A MODEL OF BOTANICAL COLLECTORS' BEHAVIOR IN THE FIELD: NEVER THE SAME SPECIES TWICE[1]

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- *Premise of the study:* Because of their numbers, specimens in natural-history museums cannot be ignored when trying to answer one of the fundamental questions in science: What determines species diversity? The nonrandom nature of collecting does not allow most statistical tests or extrapolations of species estimates, or comparison of richness between areas (which, however, is still done frequently).
- *Methods:* We present a simple simulation model, which starts from the assumption that collectors never collect the same species twice during collecting trips. The model allows the generation of the abundance distribution in a herbarium for any natural species abundance distribution, using a simple set of collecting strategies.
- *Key results:* We show that, in essence, the strategy of "never collect the same species twice" is enough to generate the relative abundance distribution as found in a herbarium. We illustrate this using real plot and specimen data from two well-collected areas, one in central Guyana and one in Suriname.
- *Conclusions:* Because of the oversampling of rare species, it is perhaps not possible to use museum data to reconstruct the community structure in the field or even estimate a proper diversity number other than the number of species in a region.

What determines species diversity? This remains among the major questions in biological science (Pennisi, 2005). Because of their sheer numbers (2.5 billion specimens worldwide; Graham et al., 2004), natural-history museum collections cannot be disregarded in the search for an answer. The original goals of the collectors were to describe the wealth of diversity of plants and animals in nature, to produce reference collections to be used by other researchers, and to produce floras and monographs of families and genera. Therefore, the collecting strategies used should meet these objectives—to collect as many new species as possible. Because time and the number of specimens that can be collected on a trip are limited, collectors typically strive to not collect the same species twice. To increase the overall number of species per trip even more, collectors will tend to move to another area when the time required to find a new species becomes too long. The consequence of this strategy is that, in principle, a large number of species is collected per expedition (Appendix S1 and S2; see online files at http://www.amjbot.org/cgi/content/full/ajb.1000215/DC1). The herbaria today are a result of many short and long expeditions. Because the expeditions did not always have the full knowledge of what was already present in the herbarium, most common species are still represented by more than one specimen. However, because all collectors use the same search strategy, the herbarium today is characterized by an overrepresentation of rare species and an underrepresentation of common species, compared

to abundance distributions in the field (see also Nelson et al., 1990). For example, in central Guyana the five most common tree species in the field—*Mora gonggrijpii*, *Eperua falcata*, *Chlorocardium rodiei*, *Dicymbe altsonii*, and *Swartzia leiocalycina* (for nomenclature, see Boggan et al., 1997)—make up 43% of all individuals over 30 cm DBH (diameter at breast height, 1.30 m) in the field (ter Steege et al., 2000a) but account for only 6% of all herbarium specimens of trees collected in that area (Ek and ter Steege, 1998). In fact, the focus on rare species has led to a staggering number of species with only one specimen (singletons) in herbaria (Fig. 1), far more than any model of relative distribution (e.g., lognormal, logseries) predicts. This hampers the comparison of areas with unequal collecting efforts (Petersen and Meier, 2003; Petersen et al., 2003; González Espinosa and María, 2004; Meier and Dikow, 2004; van Gemerden et al., 2005; Solow and Roberts, 2006; Tobler et al., 2007; Versieux and Wendt, 2007), but even those with equal collecting effort as the number of collections will not be a good representation of the community structure, as we show here.

