SAMPLING VASCULAR EPIPHYTE DIVERSITY – SPECIES RICHNESS AND COMMUNITY STRUCTURE

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Abstract. The minimum requirement for the documentation of the structure of vascular epiphyte communities comprises information on the number of co-occurring species and their abundance and distribution. Using subsampling from a comprehensive census of the epiphytes on more than 1000 trees with a diameter at breast height > 1cm in 0.4 ha of lowland rainforest in Panama as a reference, this study investigates the minimum sampling effort necessary to obtain reliable information on essential community attributes (species numbers, α-diversity, and evenness). Large trees host the majority of all vascular epiphytes and therefore only the largest trees were sampled. Comparing the resulting community attributes deduced from a sample of epiphytes on 1-12 of the largest trees with those of the entire 0.4-ha study plot indicates that a sample size of about 6-8 trees is already sufficient to obtain a representative description of this epiphyte community. *Accepted 6 March 2011.*

INTRODUCTION

Vascular epiphytes are a strikingly species-rich component of many tropical forests, and their occurrence is associated with an important role in the ecosystem, e.g. in relation to water and nutrient cycles (Benzing 1990, Hietz *et al.* 2002). However, ecological work with epiphytes presents a number of important problems. For example, their distribution is three-dimensional and access is difficult in all but small-statured forests (e.g. Zimmerman & Olmsted 1992, Moffett & Lowman 1995, Zotz *et al.* 1999). Also, epiphytic species are frequently small and rather inconspicuous, thus observations from the ground are bound to be incomplete (Flores-Palacios & García-Franco 2001, Burns & Dawson 2005). The sampling of epiphyte communities is thus a difficult logistical task, making the question of the necessary sampling effort an important topic. However, this question is still unresolved, which is probably not surprising in view of additional complicating factors, e.g. their highly patchy distribution patterns and the generally large proportion of rare species (Nieder *et al.* 2000, Jacquemyn *et al.* 2005, Zotz 2007). Sampling prob-

lems are arguably the major reason for the still limited knowledge of epiphyte community structure and dynamics, but also of regional or biogeographic patterns (Küper *et al.* 2004). The current paucity of information still hampers our ability to investigate possible large-scale changes in species richness, an urgent need in times of dramatic changes in global climate (Benzing 1998). Clearly pure species lists, which are available for a larger number of sites in the tropics, are of limited value, the study of communities rather requires an understanding of the abundance, distribution, and the number of species present (Chazdon *et al.* 1998, Leitner & Turner 2001).

There are quite a few papers dealing with the appropriate methodology to document epiphyte diversity and community structure that have been published over the last decades (Hazen 1966, Johansson 1978, Gradstein *et al.* 1996, Shaw & Bergstrom 1997, Nieder & Zotz 1998, Flores-Palacios & García-Franco 2001, Gradstein *et al.* 2003, Wolf *et al.* 2009). Those studies including recommendations on sample sizes (e.g. number and sizes of trees) invariably use data from montane forests (Flores-Palacios & García-Franco 2001, Gradstein *et al.* 2003, Wolf *et al.* 2009). In these papers, minimum sampling

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sizes are generally based on species-accumulation curves and are often concluded to coincide with (Gradstein *et al.* 2003) or even exceed (Flores-Palacios & García-Franco 2001) the maximum sample sizes actually studied. However, the estimated species richness or more complex community structure parameters can, in such cases, not really be verified, as true values for full communities are usually not available (but see Annaselvam & Parthasarathy 2001 for species numbers). To overcome this problem, the present study took advantage of a complete inventory of vascular epiphytes in 0.4 ha of a species-rich lowland forest in Panama, yielding more than 13 000 epiphytes (Zotz 2007). This unique database was used as a reference to deduce the minimum sampling effort needed to allow a representative description of an epiphyte community in terms of species diversity and community structure (Colwell & Coddington 1994, Leitner & Turner 2001).

