some commonbasic and
41	intuitive traits shared by all of them (monotonic increase of the number of recorded
42	species with sampling size, at consistently decreasing rate, see Figure 1 for an
43	example) This polymorphism of the detailed shapeof the Species Accumulation
44	curves results from its narrow dependence upon the particular species abundance
45	distribution within the sampled assemblage of species under consideration. Accordingly,
46	there are virtually as many different snapes of Species Accumulation Curves as there are

47 species assemblages differing from each other by either theirspecies richness48 and/ortheir particular distribution of species abundances.

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Figure 1 – Typical shape of aSpecies Accumulation Curve (S.A.C.), showing the basic common features pertaining to any kind of S.A.C.: monotonic increase of the number of recorded species R(N) with sampling size N, while the rate of growth is monotonically decreasing.Here is plotted the S.A.C for a partial inventory of land snails fauna in a xerothermic grassland at 'Cersot', south Burgundy (France) [from BÉGUINOT, *unpublished data*].Samplingsize is expressed in % of the size of the actually achieved sampling.Extrapolationis predicted according to Jackknife-5 estimator, selected as being the less biasedestimator for this particular inventory(see reference [9]).

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59 In spite of these causes of polymorphism, the theoretical expressions of all Species Accumulation Curves are compelled to satisfy a common constraining mathematical 60 relationship which applies to the whole series of its successive derivatives. 61 Thisconstraining relationship explicitly determines the boundaries of the yet wide range 62 of polymorphismmentioned above for the Species Accumulation Curves.On a more 63 64 practical point of view, accounting for this constraining relationship also has major importance to *improve the accuracy of extrapolations* of the species accumulation process 65 beyond actually achieved sampling. Thereby, more preciseestimations of total species 66 richness and more reliable predictions of the additional sampling effort needed to 67 achieve a given increase in sample completeness are made possible (details inreference 68 **[9]**). 69

Now, coming back to more *theoretical* ground, severalcorollaries which can be derived
from this fundamental relationship also provide useful insights into the details of the
complex process of species discovery during progressive sampling.

Let R(N) be the number of recorded species after sampling of N individuals (N thus quantifies the sampling size). Obviously, R(N) results from the additive contributions of the numbers $f_1(N)$, $f_2(N)$, $f_3(N)$,..., $f_x(N)$,... of those species respectively recorded 1, 2, 3, ..., x-times at the end of this sampling of size N:

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$R(N) = \Sigma_x f_x(N) \qquad (1)$

Thereby, the Species Accumulation Curvereveals its "*composite*" dependence upon the whole series of the $f_x(N)$. Acomposite dependence which is made still more complex by the fact that each function $f_x(N)$ has its own dependence upon N. Yet, this mutual independence of the $f_x(N)$ is not total:a kind of regulation links, step by step, the respective variations of the successive functions $f_x(N)$, as will be shown later. This regulation, indeed, is at the hearth of the mechanism of species progressive discovery and accumulation, which plays,of course, a decisive role in shaping the Species Accumulation Curve.

The main purpose of this article is precisely to highlight the mathematics underlying this regulation by mutual linkage between the successive $f_x(N)$. This, in turn,will provide a more deep understanding of the fundamentals of Species Accumulation process during progressive sampling.

90 Indeed, deriving the mathematical constraints that actually regulate the theoretical expressionofany Species Accumulation Curvesalong progressive sampling, is obviously of 91 92 prime importance, not only at the theoretical level but also at more practical points of view. In particular, accounting for these mathematical constraints is necessary to 93 reliably extrapolate the Species Accumulation Curve beyond the actually achieved 94 95 sampling size of uncomplete species inventories. Extrapolation makes it possible to accurately estimate the total species richness of partially-sampled species assemblages 96 97 and also to properly predict the level of additional sampling effort needed to improve the degree of sampling completeness. And this is all the more important, in practice, that 98 dealing with incomplete inventories is now fast becoming a fairly general issue for an 99 100 increasing part of local or regional biodiversity surveys worldwide, as more and more 101 speciose and complex taxonomic groups are progressively addressed.

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2. METHODOLOGICAL APPROACH

104 The fundamental mathematical relationship constraining the theoretical expression 105 of all Species Accumulation Curves

106 The successive derivatives $\partial^{x} R(N) / \partial N^{x}$, of the Species Accumulation Curve R(N) satisfy 107 the following equation:

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$[\partial^{x} R_{(N)} / \partial N^{x}] = (-1)^{x-1} f_{x(N)} / C_{N,x}$ (2)

109 where $f_{x (N)}$ is the number of species recorded x-times in the sample of size N and $C_{N, x} = N!/X!/(N-x)!$ is the number of combinations of x items among N. A detailed proof of this 111 general theorem is provided in Appendix.

Leaving aside the very beginning of sampling (of no practical relevance here), the sampling size N rapidly widely exceeds the numbers x of practical concern, so that, in practice, the preceding equation simplifies as:

$$[\partial^{x} R_{(N)} / \partial N^{x}] = (-1)^{x-1} (x! / N^{x}) f_{x(N)}$$
(3)

This relation has *general relevance* because its derivation does not require any specific assumption relative to the particular shape of the distribution of species abundances the sampled assemblage of species. Accordingly,equations (2), (3) actually constrain the theoretical expressions of *any kind* of Species Accumulation Curves.

120 One particular consequence of this relationship is that the successive derivatives of the 121 Species Accumulation Curve have alternating signs, since the numbers $f_{x (N)}$ of species 122 recorded x-times are necessarily positive or nil. More precisely, the derivatives of even 123 and odd orders are respectively negative and positive.

