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The epiphyte vegetation of the palm *Socratea exorrhiza* – correlations with tree size, tree age and bryophyte cover

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Abstract: We conducted a survey of the epiphyte flora growing on the stilt palm *Socratea exorrhiza* in a primary lowland rain forest in Panama by means of a canopy crane. For each palm in a 0.9-ha plot, we determined diameter at breast height, tree height, per cent bryophyte cover and the number, identity and attachment site of all vascular epiphytes. The 118 palm trees hosted a total of 701 epiphytes and hemi-epiphytes, belonging to 66 species. Trees were estimated to be *c.* 20 y old before colonization with vascular epiphytes began. Epiphyte species were highly clumped and segregated along the vertical axis of the trunk. Sequential colonization led to an increased number of species and individuals as the tree grows. Epiphytes were associated with bryophyte patches much more than expected by chance, but no species seemed to depend upon them for establishment. The influence of tree size, age and bryophyte cover on the composition of the epiphyte community are discussed.

Key Words: Araceae, Bromeliaceae, canopy dynamics, diversity, ferns, hemi-epiphytes, moss, Orchidaceae, vascular epiphytes

INTRODUCTION

The diversity of vascular epiphytes in tropical forests can be impressive: Gentry & Dodson (1987) found more than 100 species of epiphytes and stranglers, fully 35% of the total vascular flora, in a plot of 1000 m^2 in the wet forest of Rio Palenque, Ecuador. Kelly *et al.* (1994) reported an even higher percentage in an Andean forest in Venezuela: 120 of 219 species, i.e. more than 50% were true epiphytes. A single tree may support more than 50 different species (e.g. Ingram & Nadkarni 1993). However, we still know little of the dynamics of epiphyte communities (Benzing 1990).

The study of epiphyte community ecology is still hampered by the difficulty in accessing the upper strata of the forest. Consequently, the number of sampled trees is often low, e.g. one (Pupulin *et al.* 1995) or three trees (Freiberg 1996). Researchers have frequently avoided the problems associated with tall trees by studying epiphyte distributions in the lower strata of the forest (Kernan & Fowler 1995) or in forests of low stature (Zimmerman & Olmsted 1992, Zotz *et al.* 1999). The use of canopy cranes may now reduce this problem (Nieder *et al.* 1999).

Here, we report an investigation of community structure and dynamics of epiphytes on one host tree species, the stilt palm *Socratea exorrhiza*, within a 0.9-ha plot in the reach of a construction crane on the Caribbean slope of Panama. This particular study system was selected for a number of reasons. First, few studies can distinguish the effects of host tree identity and tree size on the epiphyte community over the entire size range of a tree species: the limitation to a single host tree with a large number of sampled individuals allowed this analysis. Second, knowledge of average host tree growth rates made it possible to roughly estimate tree age. Considering the almost complete lack of long-term observational data (but see Hietz 1997), simultaneous side-by-side observations allow us to approximate the temporal patterns of dynamic processes. Third, the simple architecture of this palm allowed the quantification of the substrate area available for epiphyte colonization, which has rarely been tried before for obvious reasons (see, however, Zotz 1997). Finally, the adverse establishment conditions on a vertical trunk featuring a smooth bark with relatively low water-holding capacity made this tree suitable to study the importance of bryophytes for the establishment of vascular epiphytes. Bryophyte mats supposedly play an important role for the distribution of vascular epiphytes on potential host trees: they hold water, trap seeds, provide anchorage for seedlings, and intercept nitrate from fog (Clark *et al.* 1998, Johansson 1974). Although these and other authors

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(Bennett 1987, Freiberg 1999, Hietz & Hietz-Seifert 1995*b*) reiterate the importance of mosses and liverworts for vascular epiphytes, documentation of cause and effect is rare (Laman 1995).

METHODS

This study was carried out in the late-1999 dry season at the Fort Sherman Canopy Crane site, which is located near the Atlantic coast of the Republic of Panama. Average annual rainfall is about 3500 mm (Lerdau & Throop 1999). Canopy height of this primary lowland forest is quite variable, reaching maxima of *c.* 40 m. The crane is 52 m high and has a radial length of 54 m, thus covering *c.* 9000 m^2 by means of a small gondola.