Early work of Fisher (Fisher et al., 1943) and Preston (Preston, 1962a, b) suggested that fundamental mathematical distributions underlie the structure of communities in the field. Hubbell (2001) unified these distributions in the so-called zero sum multinomial (ZSM), which resembles the lognormal in local communities and the logseries in metacommunities of large areas. Data suggest that the logseries distribution indeed fits the community structure of Amazon trees very well (Hubbell et al., 2008). The ZSM has two free parameters: θ, which is asymptotically equal to Fisher's α (one of the parameters of the logseries) and m, which can be associated with the input of new species (in the local community: immigration rate from the metacommunity; in the metacommunity: speciation). In the logseries Fisher's α is almost equal to the number of species with one individual (singletons), which is actually the first term of the logseries. The ZSM becomes similar to the logseries when m approaches 1. In that case, θ is also equal to the number of singletons.
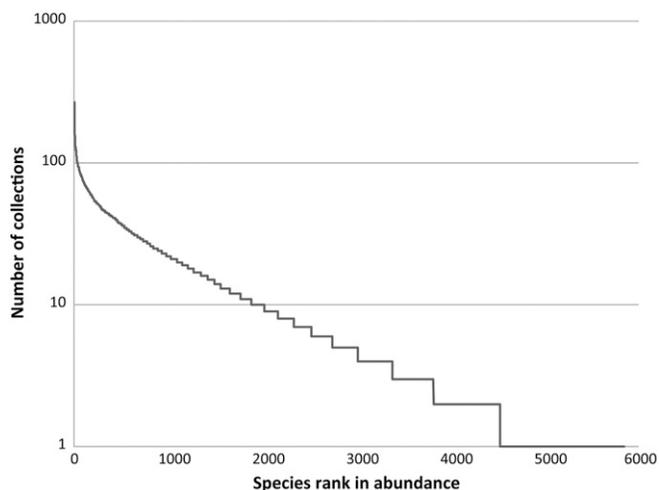
Fig. 1. Relative abundance distribution of the Guianas collections of the Utrecht Herbarium ($n = 71\,746$) that were identified to the species level (double entries removed). The number of singletons is 1318!

Because the collecting strategy used by collectors is far from random, statistical testing of the herbarium data is problematic, and this hampers estimation of diversity from herbaria. Here, we present a model that explains how the distribution of numbers of individuals of species present in herbaria develops in a nonrandom but predictable fashion from the logseries in the field.

MATERIALS AND METHODS

The model consists of two parts: (1) the construction of the relative abundance distribution in the field and (2) the sampling of that distribution by the collectors. The data for part 1 consisted of plot data (1-ha plots; full inventories of all trees with dbh > 10 cm) from two areas: Mabura Hill, central Guyana (hereafter "Mabura"; 6 plots, chosen to represent different forest types) and the bauxite mountain region of northeastern Suriname (hereafter "Bauxite"; 23 plots, chosen to represent plateaus, slopes, and lowland forest surrounding the plateaus; Bánki, 2010). For both areas, we constructed a hypothetical species abundance distribution, given below. A graphic layout of this part of the model is given in Appendix S3. We obtained the relative abundance distribution from the plot data (RAD$_{plots}$) and calculated θ and m for the associated ZSM. We used the average number of trees in the 1-ha plots and the total area encompassing all herbarium specimens collected from that area to calculate the total number of trees >10 cm dbh in the area (J_m, the metapopulation) and constructed the abundance distribution of all species and individuals of the total area (ZSM$_{area}$). Both calculations were made with MATLAB scripts provided by Brian McGill (McGill et al., 2006).

In part 2 of the model, we sampled individual specimens from the ZSM$_{area}$ (simulating botanical collecting) using MATLAB scripts written for this purpose. We simulated "expedition-type collectors"—that is, collectors who make large collecting trips and collect many specimens (100–400 specimens, typically)—and modeled three scenarios:

1. Never collect the same species twice, and keep searching for new species, regardless of the time (number of search loops) it takes;

2. As above, but when this takes more than a preset number of search loops in the program (between 5 and 50), collect whatever is the next individual (some species are now collected more than once). This simulates stress or anxiety. Although the preference in real expeditions is one individual per species, there is usually also a target number of specimens per expedition that needs to be met, relaxing rule 1;

3. As above, but sample an equal number of specimens from 4 different subareas that have no species in common (ZSM values based on one-fourth of the individuals but with similar θ and m). This simulates the sampling of β-diversity (the behavior of moving to a new terrain when the collecting of new species gets slow).

The number of specimens that were collected in different expeditions in an area also resembles a ZSM (few expeditions having many collections, many expeditions having few collections; see Appendix S4. as do many other collections of items (Nekola and Brown, 2007). We made a relative abundance distribution of specimens collected per expedition and combined this RAD with scenario 1:

4. All collectors were allowed to collect from the ZSM$_{area}$ the number of specimens they had collected for their actual expedition and never collect the same species twice.