The present study addresses two major questions: 1) how many trees have to be searched for epiphytes to obtain a reliable estimate of the local species pool, and 2) how does the community structure deduced from these samples differ from the entire inventory? The first question was addressed by using species-accumulation curves and species richness estimators, and the second by additionally calculating indices of α-diversity and evenness and by a comparison of species rankings.

METHODS

Field site and data collection. The empirical data used in this study were collected at the San Lorenzo Canopy Crane site, located within the former Fort Sherman area near the Atlantic coast of the Republic of Panama (Wright *et al.* 2003). The average annual rainfall is ca. 3500 mm. Canopy height of this primary rain forest is quite variable, a few emergents reaching a maximum of ca. 40 m.

The use of a small gondola allowed access to all strata of the forest. Each tree in a roughly square area of ca. 0.4 ha with a diameter at breast height (dbh) ≥ 1cm was inspected for the occurrence of vascular epiphytes, and all but the smallest seedlings were included in the census. With the exception of a few taxa that could not be distinguished reliably in the field, all individuals were identified to species. In the 0.4 ha that were studied in detail, we found a total of 13 099 individuals of holoepiphytes, which belonged to 103 species. In an additional 0.5 ha that was also accessible by gondola, a less comprehensive

search yielded an additional 6 species of holoepiphytes. All of these were orchids, of which only one or very few individuals were found in each case. For the purpose of the present study, 103 and 110 species are treated as the "true" number of epiphyte species in respectively 0.4 and 0.9 ha of lowland forest at San Lorenzo. Trees were mostly identified to species, and the diameter at breast height (dbh) of each individual tree was known (R. Condit, STRI, unpubl. data).

Data analysis. Data analysis was conducted with EstimateS (Version 7.5, Colwell 2005) and R (Version 2.5.1, R Development Core Team 2007). The following rationale guided the "virtual sampling" of trees from the database. Large trees usually harbor by far the majority of epiphytes (Zotz & Vollrath 2003, Flores-Palacios & García-Franco 2006, Wolf *et al.* 2009) and this was also the case in San Lorenzo (Zotz 2007). We therefore "sampled" the largest trees, as also recommended by Gradstein *et al.* (2003), starting with the one with the greatest dbh. As one would and should do in field sampling, we excluded two individuals that hosted an extraordinarily small number of epiphytes: 3 and 14 individuals (3 species each), respectively. The 12 selected trees, which belonged to 11 different species (Table 1), hosted 6638 epiphyte individuals of 83 species, which represents > 80% of the total observed on the epiphyte-bearing 389 trees in the 0.4-ha plot. Treating each of the 12

TABLE 1. List of trees sampled to compute species-accumulation curves, species richness estimators, and evenness and diversity indices. Species names follow Correa A. *et al.* (2004).

Species name	Tree dbh	Epiphytes Species	Individuals
Brosimum utile	85	45	1978
Apeiba membranacea	74	48	732
Calophyllum longifolium	73	19	259
Manilkara bidentata	66	30	1170
Tapirira guianensis	66	31	873
Humiriastrum diguense	58	22	76
Poulsenia armata	55	50	960
Brosimum utile	51	20	139
Jacaranda copaia	51	14	71
Virola surinamensis	49	37	336
Carapa guianensis	48	5	16
Lonchocarpus heptaphyllus	47	6	28

trees as a sampling unit, species-accumulation curves were obtained. Trees were randomized 50 times without replacement to obtain a stable mean curve. A range of estimators of total species richness were evaluated to determine which would be most stable at the lowest number of sampled trees. The following richness estimators as suggested by Chazdon *et al.* (1998) were chosen: five non-parametric statistics (Abundance-based Coverage Estimator (ACE), Chao 1, Chao 2, jackknife 1, jackknife 2) and an extrapolation of mean species-accumulation curves (Michaelis-Menten-Means; MMM). The alternative Michaelis Menten statistic (MMruns) and the Incidence-based Coverage Estimator (ICE) are not appropriate for small sample sizes and were therefore not used here (for a full description of these statistics see Colwell & Coddington 1994 and Colwell 2005). The estimates of species richness of the "virtual" sample were also compared with the number of species observed in the entire plot.