Within the reach of the crane we located all individuals of the stilt palm *Socratea exorrhiza* (Mart.) H. Wendl. (syn. *S. durissima* (Oerst.) H. Wendl.). Data from each palm included diameter at breast height (dbh; to the nearest mm; for trees > 50 mm dbh in 1999, data were supplied by R. Condit), height (to the nearest 0.5 m) and bryophyte cover on the trunk to the nearest 5%. Only bryophyte turfs exceeding *c.* 2 mm in height were considered. Subsequently, the trunk and stilt roots were searched for the presence of vascular epiphytes. Hemi-epiphytes were also included, whether or not they had contact with the soil. On the other hand, vines such as the abundant *Philodendron inaequilateratum* Liebm. were ignored. The gondola was positioned in the forest canopy to allow access to all epiphytes on *Socratea exorrhiza*, but in rare cases the palm trunk was inspected with binoculars. With few exceptions, we were able to identify each individual to species level, even in the case of juveniles (only tiny seedlings were ignored). In this report, ‘individual’ is used *sensu* Sanford (1968), i.e. as ‘group of stems’. For each epiphyte, the following variables were determined: height on the tree, azimuth, substrate quality (i.e. whether an epiphyte was growing in a bryophyte mat or turf), size (i.e. number and size of stems and leaves). Voucher specimens are deposited in the herbarium of the Smithsonian Tropical Research Institute, Panama (Tupper Center). Plant names of angiosperms follow the flora of Panama checklist (D’Arcy 1987), while fern names are according to Lellinger (1989).

Nearest neighbour analysis was conducted for all epiphytes occurring on *S. exorrhiza* by means of a custom-made computer program which produced null model distributions by randomly assigning each individual to one of the 701 attachment sites. A nearest neighbour was defined as that epiphyte on a given host tree with the shortest vertical distance to a focal plant, which did not differ in azimuth by more than 90°. The program was run 240 times. By discarding the six lowest and the six highest values in each category we produced 95% confidence intervals (Noreen 1989). For reasons of clarity only the results for those six epiphyte species with > 5% of all individuals will be presented. All other statistical analysis was carried out with STATISTICA software (STATISTICA 5.1, StatSoft Inc., Tulsa, OK, USA). Whenever possible, we used parametric statistics, sometimes log-transforming data before analysis (Sokal & Rohlf 1995).

RESULTS

Host tree characteristics

In contrast to most other Arecaceae, the stilt root palm *Socratea exorrhiza* increases in trunk diameter with height (Schatz *et al.* 1985). In our population, the diameter at breast height (dbh) correlated closely with the $\log_{10}$ of tree height ($\log_{10}$ (tree height) = –0.25 + 0.01 dbh, $r^2 = 0.90$, P < 0.001, n = 118). To estimate tree age, we used dbh data from repeated measurements in late 1997 and early 1999 from a larger sample of palms growing in and immediately adjacent to our study area (R. Condit *et al.*, unpubl. data). Increments (standardized for 1 y) were plotted against the initial dbh. We found a weak, but highly significant negative correlation between dbh and subsequent increment (r = –0.22, P < 0.001, n = 567). Mean annual increment in dbh gradually decreased from almost 5 mm y^{-1} in very small plants to zero growth in the largest individuals (Δdbh = 4.58 – 0.03 dbh). The modelled growth, i.e. dbh increment, of such an ‘average’ tree is depicted in Figure 1. Also given are the changes in height, using the above regression between dbh and tree height. Total bark surface (*S*), i.e. the potential target area for epiphyte diaspores, increased exponentially with dbh (log *S* = –1.670 + 0.016 dbh; $r^2 = 0.94$, P < 0.001; n = 118).

The epiphyte community

In the *c.* 9000 m^2 within reach of the crane, we located 118 individuals of *Socratea exorrhiza*. Tree height ranged 0.3–25 m, dbh 5–170 mm, and *S* 0.01–5.7 m^2. Bryophyte cover varied from 0 to 30% and was positively correlated with dbh (r = 0.58, P < 0.001, n = 118). The remaining bark was mostly covered with crustose lichens, but we also observed smaller mosses and liverworts (< 2 mm height) or algae. Vascular epiphytes were found on 57 trees, i.e. on 48% of all individuals. In total, we observed 701 epiphytes (and hemi-epiphytes) belonging to 66 species in 15 families (Appendix 1). All but 17 individuals, which were growing on the spiny stilt roots, occurred on the trunk. The highest number of individuals (85 specimens out of 12 species) was found on a large palm (dbh 140 mm), an even higher diversity, 16 species, was observed on another large tree (dbh 157 mm; 53 individuals).