Finally, we tested our model with varying number of collectors and varying number of specimens collected to understand better the effect of collecting intensity on the structure of our herbarium, using scenario 1 as the collecting scenario. For the varying number of collectors, we used the Bauxite ZSM$_{area}$ and collected 3000 specimens. The number of collectors varied from 1, who collected 3000 specimens ($\theta_{collectors} = 0$) and thus collected 3,000 species, based on scenario 1. At the other extreme were 3000 collectors, each collecting 1 individual ($\theta_{collectors} = \infty$). The latter is in fact a random sampling of the ZSM, in theory producing a smaller copy of it with the same θ (c. 145 for Bauxite). The $\theta_{collectors}$ used were 400, 200, 100, 50, 10 (close to the actual value), 5, 2, and 1. For the number of varying specimens, we sampled the ZSM$_{area}$ of Bauxite with a $\theta_{collectors}$ of 10 (which is similar to the empirical one of this area, $n = 2,998$; 57 collectors). We reduced the number of specimens collected in the area, while keeping $\theta_{collectors}$ constant by removing the collector with the highest number of collected specimens (629) for a total of 2,369 specimens (56 collectors) and repeated this to obtain a number of specimens of 1,115 (51 collectors). To obtain a higher number, we added 1 collector with 1300 specimens to the number of collectors for Bauxite ($n = 4,298$; 58 collectors). Finally, we constructed species accumulation curves for these simulations with ECOSIM (Gotelli and Entsminger, 2001), using 1000 randomizations.

RESULTS

To characterize the structure of the ecosystem, in Mabura six 1-ha plots were inventoried for a total of 3,086 trees (>10 cm dbh) and 112 species (Bánki and ter Steege unpublished data). M$_{plots}$ was 0.934, which suggests a near logseries distribution, consistent with a θ almost equal to Fisher's α and close to the number of singletons (Table 1). The relative abundance distribution of the plots (RAD$_{plots}$) and the calculated ZSM$_{Mabura}$ were also quite similar (Fig. 2A). In Bauxite, 23 plots were inventoried for a total of 13 241 trees (>10 cm dbh) and 605 species (Bánki and ter Steege, unpublished data). M$_{plots}$ was 0.954, which also suggests a near logseries distribution, again consistent with a θ almost equal to Fisher's α and close to the number of singletons (Table 1). The RAD$_{plots}$ and ZSM$_{Bauxite}$ were also very similar here (Fig. 2B). Mabura and Bauxite differ considerably in their tree diversity (see ter Steege et al., 2000b) and serve as a low- and medium-diversity test case for the Neotropics.

To characterize the herbarium, in Mabura a total of 3302 botanical specimens were collected by 47 collectors (period 1846–2004), including 853 species (Table 1; also see Appendix S4). The largest collection for one collector was 690 specimens, and there were six collectors with only one specimen. In Bauxite, a total of 2,727 specimens were collected by 46 collectors (period 1841–2003), including 713 species. The largest collection was 837 specimens (but in this case probably collected on numerous occasions: collector BW, Forest Department Suriname) and there were also six collectors with only one specimen (Table 1 and Appendix S4). Roughly half the collectors collected one specimen per species, adhering strictly to scenario 1. The numbers of specimens contributed by these collectors varied from 1 to 118. If the number of specimens per collector increased, often species were collected more than once; however, in 75% of the collectors in

TABLE 1.   Original plot and botanical collection data for Mabura Hill, Guyana, and the bauxite mountains area of Suriname.

	Mabura Hill	Bauxite Mts
1-ha plots	6	23
Number of individuals	3086	13 241
Tree density (trees ha^{-1})	514	576
Number of species	112	605
Number of singletons	27	135
θ	23.01	131.5
Fisher's α (for all plots)	22.78	130.7
m	0.934	0.954
Herbarium		
Number of collections	3302	2727
Number of species	853	713
θ	337	584
ZSM input parameters		
Area for collections (km^2)	7500	810 000
Jm calc	385 750 000	46 631 347 826
θ_calc	25	140
m_calc	0.93	0.95
ZSM_area (modeled)		
n	397 898 675	46 631 347 826
S	400	2661
Singletons	17	55
Fisher's α	24.07	135.4

Mabura and 84% of the collectors in Bauxite the S/n ratio (number of species per number of collections) was >0.75. The same species were more often collected by those collectors who visited the area on numerous occasions or were among the specimens of the forest departments of Guyana (FD) and Suriname (BW)—in fact, conglomerates of various collectors and forest scientists. The lowest S/N ratio was 0.41 in Mabura (John Pipoly, $n = 199$, $S = 83$) and 0.35 in Bauxite (BW, $n = 837$, $S = 299$).