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3. THE MATHEMATICS UNDERLYING THE REGULATION PROCESS APPLYING TO THE NUMBERS f_x OF SPECIES RECORDED x-TIMES

127 From equation (3) it comes:

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$f_{x(N)} = (-1)^{x-1} (N^x/x!) [\partial^x R_{(N)}/\partial N^x](4)$

- 129 The derivation of equation (4) according to sample size N then gives:
- 130 $[\partial f_{x(N)}/\partial N] = (-1)^{x-1}/x! \{x.N^{x-1}.[\partial^x R_{(N)}/\partial N^x] + N^x.[\partial^{x+1}R_{(N)}/\partial N^{x+1}] \}$
- 131 Accounting for the expression (3),applied to $[\partial^x R_{(N)}/\partial N^x]$ and $[\partial^{x+1}R_{(N)}/\partial N^{x+1}]$, it comes:
- 132 $[\partial f_{x(N)}/\partial N] = (1/N) [x.f_{x(N)} (x+1).f_{x+1(N)}]$ (5)

133 which may be written as well as:

 $x.f_{x(N)}-N.[\partial f_{x(N)}/\partial N] = (x+1).f_{x+1(N)}$ (6)

Note that an alternative, independent demonstration of equation (6) is provided atAppendix A.2, equation A2.1.

Being a corollary of relationship (3) above, equation (6) thus benefits from thesame*general relevance* and, thus, is valid for *all kinds* ofSpecies Accumulation Curves.

Equation (6) establishes a*mathematical linkage* between the variations of f_{x+1} (N) with N and the variations of f_{x} (N) with N. Thereby, all the f_{x} (N) are ultimately *linked together* by this "iterative chaining". In other words, although each function f_{x} (N) has its own dependence upon sampling size N, the series of f_{x} (N) nevertheless admitsa kind of connection which, if one may say, "propagates" from each f_{x} (N) to the next one, f_{x+1} (N).

145 Mathematical "chaining" between the successive numbers $f_{x(N)}$

146 The consequence of this regulation may be more easily grasped graphically, by 147 considering how the maximum of each $f_{x (N)}$ is linked to the value taken by $f_{x+1 (N)}$ at the 148 same sample size N.When $f_{x(N)}$ reaches its maximum value, its first derivative, $\partial f_{x (N)}/\partial N$, 149 falls to zero and, accordingly, from equation (6), it comes:

(7)

$$f_{x+1(N)} = [x/(x+1)].f_{x(N)}$$

Thus, when $f_{x(N)}$ reaches its maximum, in the course of progressive sampling, the corresponding value taken by f_{x+1} (N) is then exactly [x/(x+1)] times the (maximum) value taken by f_{x} (N). By reiteration of this relationship, akind of "linkage pattern" is generated, that constrains the relative locations of the successive curves $f_{x(N)}$. Figure 2 exemplifies graphically this "chaining" linkage, *propagating successively,step by step*, from f_{1} (N) to f_{2} (N), to f_{3} (N), to f_{4} (N), to f_{5} (N), etc...

As a consequence, the respective maxima of $f_{1 (N)}$, of $f_{2 (N)}$, of $f_{3 (N)}$, of $f_{4 (N)}$, of $f_{5 (N)}$, ..., succeed each other sequentially, as shown in Figure 2. The corresponding positions of these succeeding maxima are located along the Species Accumulation Curve at Figure 3, and it is worth noting (and even remarkable) that the regulating linkage between the successive $f_{x (N)}$ is such that no peculiarity is affecting the Species Accumulation Curve at any of these locations (in spite of the series of bumps constituted by the successive maxima of $f_{1 (N)}$, $f_{2 (N)}$, $f_{3 (N)}$, $f_{4 (N)}$, $f_{5 (N)}$,...).

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Figure 2 – Extrapolations of the five first numbers $f_{x (N)}(f_{1 (N)}, f_{2 (N)}, f_{3 (N)}, f_{4 (N)}, f_{5 (N)})$ along increasing 166 sampling size N, beyond the size of the actually achieved sampling(sampling size N is expressed in % 167 168 of the size of the actually achieved sampling). Here, the maxima of $f_{1(N)}$, $f_{2(N)}$, $f_{3(N)}$, $f_{4(N)}$, $f_{5(N)}$ happen to 169 be located at sample size ≈ 200%, 360%, 510%, 680%, 810%, respectively. Same inventory as in Figure 170 1; extrapolations according to Jackknife-5 estimator, selected as being the less biased for this particular inventory(see reference[9]). This figure highlights the "linkage pattern" between the 171 172 successive curves $f_{x(N)}$, imposed by the constraining relationship (7) (i.e.: $f_{x+1(N)} = [x/(x+1)].f_{x(N)}$). That is when $f_{x(N)}$ reaches its maximum, the corresponding value taken by $f_{x+1(N)}$ is then exactly [x/(x+1)]173 174 times the value of $f_{x(N)}$.

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176 Mathematical "chaining" between the successive numbersx. $f_{x(N)}$

177 Alternatively, equation (7) may be written equivalently as:

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$$x.f_{x(N)} = (x+1).f_{x+1(N)}$$

Equation (8), as equation (7), stands for $\partial f_{x(N)}/\partial N = 0$, and thus stands as well for $\partial (x.f_x _{(N)})/\partial N = 0$. It follows that the curve $(x+1).f_{x+1(N)}$ intersects the curve $x.f_{x(N)}$ exactly when the latter reaches its maximum value (i.e. when $\partial (x.f_{x(N)})/\partial N = 0$) : Figure 4. Keeping in mindthe significance of $x.f_{x(N)}$, which is the total number of recorded individuals belonging to any one of those species recorded x-times.

(8)



Figure 3–The locations, along the Species Accumulation Curve, of the successive maximum of $f_{1 (N)}$, f_{2}

- 187 (N), $f_{3(N)}$, $f_{4(N)}$, $f_{5(N)}$, according to Figure 2.Same inventory as in Figure 1.
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Figure 4 - The computed variations, with increasing sampling size N, of the five first numbers $x.f_{x (N)}$ of recorded individuals belonging to any one of species recorded x-times $(1.f_{1 (N)}, 2.f_{2 (N)}, 3.f_{3 (N)}, 4.f_{4 (N)}, 5.f_{5 (N)})$. As prescribed by the constraining equation (8), for any value of x, the curve $(x+1).f_{x+1 (N)}$ intersects the curve $x.f_{x (N)}$ exactly when the latter reaches its maximum value. Samplingsize is expressed in % of the size of the actually achieved sampling.Same inventory as in Figure 1.