As described in detail by Chazdon *et al.* (1998), EstimateS allows the study of the effect of non-randomness in spatial distributions on the performance of richness estimators. When the "patchiness parameter" A is set to 0, sample affiliations of individual epiphytes are randomized within species, which removes any patchiness of the original data. Conversely, a value of 1 yields maximum patchiness. In this paper, we use modifications of A to quantify the patchiness of the original samples by comparing species-accumulation curves of varying degrees of patchiness with the one obtained with the original data set, comparing the differences graphically.

Apart from species richness, the evenness of relative abundances is another key component of the quantitative description of the structure of plant communities. Although some evenness indices are significantly correlated with species richness, evenness and species richness are generally not redundant (Stirling & Wilsey 2001). Therefore we analyzed the variation in evenness indices as a function of sampling effort and compared these values with indices obtained for the entire data set. Smith & Wilson (1996) compared 12 different indices of evenness and recommended $E_{1/D}$ when it is required that the index be less affected by minor species. This index is derived from Simpson's dominance index, D, and is defined as

$$E_{1/D} = \frac{1/D}{S} \qquad (1),$$

where S is the number of species in the sample.

Simpson's D in turn is defined as

$$D = \sum_{s=1}^{S} p_s^2 \qquad (2)$$

where $p_s = x_s / \sum x$ and x_s is the abundance of the sth species.

The popular index J, which is based on the Shannon-Wiener diversity index, H′, as

$$J = \frac{H'}{\ln(S)} \qquad (3)$$

depends on species richness and is only given for comparison with literature values. Similar evenness may be observed in spite of a substantial shift in the ranks of individual species. A particularly strong shift would be expected if there were epiphyte species that prefer smaller trees as hosts (Johansson 1974, Krömer *et al.* 2007, Zotz 2007), and would therefore be under-sampled or even missing in a sampling scheme that is restricted to large trees. The relationship of rank order in the "virtual" sample and the total was explored with correlation analysis.

Finally, we studied the behaviour of two commonly used proportional statistics that combine both species counts and evenness, the Shannon-Wiener index H′ and the Simpson index (1/D) (Krebs 1989).