The RAD$_{herbarium}$ for each of the areas was much flatter than that for the RAD$_{plots}$ and ZSM$_{plots}$ (Fig. 2A, B), which is consistent with the expected undercollecting of common species (less dominance) and overcollecting of rare species (long tail). Complete random collecting from the metacommunity in the field

(ZSM$_{area}$) would in principle have led to an RAD$_{herbarium}$ very comparable to RAD$_{plots}$ and ZSM$_{area}$. The 10 most common species in the area (*Eperua falcata*, *E. grandiflora*, *Catostemma fragrans*, *Licania buxifolia*, *Dicymbe altsonii*, *Oxandra asbeckii*, *Talisia squarrosa*, *Eschweilera sagotiana*, and *Chlorocardium rodiei*) amounted to 69% of all individuals on the plots but only 4% of the number of herbarium specimens. Similarly, the 10 most common species in Bauxite (*Lecythis corrugata*, *Eperua falcata*, *Micrandra brownsbergensis*, *Eschweilera* sp., *Elvasia elvasioides*, *Croton argyrophylloides*, *Qualea rosea*, *Astrocaryum sciophilum*, *Quararibea duckei*, and *Bocoa prouacensis*) accounted for 22% of the individuals of the plots but only 2% of the herbarium specimens. Theta calculated for the herbarium specimens for Mabura was 337, an extremely high number, compared with the θ of the plots (Table 1). The same is true for Bauxite, where θ of the herbarium specimens was 584.

So far, we have characterized the original herbarium structure and the structure of the ecosystem from which this collection of specimens was obtained. Simulated herbarium structures based on the sampling scenarios introduced above show that in the case of a relatively few large-scale expeditions with the rule "never the same species twice" (scenario 1: Mabura, 15 collectors, 150 specimens, Fig. 3A1; Bauxite: 15 collectors, 200 specimens, Fig. 3B1), the relative abundance distributions of the herbaria are rather flat. This was especially clear in Mabura (Fig. 3A1), where all collectors collect at least the most common species once; hence, the number of specimens of all common species is equal to the number of collectors (15). Rarer species are collected less than the number of collectors, and this causes the horizontal line to drop off. Because there are not that many very common species in Bauxite, this happened much earlier there (Fig. 3B1). Extending the collecting strategy with a stress factor (scenario 2) results in an upward shift at the position of the common species, which are now collected more often than the number of collectors in the area (Fig. 3A2, B2). The same result can be obtained by modeling scenario 1 and adding a few collectors who collect just a few specimens. Hence, the more collectors visiting an area, the more often the most common species will
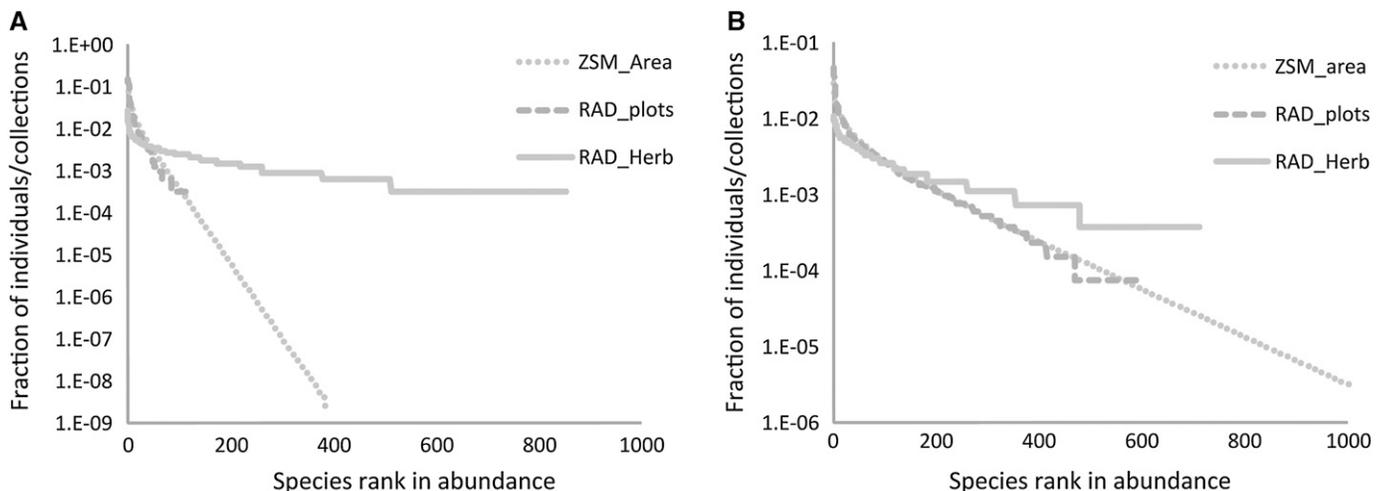