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196 The regularly repetitive shift from any one curve, $x.f_{x (N)}$, to the next one, $(x+1).f_{x+1 (N)}$, 197 resulting from this regulating process (Figure 4) is particularly demonstrative. This, 198 indeed, likely offers the best visual evidence of the sequential linkage existing between 199 each of the numbers $f_{x (N)}$ successively.

Note, incidentally, that while the cumulative addition of all the $f_{x (N)}$ leads to the number R(N) of recorded species (*cf.* equation (1)); on the other hand the addition of the $x.f_{x (N)}$ leads "symmetrically" to the number N of recorded individuals:

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$$\Sigma_x [f_x(N)] = R(N) \text{ and } \Sigma_x [x.f_x(N)] = N$$
 (9)
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Mathematical "chaining" between each $f_{x(N)}$ and the series of the first derivatives 205 of the preceding $f_{x(N)}$ 206 This is a third alternative way to express the inter-relationship within the series of the 207 $f_x(N)$. Referring once more to equation (6), that is: 208 $x.f_{x(N)} - N.[\partial f_{x(N)} / \partial N] = (x+1).f_{x+1(N)}$ 209 210 letnow consider the successive forms taken by this equation for increasing values of x. It comes: 211 212 $0.f_{0(N)} - N.[\partial f_{0(N)} / \partial N] = 1.f_{1(N)}$ $1.f_{1(N)} - N.[\partial f_{1(N)} / \partial N] = 2.f_{2(N)}$ 213 $2.f_{2(N)} - N.[\partial f_{2(N)}/\partial N] = 3.f_{3(N)}$ 214 215 $(x - 1).f_{x-1(N)} - N.[\partial f_{x-1(N)}/\partial N] = x.f_{x(N)}$ 216 217 By summing these equations, the following relationship is immediately derived: $f_{x(N)} = -(N/x) \sum_{i} [\partial f_{i(N)}/\partial N]$ 218 (10)219 with the summation Σ_i extended from i = 0 to i = (x - 1) That is, namely, the number $f_{x(N)}$ of species recorded x-times in a sampling of size N is 220 proportional [via the factor- (N/x)] to the sum of the first derivatives (with respect to N) 221 222 of the series of the preceding $f_{i(N)}$. In more practical terms, this means that the number f_x 223 (N) of species recorded x-times, in a sample of size N, is proportional to the sum of the variations of the preceding $f_{x(N)}$ when sampling size increases of one observation (N \rightarrow 224 225 N+1). Another way to understand relation (10) results from re-writing it as follows: 226 227 $(x.f_{x(N)})/N = -\Sigma_i [\partial f_{i(N)}/\partial N]$ (11)with the summation Σ_i extended from i = 0 to i = (x – 1). 228 This means that the proportion, among all sampled individuals, of those ones that belong 229 to any species recorded x-times $[= (x.f_{x (N)})/N]$ is equals to minus the sum of the 230 variations of the preceding $f_{x(N)}$ when sampling size increases of one observation. 231 232 Accordingly, relationships (10) or (11) both express, once again but in another way, the continuous linkage between each $f_{x (N)}$ and the *whole series of its predecessors*, thereby 233 highlighting still more clearly the strong "chaining" between the successive numbers f_x 234 (N), which together rule the kinetics of species accumulation during progressive 235 sampling. 236 237 Still another remarkable relationship may be derived from equation (10), which only 238 involves, this time, the first derivatives of all the $f_{x(N)}$. Let X be the recorded number of individuals belonging to the species most frequently met 239 in the sampling under consideration. In other words, X is the largest value of x for which 240 $f_{x(N)} \neq 0$ in this particular sampling. The sum of the numbers of sampled individuals that 241 belong to anyone of those species recorded x-times $[=(x.f_{x(N)})]$ for x up to its maximum 242 243 value X is equal to N. Accordingly, the summation of equation (11) for x up to its maximum value X yields: 244 $\Sigma_{x} \left[(x.f_{x(N)})/N \right] = N/N = 1 = \Sigma_{x} \left[-\Sigma_{i} (\partial f_{i(N)}/\partial N) \right]$ 245 with the summation Σ_x extended from x = 1 to x = X and the summation Σ_i extended from 246 i = 0 to i = (x - 1). This finally leads to: 247 248 $1 = -\Sigma_{i}[(\partial f_{i(N)}/\partial N).(X-i)]$ (12)249 with the summation Σ_i extended from i = 0 to i = (X – 1). 250 251

4. COMPLEMENTARY ILLUSTRATIVE EXAMPLES OF THE REGULATION PROCESS GOVERNING THE NUMBERS OF SPECIES RECORDED 1-, 2-, 3-, 4-, 5 ,...TIMES

The same trends demonstrated above on a theoretical basis, and illustrated by a first example at Figures 2 to 4, are illustrated again in the following complementary examples. I shall only consider,hereafter, the variations of $x.f_{x}$ (N) (i.e. the number of recorded individuals belonging to any one of species recorded x-times) as they provide the more graphically speaking feature, highlighting at bestthe specific"chaining" linkage, step by step, between the successive numbers f_1 (N), f_2 (N), f_3 (N), f_4 (N), f_5 (N).