RESULTS

Species richness. The number of species found on the 12 sampled trees was 83, which represents over 80% of the observed number of species in the 0.4-ha plot (Zotz & Schultz 2008). Sampling the 8 largest trees yielded 81 species, whereas only 66 taxa were detected on the 4 largest trees. The species-accumulation curve showed no sign of saturation (Fig. 1A). After a strong initial increase until about 5 trees were included, species numbers increased in a slow and rather steady manner with about 2 additional species per tree. All richness estimators increased similarly with the number of samples. Jackknife 2 yielded the highest estimates, Chao 1 the lowest. Least affected by sample size was Michaelis-Menten Means (MMM); the MMM species estimate increased by only 5% (from 95 to 100 species) from 3 to 12 sampled trees (Fig. 1B). Results for the five non-parametric richness estimators ranged from 94 (Chao 1) to 113 species (Jackknife 2), thus centering on the "true" (observed) number of species in the entire plot (103 species in 0.4 ha and ca. 110 species in 0.9 ha, Zotz & Schultz 2008).
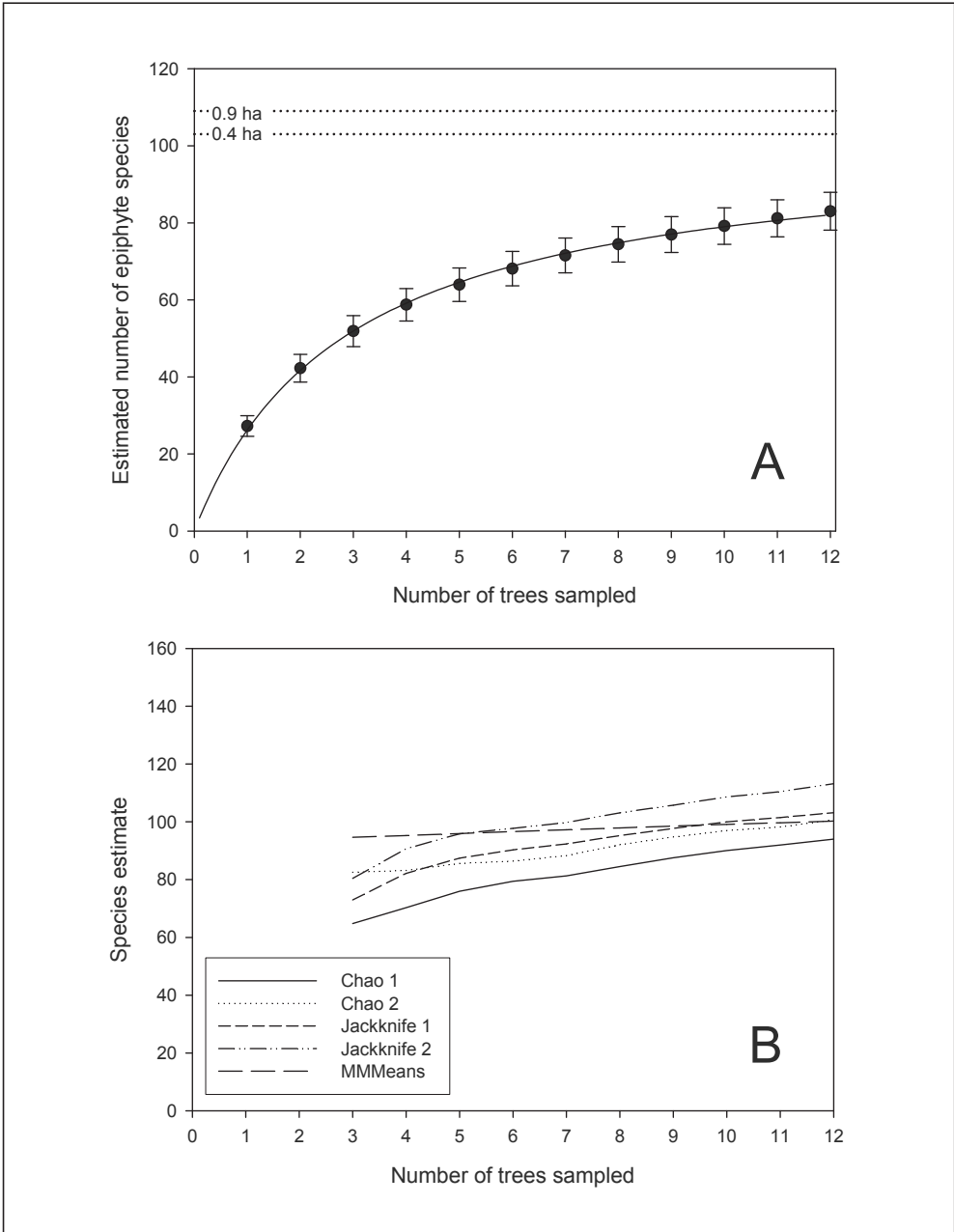
FIG. 1A. Cumulative species count versus number of trees sampled at the San Lorenzo crane site. Data are means ± SD of 50 randomizations. Dotted lines indicate the observed species numbers in the 0.4- and 0.9-ha study plots. B. Estimated species numbers from five richness estimators as a function of the number of trees sampled. Sample accumulation order of all curves was randomized 50 times, data points are means of these 50 estimates or extrapolations of the mean curves (MMMeans). The Abundance-based Coverage Estimator (ACE) yielded virtually identical results to Chao 1 and is not shown.

Patchiness. The degree of patchiness in this epiphyte community was very high, with an A between 0.75 and 0.9 (Fig. 2).

Evenness and rank abundance. The evenness index recommended by Smith & Wilson (1996), $E_{1/D}$, was rather constant and comparable to the value calculated for the entire 0.4 ha-plot when at least 6 trees were sampled (Fig. 3). The other index of evenness, *J*, showed very little change with the number of trees included in the sample.