The three most common species were all ferns

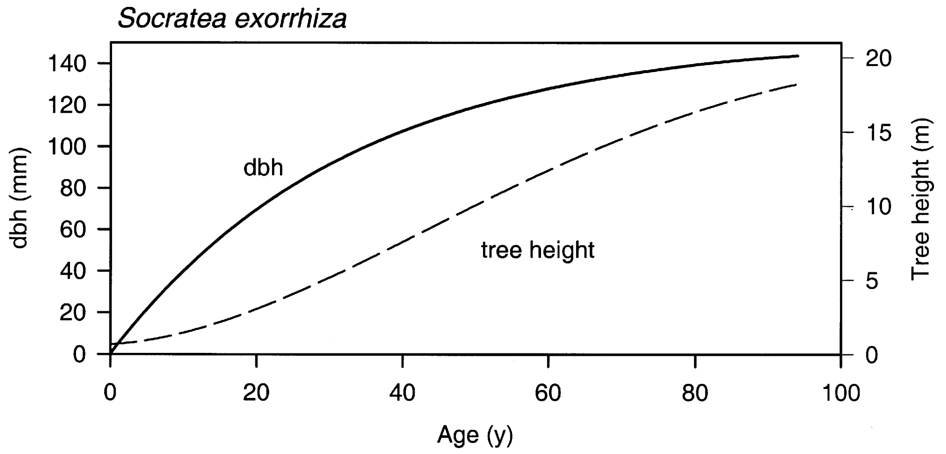

Figure 1. Model growth in *Socratea exorrhiza*. Based on the regression of tree size and subsequent annual increment in dbh an average relationship of age and dbh is simulated. Tree height was then calculated from dbh as log(tree height) [m] = –0.25 + 0.01 dbh [mm].

(*Ananthacorus angustifolius*, *Elaphoglossum sporadolepis*, *Dicranoglossum panamense*), accounting alone for almost 30% of all individuals. Other common species representing more than 5% of the total were *Scaphyglottis longicaulis* (Orchidaceae), the secondary hemi-epiphyte *Philodendron schottianum* (Araceae) and *Guzmania subcorymbosa* (Bromeliaceae). On the other hand, almost half of all species were rare, i.e. occurred with just 1–3 individuals on our population of palms (Appendix 1).

Attachment heights, which were analysed for the 13 most abundant species, differed significantly (one-way ANOVA, $F_{12,497} = 23.2$, $P < 0.001$; Figure 2). While some taxa (e.g. *Ananthacorus angustifolius*, *Elaphoglossum sporadolepis*) were found at almost any possible height along the trunk, most species showed a rather narrow range. It was possible to distinguish between understorey (e.g. *Anthurium clavigerum*), midstorey (e.g. *Guzmania subcorymbosa*) and 'canopy' species (e.g. *Scaphyglottis graminifolia*).

Trees with epiphytes were significantly larger than those without epiphytes (t-test, $P < 0.001$). The relationship between tree size and epiphyte abundance was further explored with a best-fit polynomial regression model (Figure 3b): the regression explained 34% of the variation. Only on two of the 50 trees smaller than about 80 mm dbh were vascular epiphytes found (two individuals of *Trichomanes* spp. and one of *Asplenium serratum*). Excluding these two cases, we estimate that trees are about 20 y old before colonization by vascular epiphytes begins (based on average growth rates of this palm; Figure 1). Because the number of species and individuals were closely correlated (log species = 0.13 + 0.58 log individuals, $r^2 = 0.86$, $P < 0.001$, n = 57 trees with epiphytes), we expected and found similar results in an analysis with species numbers ($r^2 = 0.47$; Figure 3c), The regression coefficient of the above equation was smaller than 1, i.e. the number of individuals per species increased significantly with the number of species per tree ($r = 0.57$, $P < 0.001$). Higher abundance and diversity of epiphytes with tree size was not simply the consequence of the exponential increase in substrate area with dbh. The density of epiphyte individuals was significantly higher on larger trees (Spearman $r = 0.26$, $t_{(n-2)} = 2.01$, $P = 0.049$, n = 57): while small trees with epiphytes (dbh = 80–90 mm) supported less than one specimen per m^2, this density approximately tripled in the largest palms (the maximum was 5.6 individuals m^{-2}). In contrast to density, diversity did not change with size (Spearman rank order correlation, $r = 0.12$, $t_{(n-2)} = 0.89$, $P = 0.38$, n = 57) with 0.4 species m^{-2} on average. Larger trees frequently hosted larger specimens (Table 1). We found a significant increase in plant size with host tree dbh in three of the 13 species; the trend in a fourth species, *Dichaea panamensis*, was marginally significant.