Fig. 2.   Relative abundance distribution of plots (RAD$_{plots}$) in (A) Mabura and (B) Bauxite ($100*n_{species\_}/n_{tot}$). The modeled relative abundance distribution (ZSM$_{area}$) for each area follows the RAD$_{plots}$ quite well. There is a great difference in the relative abundance distributions of plot data and of herbarium data (data from Herbarium Utrecht). The relative abundance distribution of the herbarium (RAD$_{herb}$) is much flatter, with less dominance and much more rare species (large tail), especially in Mabura.
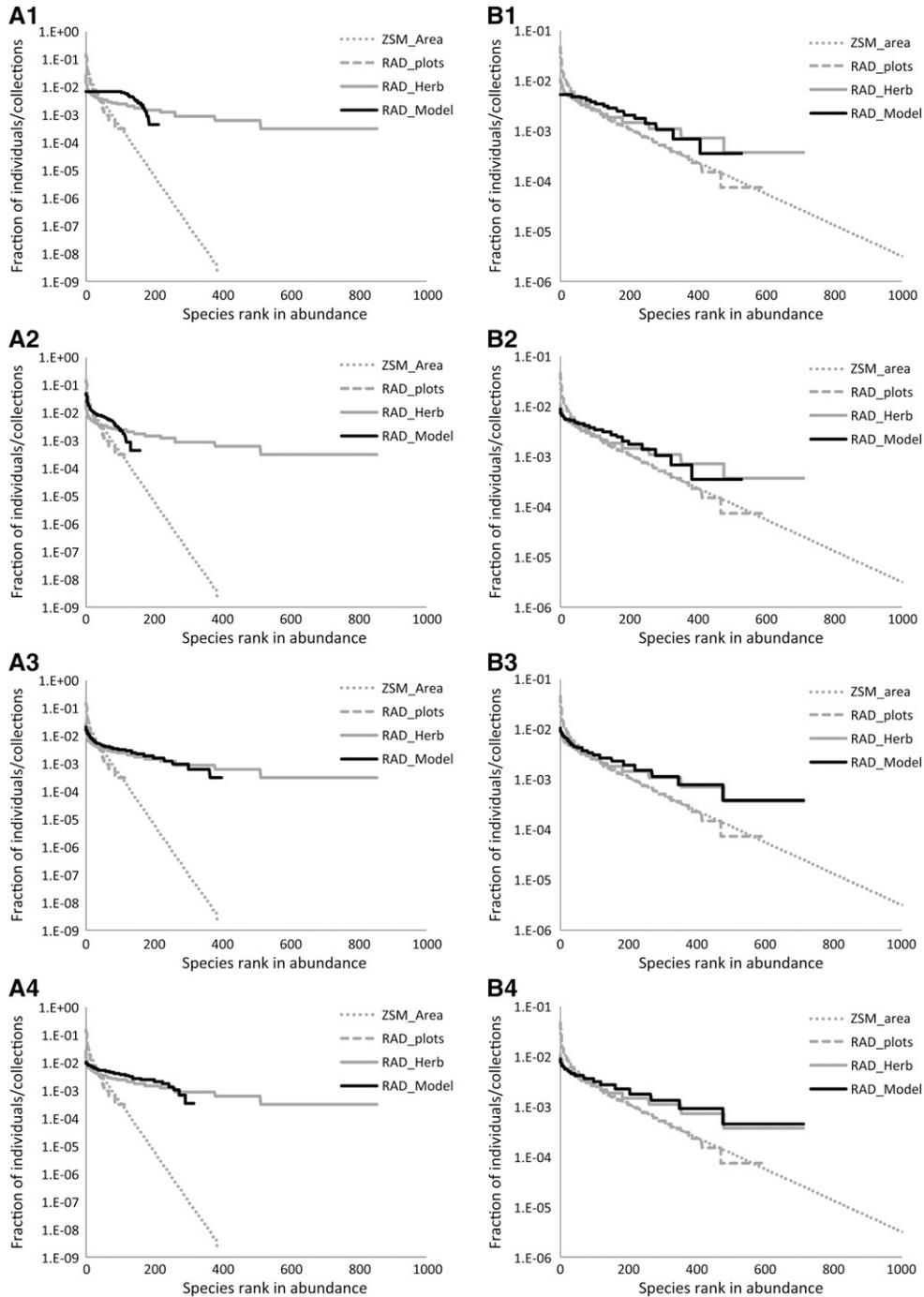
Fig. 3. Output of simulations based on scenarios 1 to 4 (top to bottom) in (A) Mabura and (B) Bauxite. Light gray curves and axis legends are as in Figure 1. Black line = simulation result.