FIG. 2. Effect of various levels of spatial patchiness on the rate of species-accumulation. The solid line represents the unchanged abundances of epiphytes from the observed field data, the other lines various levels of patchiness from random (*A* = 0) to extremely patchy (*A* = 0.99).
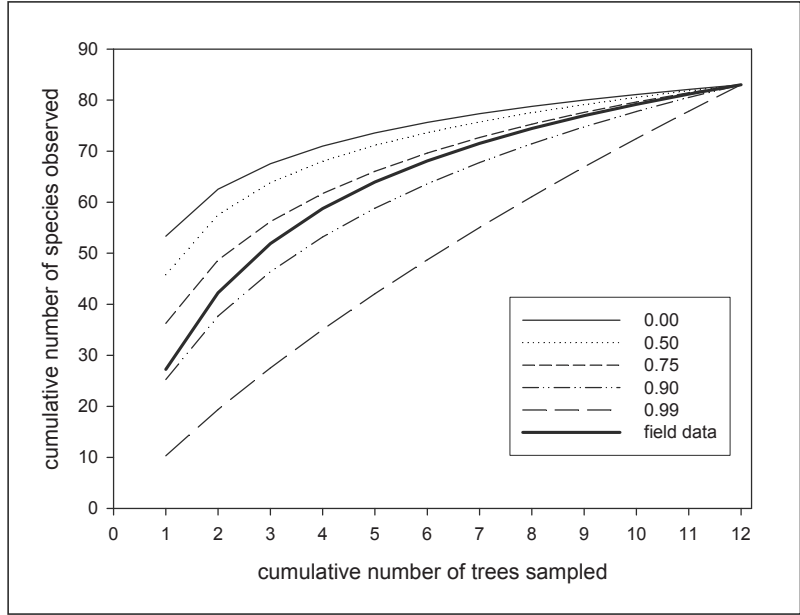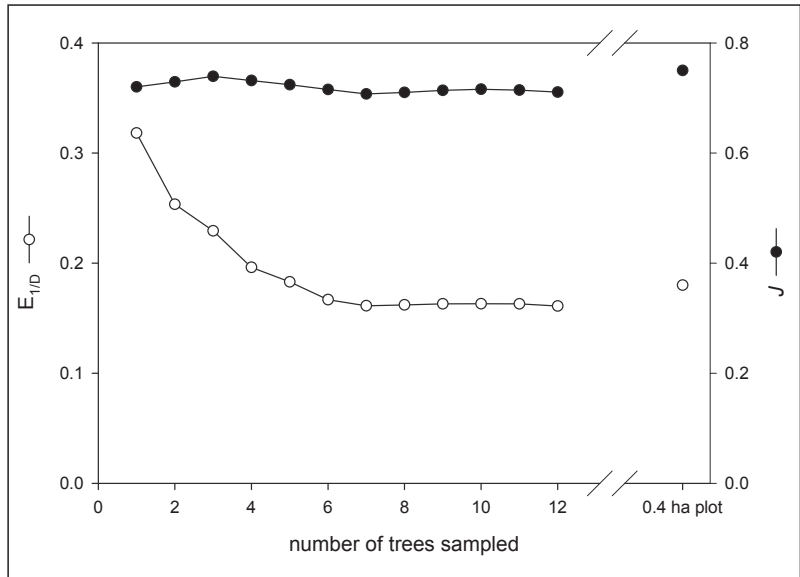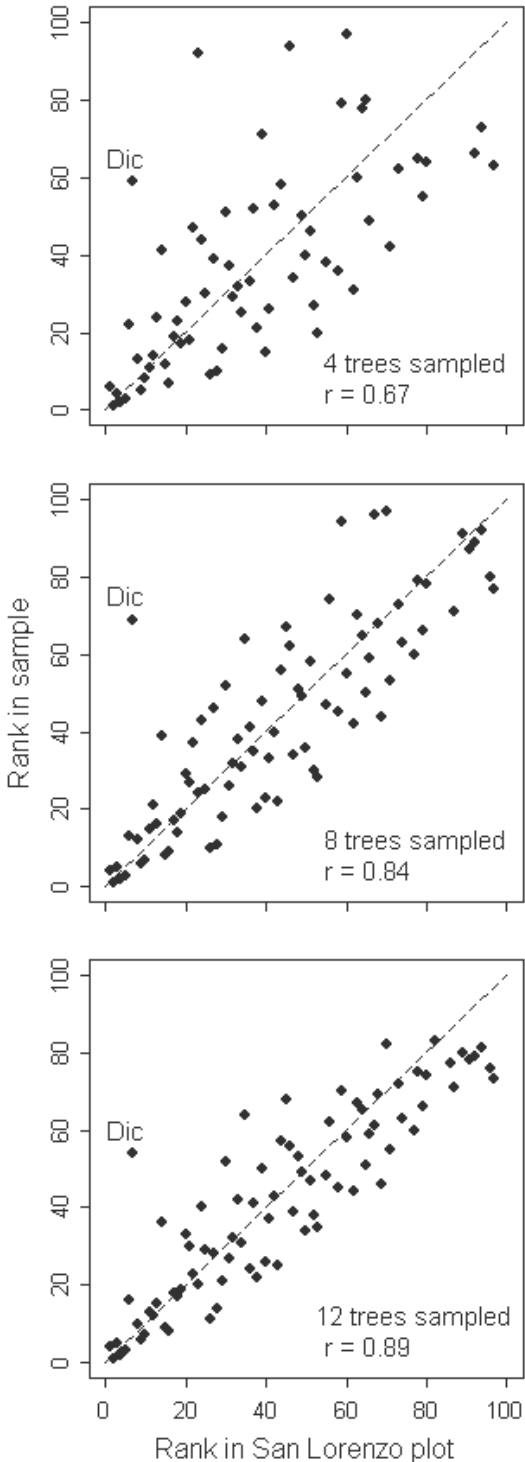