The sequence of colonization of *Socratea* trees is analysed in Table 2 and Figure 4. Figure 4 gives representatives of three groups: the first, represented by *Philodendron schottianum* among others, was frequently the first to colonize a tree, but was also consistently found in more complex species assemblages. The second group with, for example, *Dicranoglossum panamense*, *Ananthacorus angustifolius* or *Anthurium clavigerum* showed a continuous increase with species numbers. The last group, finally, was never present in species-poor assemblages: typical examples are *Niphidium crassifolium* and *Scaphyglottis* spp.

We also analysed nearest neighbour relationships for the six most abundant species (Table 3). Invariably, the nearest neighbour being a conspecific was observed much more often than expected by chance. There were few other deviations from the expected frequencies of species pairs. For example, the two ferns *Ananthacorus angustifolius* and *Dicranoglossum panamense* were found next to each other more often than expected by chance, while the latter species was never nearest neighbour of either

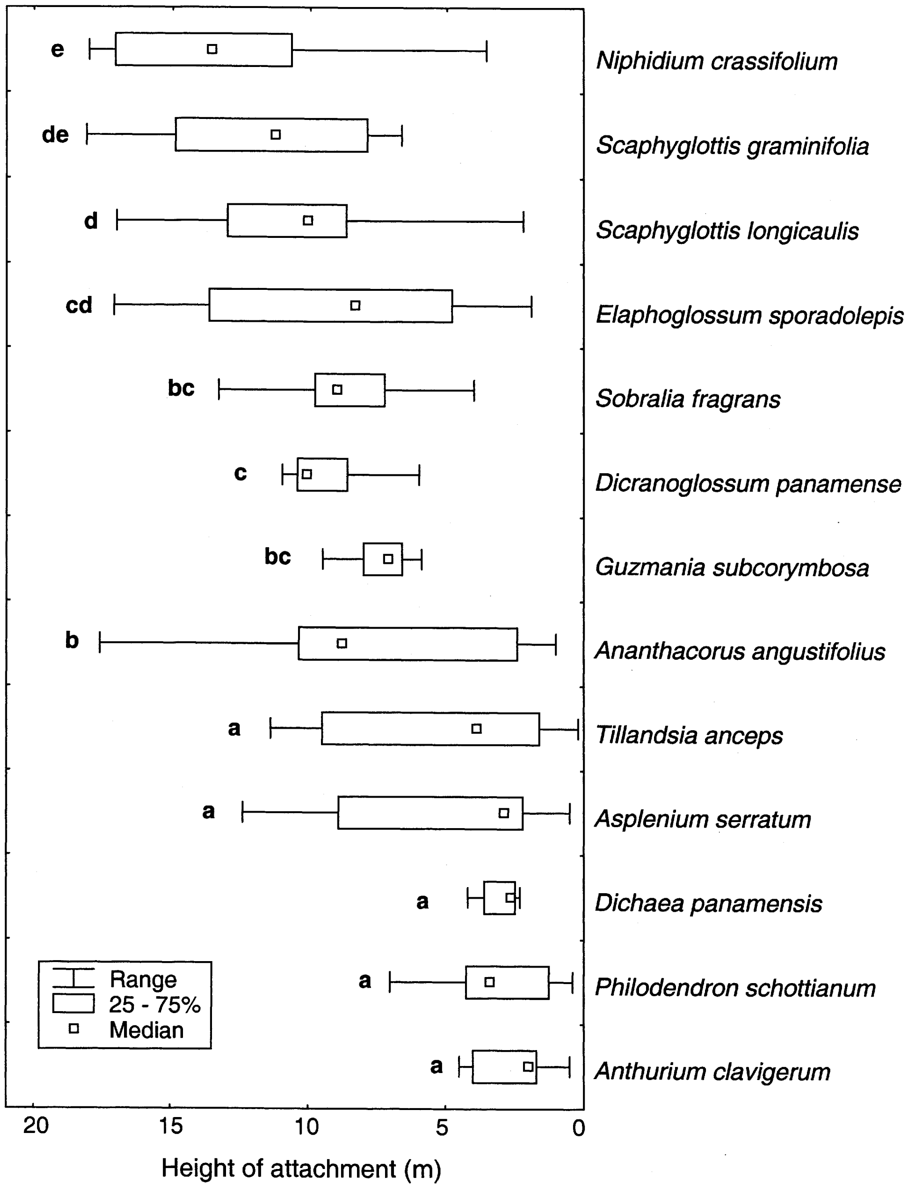

Figure 2. Vertical distributions of the 13 most abundant epiphyte species on *Socratea exorrhiza*. Different letters beside each box plot indicate significant differences in a post-hoc LSD test ($P < 0.05$). For reasons of clarity outliers are not shown.