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4.1. Butterfly inventory on the slopes of MountGariwang-san (S-Korea)

Field data from reference [10]. Figure5 relates to an inventory carried out during year 265 2015. The realised sampling size was $N_0 = 181$ individuals; the number of recorded 266 species was $R(N_0) = 39$ species and the values of the f_{x_x} were: $f_1 = 17.0$, $f_2 = 8.0$, $f_3 =$ 267 3.7, $f_4 = 2.0$, $f_5 = 1.4$ (values obtained after regression applied to the crude values of the f_{x_x} 268 in order to reduce the consequences of stochastic dispersion, as prescribed in [9]. 269



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Figure 5 - The computed variations, with increasing sampling size N, of the five first numbers $x.f_{x (N)}$ of recorded individuals belonging to any one of species recorded x-times $(1.f_{1 (N)}, 2.f_{2 (N)}, 3.f_{3 (N)}, 4.f_{4 (N)}, 5.f_{5 (N)})$. Butterfly inventory on the slopes of Mount Gariwang-san (field data from reference [10]). As prescribed by the constraining equation (8), for all values of x, the curve (x+1).f_{x+1 (N)} intersects the curve $x.f_{x (N)}$ exactly when the latter reaches its maximum value.Samplingsize is expressed in % of the size of the actually achieved sampling.

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278 **3.2 Butterfly inventories at Bifeng Valley (Ghansu, China)**

Field data from reference[11]. Figure 6 relates to an inventory conducted at site 1, in the upper part of the valley of Bifeng (province of Ghansu), where species richness of butterfly fauna proves to be the highest in the valley, with $R(N_0) = 28$ recorded species for $N_0 = 68$ recorded individuals. The values of the f_x , were: $f_1 = 14.0$, $f_2 = 6.0$, $f_3 = 2.6$, $f_4 = 1.5$, $f_5 = 1.2$ (values obtained after regression applied to the crude values of the f_x , in order to reduce the consequences of stochastic dispersion, as prescribed in [9].



Figure 6 - The computed variations, with increasing sampling size N, of the five first numbers $x.f_{x (N)}$ of recorded individuals belonging to any one of species recorded x-times $(1.f_{1 (N)}, 2.f_{2 (N)}, 3.f_{3 (N)}, 4.f_{4 (N)},$ 5. $f_{5 (N)})$. Butterfly inventory at Bifeng valley, site 1 (field data from reference [11]). As prescribed by the constraining equation (8), *for all values of x*, the curve (x+1). $f_{x+1 (N)}$ intersects the curve $x.f_{x (N)}$ exactly when the latter reaches its maximum value.Samplingsize is expressed in % of the size of the actually achieved sampling.

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5. THE GENERAL RELATIONSHIP GOVERNINGTHE DECREASING **PROPORTION** OF OBSERVATIONS PROVIDING NEWLY RECORDED SPECIES, WITH INCREASING SAMPLING SIZE

So far, we have approached the Species Accumulation Curve,R(N), in a deliberately analytical manner: each new observation was considered as equally informative, whether or not it gives rise to the detection of a new species. Indeed, in any case, each individual observation actually plays the same kind of role: it determines a transition of the kind $f_x(N) \rightarrow f_{x+1}(N+1)$.

Now, letconsider,*alternatively*, a more usual and pragmatic approach, now payingattention to those observations *only* giving rise to the detection of a new species and neglecting, accordingly, all the other observations (in spite of their equal role in the analytical approach considered above). In this purely "accounting" approach, the focus is put on the proportion p(N) = R(N)/N of those observations exclusively, which have provided positive records of new species. In other words, instead ofpaying attention to $R(N) = \Sigma_x f_x(N)$, as previously, the focus is placed now upon:

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R(N) = N.p(N) (13)

This proportion p(N) is pragmatically interesting in that it quantifies the gradual weakening of sampling efficiency, i.e. the ever-slowing rate of detection of newly recorded species, as sampling is going on further.

As for the Species Accumulation Curve, the proportion p(N)of those observations providing positive records of new speciesis highly polymorphic and this polymorphism,

here also, is limited by a constraining relationship applying to the expression of p(N).



352 **6. DISCUSSION**

Fivemain features are emerging from the theoretical treatment (and the corresponding illustrative examples), regarding the variations,with sampling size N, of the numbers $f_x(N)$ of species respectively recorded x-times during sampling. It should bewell understood that these features, all derived on theoretical basis, are *focal tendencies*, towardswhich the empirical data, obtained from real samplings, actually converges (but may yet more or less slightly deviate, due to sampling stochasticity).

359 Twotrendswere expected, being in obvious*accordance with intuition*:

1) all the numbers $f_{x (N)}$ of species recorded x-times are first increasing, then pass by a maximum and finally decrease to zero.Also, in addition, the curves describing the variations of each $f_{x (N)}$ (and the positions of their respective maxima) are regularly shifted towards higher values of sampling size N, when x takes increasing values (Figure 2);

365 2) thesame holds true, *mutatis mutandis*, for the numberx. $f_{x (N)}$ of those recorded 366 individuals belonging to anyone of species recorded x-times, whatever the value of x.

Now, three other trends, *by no means intuitive*, were newly derived above, related to the general mathematical relationship (6) which constrains the expressions and shapes of the $f_{x(N)}$:

370 3) when $f_{x(N)}$ reaches its maximum, in the course of progressive sampling, the 371 corresponding value taken by $f_{x+1}(N)$ is then exactly [x/(x+1)] times the maximum value 372 taken by $f_{x(N)}$ (see Figure 2);

4) regarding now the number $x.f_{x (N)}$ of recorded individuals belonging to anyone of those species recorded x-times, it consistently happens that the curve describing the variations of $(x+1).f_{x+1 (N)}$ intersects the curve of $x.f_{x (N)}$ exactly when the latter reaches its maximum value (see Figures 4, 5, 6);

5) at last, the number $f_{x (N)}$ of species recorded x-times in a sampling of size N is proportional to the sum of the variations of the preceding $f_{x (N)}$, when sampling size increases by one observation.

380 The three latter trends have *major importance* in that they determine the "chaining 381 linkage" between the successive numbers $f_{x (N)}$ of species recorded x-times. And this is of 382 importance because the successive numbers $f_{x (N)}$ actually regulate the process of 383 cumulative species discovery during progressive sampling.