FIG. 3. Change in two evenness indices with an increasing number of trees sampled. Data are means. The respective values for the entire 0.4-ha plot are shown for comparison.

When the abundances of individual species were considered (Fig. 4), the correlation of rank orders was surprisingly good, but some species could show large discrepancies. These were primarily found in species that are known to prefer substrates of small diameter at lower to intermediate heights within the forest (Zotz 2007). Examples were *Peperomia rotundifolia* (Piperaceae) and *Microgramma reptans* (Polypodiaceae), but the most conspicuous deviation was observed in the fern *Dicranoglossum panamense*, which was among the 10 commonest species in the 0.4-ha plot, but only reached rank 54 in the sample of the 12 large trees. The 12-tree sample included nearly all of the common species, missing only 4 species with abundances > 10 individuals in the 0.4-ha plot (*Trichocentrum capistratum, Stenospermation angustifolium, Notylia albida, Polypodium triseriale*), which were all restricted to a small number of trees (4-10) in the plot.
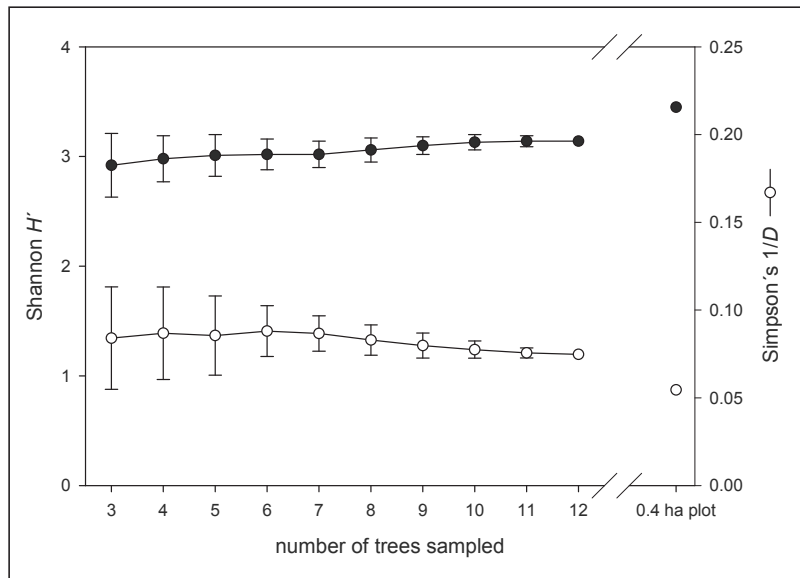
Diversity indices. The averages of the Shannon-Wiener Index (H') and the Simpson index ($1/D$) varied very little between samples of 3 and 12 trees, but deviated from the estimates of H' and $1/D$ derived from the entire data set by about 10 and 25 percent, respectively (Fig. 5).