be collected (this is in essence scenario 4). Allowing the collectors to use the β-diversity of an area (scenario 3) produced the long tail that is so characteristic of the relative abundance distribution of the herbarium (Fig. 3A3, B3). Simulating the collecting with the rule "never the same species twice" with the actual numbers of collectors and their actual collection sizes (Appendix S4) (scenario 4) also results in a relative abundance distribution that closely resembles that of the herbaria (Fig. 3A4, B4). This is the result of the collectors that

collect many specimens and find several rare ones (as they never collect the same species twice) and collectors that collect only one or two specimens and invariably end up with the most common species.

Collecting the ZSM_{area} of Bauxite with varying relative abundance distribution of the number of specimens over the collectors, with $\theta_{collectors} = 0$ (1 collector collects all 3000 specimens) to $\theta_{collectors} = \infty$ (3000 collectors each collecting 1 specimen) resulted in greatly varying number of species and species
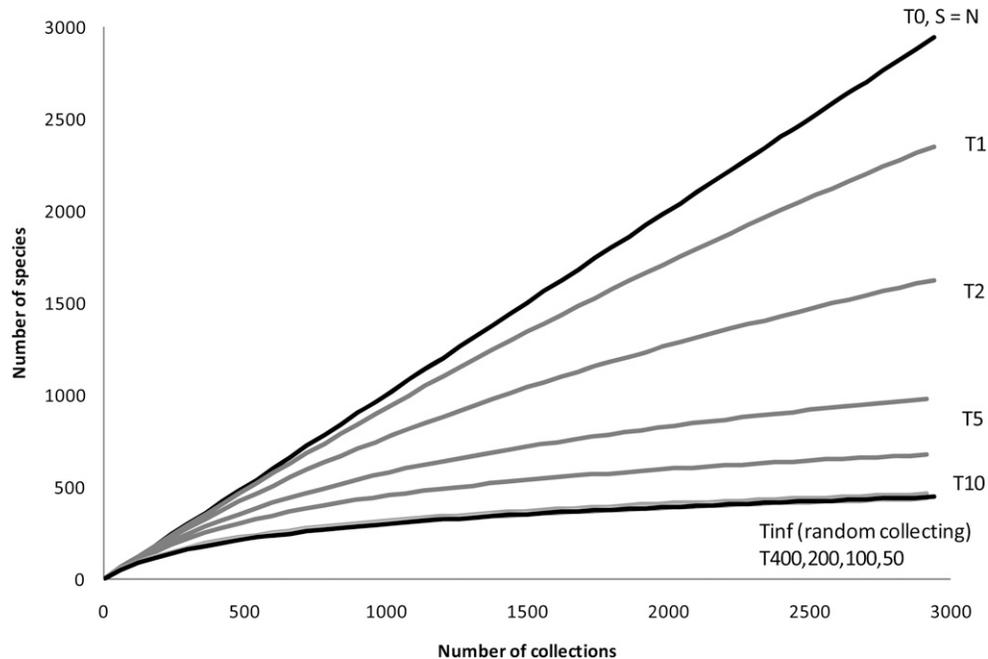
Fig. 4.   Species accumulation curves based on sampling the ZSM$_{area}$ of Bauxite with collectors with differing relative abundance distributions of the specimens collected per collector. T0, $\theta_{collectors} = 0$, 1 collector collects all specimens, hence $S = n$; Tinf, $\theta_{collectors}$ = infinite, 3000 collectors all collecting 1 random specimen. All other $\theta_{collectors}$ fall within this range (as should their curves); those with $\theta_{collectors}$ = 50–400 are very close to $\theta_{collectors}$ = infinite.