- As already stressed, the general mathematical relationship (6)
 - $x.f_{x(N)}-N.[\partial f_{x(N)}/\partial N] = (x+1).f_{x+1(N)}$

which constrains the expressions and the shapes of the $f_{x(N)}$, is a corollary of the general relationship (A2.1), derived in Appendix A.2, which, in turn, constrains the theoretical expressions of all Species Accumulation Curves R(N). Thus, to get a full understanding of the underlying process of species accumulation during sampling, it is advisable to refer to the detailed demonstration leading to equation (A2.1) in Appendix.

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7. CONCLUSION

The increasing number of newly recorded species (i.e. the "species accumulation") during progressive sampling gives rise to a rather simple shaped "Species Accumulation Curve".Paradoxically, this apparent simplicitydoes not incite to imagine the underlying complexity of the detailed process of species discovery and progressive accumulation, as detailed above. In fact, each new individual observation may alternatively result in one or the other of a series of different consequences. More precisely, each observation of a

399	new individual (i.e. N \rightarrow N + 1) will contribute to increase by one unity either f _{1 (N)} , orf ₂
400	(N), $orf_{3}(N)$,, $f_{x}(N)$,
401	Now, althougheach of the numbers $f_{x (N)}$ of species recorded x-times varies with N at <i>its</i>
402	own pace and out of phase with the others (Figure 2), the process of species
403	accumulation proves to be regulated, however, due to the above mentioned "chaining
404	linkage" between the successive $f_{x (N)}$ (Figures 4, 5, 6). And this, indeed, is at the very
405	heart of the detailed process of species discovery and accumulation during progressive
406	sampling. A process of major practical importance since it is involved in all biodiversity
407	surveys and, more specifically, it is involved in the accurate extrapolation of the Species
408	Accumulation Curve. Accurate extrapolation which, in turn, determines the precise
409	estimate of the total species richness of a partially sampled assemblage of species and
410	the reliableprediction of the additional sampling effort required to obtain a given
411	increase in sample completeness.
412	
413	The constraining mathematical relationships highlighted above
414	aresummarized as follows :
415	* <u>relationship applying to the Species Accumulation Curve, R(N),itself</u> :
416	equations (2) & (3):
417	$[\partial^{x} R_{(N)} / \partial N^{x}] = (-1)^{x-1} f_{x(N)} / C_{N, x} \approx (-1)^{x-1} (x! / N^{x}) f_{x(N)}$
418	* relationship applying to the proportion of efficient observations, $p(N) = R$
420	(N)/N:equation (21):
421	$[\partial^{x} \mathbf{p}(\mathbf{N}) / \partial \mathbf{N}^{x}] = (-1)^{x} (\mathbf{x}! / \mathbf{N}^{x+1}) \sum_{i>x} [\mathbf{f}_{i}(\mathbf{N})]$
422	
423	* relationshipapplying to the numbers $f_1(N)$, $f_2(N)$, $f_3(N)$,, $f_x(N)$,
424	of those species respectively recorded 1, 2, 3,, x-times during sampling:
425	equation (6):
426 427	$\mathbf{x} \cdot \mathbf{f}_{\mathbf{x}(\mathbf{N})} - \mathbf{N} \cdot \left[\frac{\partial \mathbf{f}_{\mathbf{x}(\mathbf{N})}}{\partial \mathbf{N}} \right] = (\mathbf{x} + 1) \cdot \mathbf{f}_{\mathbf{x} + 1}(\mathbf{N})$
428	* and its three <i>corollaries</i> :
429	equations (7), (10) and (12):
430	$f_{x+1 (N)} = [x/(x+1)] f_{x (N)}$ valid when $\partial f_{x (N)}/\partial N = 0$
431	
432	$f_{x(N)} = -(N/x) \Sigma_i [\partial f_{i(N)}/\partial N]$
433	with the sum Σ_i extended from $i = 0$ to $i = (x - 1)$
434	and, at last:
435	$-\Sigma_{i}[(\partial T_{i}(N)/\partial N).(X-1)] = 1$
436	with X as the larger value of x for which $f_{X(N)} \neq 0$
437	and the sum Σ_i extended from $i = 0$ to $i = (X - 1)$
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439	
440	APPENDICES
441	A.1 - Derivation of the constraining relationship between $\partial^{x}R_{(N)}/\partial N^{x}$ and $f_{x(N)}$
442	I ne snape of the theoretical Species Accumulation Curve is directly dependent upon the
443	particular Species Abundance Distribution (the "S.A.D.") within the sampled assemblage
444	or species. That means that beyond the common general traits shared by all Species
445	Accumulation Lurves, each particular species assemblage give rise to a specific Species
446	Accumulation Curve with its own, unique shape, considered in detail. Now, it turns out
447	that, in spite of this diversity of particular shapes, all the Species Accumulation Curves

448 are, nevertheless, constrained by a same mathematical relationship that rules their successive derivatives (and, thereby, rules the details of the curve shape since the 449 450 successive derivatives altogether define the local shape of the curve in any details). Moreover, it turns out that this general mathematical constraint relates bi-univocally 451 each derivative at order x $\left[\frac{\partial^{x} R_{(N)}}{\partial N^{x}}\right]$ to the number, $f_{x(N)}$, of species recorded x-times 452 453 in the considered sample of size N. And, as the series of the $f_{x(N)}$ are obviously directly dependent upon the particular Distribution of Species Abundance within the sampled 454 455 assemblage of species, it follows that this mathematical relationship between $\partial^{x} R_{(N)} / \partial N^{x}$ and $f_{x(N)}$, ultimately reflects the indirect but strict dependence of the shape of the Species 456 Accumulation Curve upon the particular Distribution of the Species Abundances (the so 457 called S.A.D.) within the assemblage of species under consideration. In this respect, this 458 constraining relationship is central to the process of species accumulation during 459 460 progressive sampling, and is therefore at the heart of any reasoned approach to the extrapolation of any kind of Species Accumulation Curves. 461

462 This fundamental relationship may be derived as follows.

463 Let consider an assemblage of species containing an unknown total number 'S' of 464 species. Let R be the number of recorded species in a partial sampling of this assemblage 465 comprising N individuals. Let p_i be the probability of occurrence of species 'i' in the 466 sample This probability is assimilated to the relative *abundance* of species 'i' within this 467 assemblage or to the relative *incidence* of species 'i' (its proportion of occurrences) 468 within a set of sampled sites. The number Δ of missed species (unrecorded in the 469 sample) is $\Delta = S - R$.