DISCUSSION

For a detailed understanding of community structure, sampling all epiphytes on a relatively small number of trees is by no means a substitute for a comprehensive census with individually marked plants. However, the present study suggests that a rather limited effort in the field, i.e. the sampling of about 6-8 large trees, may yield a satisfactory description of the structure of a species-rich epiphyte community in terms of 1. the total species number (when using richness estimators; Fig. 1), 2. α-diversity (Fig. 5), and 3. evenness (Fig. 3). Moreover, the relative ranking of species derived from such a limited sampling effort was quite similar to that of the entire data set when 8 or more trees were sampled (Fig. 4).

FIG. 4. Correlation between the rank orders of the epiphytes sampled on a varying number of largest (4, 8, and 12 trees) and rank order of all epiphytes in the 0.4-ha San Lorenzo plot. One species which is typically found on small-diameter substrates in intermediate heights of the forest is indicated (Dic = *Dicranoglossum panamense*). Dotted lines are the 1:1 relationship, r = Pearson's correlation coefficient.

FIG. 5. Change in the Shannon-Wiener Index (H′) and the Simpson index (1/*D*) with an increasing number of trees sampled. Data are means ± SD. The respective values for the entire 0.4-ha plot are also given for comparison.

Thus even the relative abundance and dominance of most species is adequately captured in a rather small sample. This was unexpected in view of the documented patchiness of individual species (Fig. 2) and the repeated observation that a noticeable number of epiphyte species is uncommon on large trees, growing preferentially at lower and intermediate heights of the forest on substrates of small diameter (Johansson 1974, Gradstein *et al.* 2003, Krömer *et al.* 2007, Zotz 2007). Species like the fern *Dicranoglossum panamense*, a typical representative of this group (Johansson 1974, Gradstein *et al.* 2003, Zotz 2007), were indeed greatly underrepresented in the large-tree samples (Fig. 4), but not completely absent.

Overall, sampling only larger trees seems sufficient since there is no indication that any epiphyte species occurs exclusively on smaller trees in this forest (Zotz 2007). This may not be the case in other forest types, for instance montane forests where the lower strata may receive more light and support more epiphytes. In montane sites in Bolivia, for example, Krömer *et al.* (2007) identified a large number of epiphyte species that were not found at all on larger trees. For such forests additional sampling of smaller trees has been recommended (Flores-Palacios & García-Franco 2001,Gradstein *et al.* 2003, Wolf *et al.* 2009). Unfortunately, our current database does not allow us to evaluate whether varying importance of small trees is idiosyncratic or a general difference between the lowlands and montane sites.

The performance of the richness estimators varied considerably (Fig. 1B). All estimators increased with sample size, but MMM was least affected by the number of trees included. This justifies the use of this particular statistic, although MMM slightly underestimated the number of species, even when sampling 12 trees. Other studies on richness estimator methods also identified MMM as the most appropriate statistic (e.g. Flores-Palacios & García-Franco 2001, Herzog *et al.* 2002), but there is certainly no universal species richness estimator (*cf.*, e.g., Chazdon *et al.* 1998, Walther & Morand 1998, Leitner & Turner 2001).

The selection of trees to be included in this study was based mainly on size (dbh). Tree species identity has been shown to influence the spectrum of species growing on them (Laube & Zotz 2006), which could potentially cause a bias, although it seems likely that the chosen selection criterion will mostly lead to a diverse selection of tree species in such species-rich forests (Table 1). Spatial structure could also be problematic, if large trees were clumped and if trees closer to each other hosted more similar epiphyte assemblages. Again, although vascular epiphytes are highly clumped on individual host trees (Fig. 2), the proximity of host trees explained only a very small percentage (<10%) of the species compositions of their epiphyte assemblages (Zotz & Schultz 2008). Thus, the parsimonious sampling scheme described here seems sufficient.