accumulation curves (Fig. 4). When high $\theta_{collectors}$ were used (from infinite [= random sampling] to 50; i.e., many collectors collecting small numbers of specimens), near similar accumulation curves were produced with near similar number of species collected (c. 460; Fig. 4). When $\theta_{collectors}$ was <50, the accumulation curves became steeper because there was a larger number of collectors collecting high numbers of specimens and, thus, species. The highest number of species was, obviously, from the single collector with 3000 specimens (and, thus, 3000 species). Search time for this simulation was (expectedly) very long.

Collecting the ZSM$_{area}$ of Bauxite with varying number of specimens collected but with constant $\theta_{collectors} = 10$ also resulted in widely varying species accumulation curves (Fig. 5). The lowest number of species was found with a small number of specimens collected, and the number of species logically increased when the number of specimens collected was higher. It grew increasingly faster with higher numbers; hence, the steepness of the accumulation curve depends on the number of specimens collected. This is because with a large number of total specimens collected, the collector with the highest number of specimens strongly determines the total number of species.

DISCUSSION

We have two models that are quite good for producing the relative abundance distribution in the herbarium from the actual abundance distribution of trees in the field—scenario 3 and scenario 4. Although scenario 4, combining the actual number of collectors and their actual collection sizes, is arguably the most parsimonious model, we argue that it can be only partly correct. First, the data clearly show that more than half the collectors did not follow scenario 1 (see Appendix S1)—that is, collected more than one individual of several species. We know that this is caused by the need to collect a certain amount of specimens during an expedition (a common goal is often 400–500 specimens), and the time to find new species may become too long. Resident collectors, for instance, are often hired to collect a fixed number of specimens per month and cannot fill this quota with unique species. Collectors may also collect the same species more than once if, for instance, they find a new individual of a species at a different place, find a more representative individual (flowers, fruits, better specimen), are unsure whether the species is the same, focus on a particular taxon and wish to have many specimens, or if the group is poorly known, specimens are part of an ecological study or molecular study, and reference collections are made. Second, scenario 3 (including habitat diversity in the collecting strategy) is definitely employed by experienced botanists, who specifically aim to collect in all different vegetation types in an area during their expeditions (personal observation) and thus find a larger number of rare species.