- 470 The estimated number Δ of those species that escape recording during sampling of the 471 assemblage is a decreasing function $\Delta_{(N)}$ of the sample of size N, which depends on the 472 particular distribution of species abundances p_i :
- 473 Δ(

$$\Delta_{(N)} = \Sigma_i (1 - p_i)^N (A1.1)$$

474 with Σ_i as the operation summation extended to the totality of the 'S' species 'i' in the 475 assemblage (either *recorded* or *not*)

476 The expected number f_x of species recorded *x times* in the sample, is then, according to 477 the binomial distribution:

478
$$f_{x} = [N!/X!/(N-x)!] \Sigma_{i}[(1-p_{i})^{N-x}p_{i}^{x}] = C_{N,x} \Sigma_{i}(1-p_{i})^{N-x}p_{i}^{x}$$
(A1.2)

479 with $C_{N,x} = N!/X!/(N-x)!$

480 We shall now derive the relationship between the successive derivatives of $R_{(N)}$, the 481 theoretical Species Accumulation Curve and the expected values for the series of 'f_x'.

482 According to equation (A1.2):

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$$\blacktriangleright$$
 $f_1 = N \Sigma_i[(1-p_i)^{N-1} p_i] = N \Sigma_i[(1-p_i)^{N-1} (1-(1-p_i))] = N \Sigma_i[(1-p_i)^{N-1}] - N \Sigma_i[(1-p_i)^{N-1}(1-p_i))]$

485 = N
$$\Sigma_i[(1-p_i)^{N-1}]$$
 - N $\Sigma_i[(1-p_i)^N]$.

486 Then, according to equation (A1) it comes: $f_1 = N (\Delta_{(N-1)} - \Delta_{(N)}) = -N (\Delta_{(N)} - \Delta_{(N-1)})$

487 = - N
$$(\partial \Delta_{(N)}/\partial N)$$
 = - N $\Delta'_{(N)}$

488 where $\Delta'_{(N)}$ is the first derivative of $\Delta_{(N)}$ with respect to N. Thus:

 $f_1 = -N \Delta'_{(N)} (= -C_{N,1} \Delta'_{(N)})$ (A1.3)

490 Similarly:

491 **•**
$$f_2 = C_{N, 2} \Sigma_i [(1-p_i)^{N-2} p_i^2]$$
 according to equation (A1.2)

492 = $C_{N, 2}\Sigma_i[(1-p_i)^{N-2}(1-(1-p_i^2))] = C_{N, 2}[\Sigma_i[(1-p_i)^{N-2}] - \Sigma_i[(1-p_i)^{N-2}(1-p_i^2)]]$