The results presented in this paper suggest that it may be relatively easy to obtain a database that contains the structure of epiphyte communities from a number of field sites, and which will enable us to identify conservation priorities, allow comparative studies of regional or even larger scales, or assess long-term changes in community structure. However, yet another issue has to be addressed before such large-scale meta-analyses lead to consistent results: there is no real consensus in the literature how "epiphytes" are defined. Hence epiphyte studies may be restricted to holo-epiphytes (non-parasitic plants that germinate on trees and remain dependent for their entire life, e.g. Zotz 2004), hemi-epiphytes (plants that are epiphytic for some part of their ontogeny, but are otherwise tree-like or vine-like, e.g. Todzia 1986), or plants that mix both life-forms (e.g. Nieder *et al.* 2000, Benavides *et al.* 2005). Some studies even include parasitic mistletoes (ter Steege & Cornelissen 1989). Although a more comprehensive approach that includes several or even all dependent flora, i.e. vascular epiphytes, non-vascular epiphytes, hemi-epiphytes, mistletoes, vines and lianas, should be encouraged (see, e.g,. Kelly *et al.* 2004, Burns & Dawson 2005) because of the potentially important insights into conceivable positive or negative interactions between life forms (*cf.* Galeano *et al.* 1999), the frequent practice of lumping them in the analysis seems problematic. While the ecology of primary hemi-epiphytes is very similar to that of true epiphytes at least during the early stages of their ontogeny (Zotz & Winter 1994), the ecology of vine-like secondary hemi-epiphytes (e.g. many aroids) and truly epiphytic flora differs fundamentally. Lumping life forms makes comparisons among studies difficult or even impossible because different results may simply be due to the inclusion/exclusion of hemi-epiphytes. Arguably, this is the probable reason for highly divergent reports on vertical distribution patterns of "epiphytes" within a forest (e.g. Zotz 2004, Benavides *et al.* 2005). Including hemi-epiphytes will artificially increase the proportion of "epiphytes" near the base of tree trunks. It would be much more informative to document and study a likely negative interaction, e.g. a reduction of true epiphytes with an increased abundance of creeping hemi-epiphytes in lower strata of the forest. A similar problem emerges when the taxonomic participation at different sites is compared. The inclusion of hemi-epiphytes seemingly increases the importance of aroids in particular among local "epiphyte" communities. It should be acknowledged, however, that separating holo-epiphytes and hemi-epiphytes is frequently not trivial: especially among aroids, individuals of the same species may occur both as true epiphytes or as soil-rooted hemi-epiphytes (Croat 1988, Zotz 2004, Benavides *et al.* 2005). However, this problem can be solved at least in part by separate analyses depending on the particular research question (see, e.g., Zotz 2004)

Clearly, not all epiphyte-related ecological parameters can be well represented by sampling a few of the largest trees. For estimating (e.g.) epiphyte biomass per unit ground area an estimate of epiphyte cover on trees in different size classes will be necessary (Wolf *et al.* 2009). Also, the largest (and probably oldest) trees may not adequately represent the demographic structure of populations and communities. On the other hand, if sampling only a few trees gives reliable information on epiphyte community structure in terms of species composition and abundances, as appears to be the case, this provides an important basis for further studies, such as functional analyses of epiphyte distributions (Zotz 2004).

In summary, the present study confirms and extends earlier suggestions from a montane setting (Gradstein *et al.* 2003) that a small number of censused trees may yield a reliable representation of the structure of a local epiphyte community, including not only species richness but also other diversity measures, evenness, and species rank abundances. Given a common definition of epiphytic plants, the resulting database may enable us to address more general questions concerning the structure of epiphyte communities and biogeographic patterns, and also allow comparative studies in the context of the current debate on the neutral theory of biodiversity (Hubbell 2001) or in the context of global change (Benzing 1998).

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