Our simple model shows that just one rule, "never collect the same species twice," may be responsible for the flat relative abundance distribution of herbarium specimens, while a significant addition to the flatness (tail with rare species) is caused by trying to include as many vegetation types as possible. Our vegetation types were unrealistically distinct (no species in common), so the effect is likely to be smaller in real life. The fact that common species are still relatively abundant in the herbarium is caused by (1) the fact that they tend to be collected by all collectors, as opposed to the rare species; and (2) the fact that some collectors spend only a small amount of time in the field and then collect mainly the most common species in flower or fruit. Many estimators of diversity, such as Fisher's α and Chao's estimator, are very sensitive to the large number of singletons, and the use of these estimators on herbarium data will thus provide a serious overestimate of diversity.
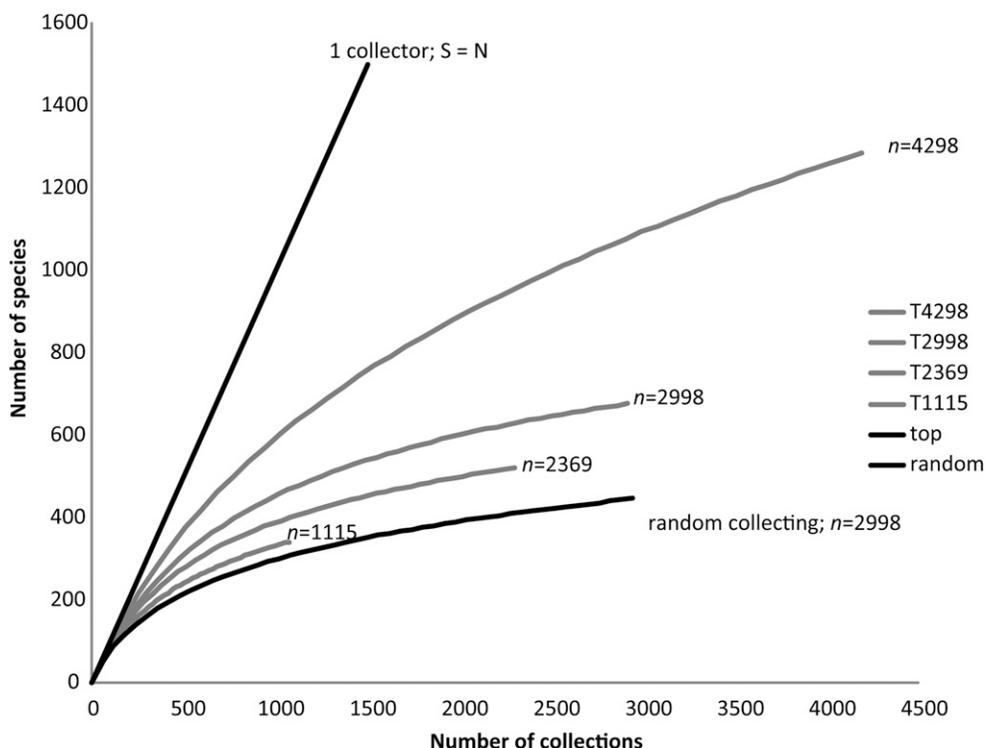
Fig. 5.   Species accumulation curves based on sampling the ZSM$_{area}$ of Bauxite, with collectors with differing relative numbers of specimens and relative abundance distributions among the collectors with constant theta (c. 10). "1 collector" = one collector collects all specimens, hence $S = n$; random collecting 2998 random draws from the ZSM$_{area}$. All other curves are based on randomizations of model output with rule "never the same species twice" and varying numbers of specimens collected (1115, 2369, 2998, 4298).

Sampling the modeled relative abundance distribution of the field with a logseries of specimens collected per collector may allow a mathematical model to reverse-engineer the relative abundance distribution of the field (and, hence, diversity measures) from herbarium specimens. Our results, however, show that this reverse-engineering will suffer from nonlinear relationships. Only with relatively high $\theta_{collectors}$—that is, many collectors with a small number of specimens per trip—does $\theta_{herbarium}$ approach the θ of the ZSM$_{area}$. Given that the $\theta_{collectors}$ of our total herbarium is rather high (98 for the collectors in Guyana and 104 for those of Suriname), we might assume that the $\theta_{herbarium}$ can be used to estimate the number of species in the field. The $\theta_{herbarium}$ values for trees are extremely high, though (598 for Guyana; 583 for Suriname). With an average of 500 trees ha^{-1} and a surface area of 21 million ha for Guyana (85% of which is forest), this leads to a number of species in the order of 9500 for Guyana alone. The total estimate for the Amazon (Hubbell et al., 2008) was 12 500. These numbers are difficult to reconcile. We therefore conclude that our herbarium still contains far too many singletons to make accurate estimates. Perhaps, as seems to be the case for the many forest stations, collectors had prior knowledge of what species were already present in the herbarium and they extended the rule "never the same species twice" over different expeditions.

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