 $= C_{N,2} \left[\sum_{i} \left[(1-p_i)^{N-2} \right] - \sum_{i} \left[(1-p_i)^{N-2} (1-p_i) (1+p_i) \right] \right] = C_{N,2} \left[\sum_{i} \left[(1-p_i)^{N-2} \right] - \sum_{i} \left[(1-p_i)^{N-1} (1+p_i) \right] \right]$ 493 = $C_{N,2} \left[\left(\Delta_{(N-2)} - \Delta_{(N-1)} \right) - f_1 / N \right]$ according to equations (A2.1) and (A1.2) 494 $= C_{N,2} \left[-\Delta'_{(N-1)} - f_1/N \right] = C_{N,2} \left[-\Delta'_{(N-1)} + \Delta'_{(N)} \right] \text{ since } f_1 = -N \Delta'_{(N)} \quad (cf. \text{ equation (A1.3)}).$ 495 $= C_{N,2} \left[\left(\partial \Delta'_{(N)} / \partial N \right) \right] = \left[N(N-1)/2 \right] \left(\partial^2 \Delta_{(N)} / \partial N^2 \right) = \left[N(N-1)/2 \right] \Delta''_{(N)}$ 496 where $\Delta''_{(N)}$ is the second derivative of $\Delta_{(N)}$ with respect to N. Thus: 497 $f_2 = [N(N-1)/2] \Delta''_{(N)} = C_{N,2} \Delta''_{(N)}$ 498 (A1.4) • $f_3 = C_{N,3}\Sigma_i[(1-p_i)^{N-3} p_i^3]$ which, by the same process, yields: 499 $= C_{N,3} \left[\sum_{i} (1-p_i)^{N-3} - \sum_{i} (1-p_i)^{N-2} - \sum_{i} \left[(1-p_i)^{N-2} p_i \right] - \sum_{i} \left[(1-p_i)^{N-2} p_i^2 \right] \right]$ 500 = $C_{N,3} [(\Delta_{(N-3)} - \Delta_{(N-2)}) - f_1*/(N-1) - 2 f_2/(N(N-1))]$ according to equations (A2.1) and 501 502 (A1.2) where f_1^* is the number of singletons that would be recorded in a sample of size (N - 1) 503 instead of N. 504 According to equations (A1.3) & (A1.4): 505 $f_1^* = -(N-1)\Delta'_{(N-1)} = -C_{N-1,1}\Delta'_{(N-1)}$ and $f_2 = [N(N-1)/2]\Delta''_{(N)} = C_{N-1,2}\Delta''_{(N)}$ (A1.5) 506 where $\Delta'_{(N-1)}$ is the first derivate of $\Delta_{(N)}$ with respect to N, at point (N-1). Then, 507 $f_{3} = C_{N,3} \left[\left(\Delta_{(N-3)} - \Delta_{(N-2)} \right) + \Delta'_{(N-1)} - \Delta''_{(N)} \right] = C_{N,3} \left[-\Delta'_{(N-2)} + \Delta'_{(N-1)} - \Delta''_{(N)} \right]$ 508 $= C_{N,3} \left[\Delta''_{(N-1)} - \Delta''_{(N)} \right] = C_{N,3} \left[-\partial \Delta''_{(N)} / \partial N \right] = C_{N,3} \left[-\partial^3 \Delta_{(N)} / \partial N^3 \right] = C_{N,3} \Delta'''_{(N)}$ 509 where $\Delta'''_{(N)}$ is the third derivative of $\Delta_{(N)}$ with respect to N. Thus : 510 $f_{3} = -C_{N,3}\Delta'''(N)$ 511 (A1.6) Now, generalising for the number f_x of species recorded *x times* in the sample: 512 513 \blacktriangleright f_x = C_{N,x} Σ_i [(1-p_i)^{N-x}p_i^x] according to equation (A1.2), $= C_{N,x} \sum_{i} [(1-p_i)^{N-x} (1 - (1 - p_i^x))] = C_{N,x} [\sum_{i} (1-p_i)^{N-x} - \sum_{i} [(1-p_i)^{N-x} (1 - p_i^x)]]$ 514 $= C_{N,x} \left[\sum_{i} (1-p_i)^{N-x} - \sum_{i} \left[(1-p_i)^{N-x} (1-p_i) (\sum_{j} p_i^{j}) \right] \right]$ 515 516 with Σ_i as the summation from j = 0 to j = x-1. It comes: 517 $f_x = C_{N,x} [\Sigma_i (1-p_i)^{N-x} - \Sigma_i [(1-p_i)^{N-x+1} (\Sigma_i p_i^j)]]$ $= C_{N,x} \left[\sum_{i} (1-p_i)^{N-x} - \sum_{i} (1-p_i)^{N-x+1} - \sum_{k} \left[(\sum_{i} (1-p_i)^{N-x+1} p_i^k) \right] \right]$ 518 with Σ_k as the summation from k = 1 to k = x-1; that is: 519 $f_x = C_{N,x} \left[(\Delta_{(N-x)} - \Delta_{(N-x+1)}) - \Sigma_k (f_k^* / C_{(N-x+1+k),k}) \right]$ according to equations (A1.1) and 520 521 (A1.2)) 522 where $C_{(N-x+1+k),k} = (N-x+1+k)!/k!/(N-x+1)!$ and f_k^* is the expected number of species 523 recorded k times during a sampling of size (N-x+1+k) (instead of size N). The same demonstration, which yields previously the expression of f_1^* above (equation 524 525 (A1.5)), applies for the f_k^* (with k up to x-1) and gives: 526 $f_k^* = (-1)^k (C_{(N-x+1+k),k}) \Delta^{(k)}_{(N-x+1+k)}$ (A1.7) where $\Delta^{(k)}(N-x+1+k)$ is the kth derivate of $\Delta_{(N)}$ with respect to N, at point (N-x+1+k). Then, 527 $f_x = C_{N,x} \left[(\Delta_{(N-x)} - \Delta_{(N-x+1)}) - \Sigma_k ((-1)^k \Delta^{(k)}_{(N-x+1+k)}) \right]$ 528

529 which finally yields :

530 $f_x = C_{N,x} [(-1)^x (\partial \Delta^{(x-1)}(N) / \partial N)] = C_{N,x} [(-1)^x (\partial^x \Delta^{(N)} / \partial N^x)].$ That is:

$$f_{x} = (-1)^{x} C_{N, x} \Delta^{(x)}(N) = (-1)^{x} C_{N, x} \left[\frac{\partial^{x} \Delta_{(N)}}{\partial N^{x}} \right]$$
(A1.8)

532 where $[\partial x \Delta_{(N)} / \partial N^x]$ is the xth derivative of $\Delta_{(N)}$ with respect to N, at point N. 533 Conversely:

$$[\partial^{\mathbf{x}} \Delta_{(\mathbf{N})} / \partial \mathbf{N}^{\mathbf{x}}] = (-1)^{\mathbf{x}} f_{\mathbf{x}} / C_{\mathbf{N}, \mathbf{x}}$$
(A1.9)

Note that, in practice, leaving aside the beginning of sampling, N rapidly increases muchgreater than x, so that the preceding equation simplifies as:

(A1.11)

$$[\partial^{x} \Delta_{(N)} / \partial N^{x}] = (-1)^{x} (x! / N^{x}) f_{x(N)}$$
(A1.10)

 $[\partial \Delta_{(N)}/\partial N] = f_{1(N)}/N$

538 In particular:

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 $\left[\frac{\partial^2 \Delta_{(N)}}{\partial N^2}\right] = 2 f_{2(N)}/N^2$ (A1.12) This relation (A1.9) has general relevance since it does not involve any specific 541 assumption relative to either (i) the particular shape of the distribution of species 542 abundances in the sampled assemblage of species or (ii) the particular shape of the 543 544 species accumulation rate. Accordingly, this relation constrains any theoretical form of species accumulation curves. As already mentioned, the shape of the species 545 accumulation curve is entirely defined (at any value of sample size N) by the series of 546 the successive derivatives $\left[\partial^{x}R_{(N)}/\partial N^{x}\right]$ of the predicted number R(N) of recorded 547 548 species for a sample of size N:

$$[\partial^{x} R_{(N)} / \partial N^{x}] = (-1)^{(x-1)} f_{x} / C_{N,x}$$
(A1.13)

with $[\partial^{x}R_{(N)}/\partial N^{x}]$ as the xth derivative of $R_{(N)}$ with respect to N, at point N and $C_{N, x} = N!/(N-x)!/x!$ (since the number of recorded species $R_{(N)}$ is equal to the total species richness S minus the expected number of missed species $\Delta_{(N)}$).

As above, equation (A1.13) simplifies in practice as:

 $\partial^{x} R_{(N)} / \partial N^{x} = (-1)^{(x-1)} (x! / N^{x}) f_{x(N)}$ (A1.14)

Equation (A1.13) makes quantitatively explicit the dependence of the shape of the species accumulation curve (expressed by the series of the successive derivatives $[\partial^x R_{(N)}/\partial N^x]$ of R(N)) upon the shape of the distribution of species abundances in the sampled assemblage of species.

A2 - An alternative derivation of the relationship between $\partial^x R_{(N)} / \partial N^x$ and $f_{x(N)}$

Consider a sample of size N (N individuals collected) extracted from an assemblage of S 561 562 species and let G_i be the group comprising those species collected i-times and $f_{i(N)}$ their number in G_i . The number of collected individuals in group G_i is thus i.f_{i(N)}, that is a 563 proportion i.f_{i(N)}/N of all individuals collected in the sample. Now, each newly collected 564 individual will either belong to a new species (probability $1.f_1/N = f_1/N$) or to an already 565 566 collected species (probability $1 - f_1/N$), according to reference [12]. In the latter case, the proportion i.f_{i(N)}/N of individuals within the group G_i accounts for the probability that 567 the newly collected individual will contribute to increase by one the number of species 568 that belong to the group G_i (that is will generate a transition $[i-1 \rightarrow i]$ under which the 569 species to which it belongs leaves the group G_{i-1} to join the group G_i). Likewise, the 570 571 probability that the newly collected individual will contribute to reduce by one the 572 number of species that belong to the group G_i (that is will generate a transition $[i \rightarrow i+1]$ under which the species leaves the group G_i to join the group G_{i+1} is (i+1). $f_{i+1(N)}/N$. 573

574 Accordingly, for $i \ge 1$:

$$\partial f_{i(N)} / \partial N = [i.f_{i(N)} / N - (i+1).f_{i+1(N)} / N](1 - f_1 / N)$$
 (A2.0)

Leaving aside the very beginning of sampling, and thus considering values of sample size 576 N substantially higher than f₁, it comes: 577 578 $\partial f_{i(N)}/\partial N = i f_{i(N)}/N - (i+1) f_{i+1(N)}/N$ (A2.1) 579 Let consider now the Species Accumulation Curve R(N), that is the number R(N) of species that have been recorded in a sample of size N. The probability that a newly 580 collected individual belongs to a still unrecorded species corresponds to the probability 581 of the transition $[0 \rightarrow 1]$, equal to i.f_{i(N)}/N with i = 1, that is: f_{1(N)}/N (as already 582 583 mentioned). Accordingly, the first derivative of the Species Accumulation Curve R(N) at point N is 584 $\partial R_{(N)} / \partial N = f_{1(N)} / N$ 585 (A2.2) In turn, as $f_{1(N)} = N \cdot \partial R_{(N)} / \partial N$ (from equation (A2.2)) it comes: 586 $\partial f_{1(N)}/\partial N = \partial [N(\partial R_{(N)}/\partial N)]/\partial N = N(\partial^2 R_{(N)}/\partial N^2) + \partial R_{(N)}/\partial N$ 587 588 On the other hand, according to equation (A2.1): $\partial f_{1(N)} / \partial N = 1.f_{1(N)} / N - 2.f_{2(N)} / N = f_{1(N)} / N - 2f_{2(N)} / N$, and therefore: 589 $N(\partial^2 R_{(N)}/\partial N^2) + \partial R_{(N)}/\partial N = f_{1(N)}/N - 2f_{2(N)}/N$ 590 591 And as $\partial R_{(N)}/\partial N = f_{1(N)}/N$ according to equation (A2.2): $\partial^2 R_{(N)}/\partial N^2 = -2f_{2(N)}/N^2$ 592 (A2.3) 593 Likewise, as $f_{2(N)} = -N^2/2.(\partial^2 R_{(N)}/\partial N^2)$, it comes: $\partial f_{2(N)}/\partial N = \partial [-N^2/2.(\partial^2 R_{(N)}/\partial N^2)]/\partial N = -N(\partial^2 R_{(N)}/\partial N^2) - N^2/2.(\partial^3 R_{(N)}/\partial N^3)$ 594 As $\partial f_{2(N)}/\partial N = 2f_{2(N)}/N - 3f_{3(N)}/N$, according to equation (A2.1), it comes: 595 $-N(\partial^2 R_{(N)}/\partial N^2) - N^2/2.(\partial^3 R_{(N)}/\partial N^3) = 2f_{2(N)}/N - 3f_{3(N)}/N$ 596 and as $\partial^2 R_{(N)} / \partial N^2 = -2f_{2(N)} / N^2$, according to equation (A2.3), it comes: 597 598 $\partial^3 R_{(N)} / \partial N^3 = + 6 f_{3(N)} / N^3$ (A2.4) 599 More generally: $\partial^{x} R_{(N)} / \partial N^{x} = (-1)^{(x-1)} (x! / N^{x}) f_{x(N)}$ (A2.5) 600 601 602 **ACKNOWLDGEMENTS** 603 604 To Nick GOTELLI for his stimulating appreciation regarding my derivation of the general 605 relationship constraining the successive derivatives (and thereby the shape) of the 606 theoretical expression of all kinds of Species Accumulation Curves. 607 608 609 REFERENCES 610 1. Chiarucci A, Bacaro G, Rocchini D & FattoriniLDiscovering and rediscovering the 611 sample based rarefaction formula in the ecological literature. *Community Ecology*. 612 2008;9(1):121-123. 613 614 2. Gotelli NJ & Chao A Measuring and Estimating Species Richness, Species 615 Diversity, and Biotic Similarity from Sampling Data. In: Levin SA (ed.) 616 Encyclopedia of Biodiversity, second edition. 2013; vol.5;pp. 195-211. Waltham, 617 MA: Academic Press. 618 619 620 3. Soberon JM & Llorent JB The Use of Species Accumulation Functions for the Prediction of Species Richness. Conservation Biology. 1993;7(3):480-488. 621 622

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