Scaphyglottis longicaulis or *Philodendron schottianum*. The latter finding is not surprising, however, considering the vertical distributions of the three species (Figure 2).

The temporal pattern of the colonization of *Socratea* by bryophytes was not distinguishable from that of vascular epiphytes (Figure 3). The spatial association of these two plant groups was analysed by comparing the number of vascular epiphytes occurring directly on bark to those found rooted in patches of bryophytes. First, we estimated the bark area covered by bryophytes. We obtained 7.9 m^2, i.e. 5% of the total bark surface (155 m^2) of all of the palms in the study area. The number of epiphytes growing in patches of mosses and liverworts, however, was considerably higher than expected from this surface area, i.e. 267 or 38% of all 701 individuals ($\chi^2 = 1509$; $P < 0.001$). This association with bryophytes was highly variable (Table 4). While some species, for example *Ananthacorus angustifolius* or *Dicranoglossum panamense* almost always anchored in patches of mosses and liverworts, others like *Scaphyglottis longicaulis* were rarely associated with them.

DISCUSSION

Even architecturally simple trees like *Socratea exorrhiza* may host an impressive number of vascular epiphytes

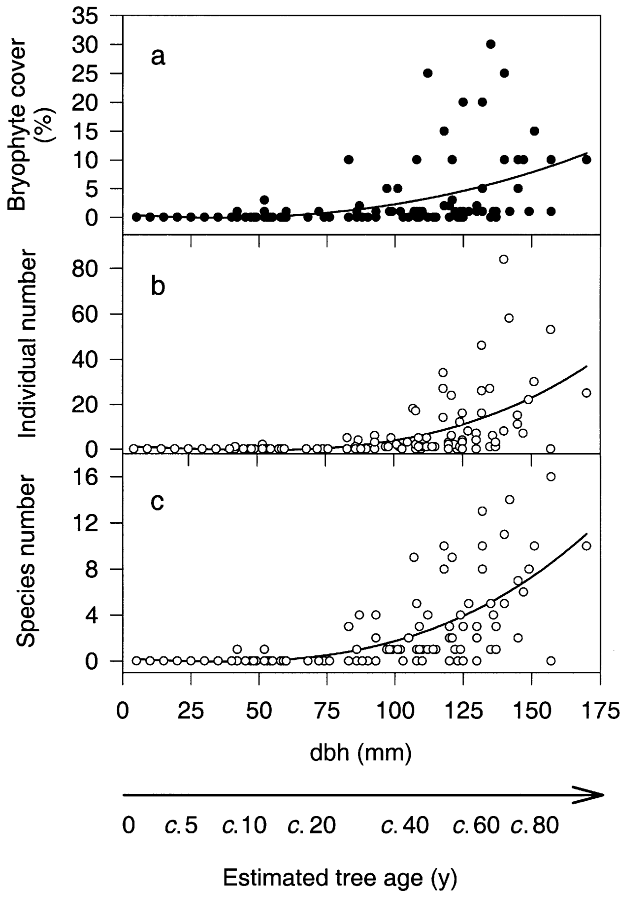

Figure 3. Relationships of the relative bryophyte cover (a), the number of epiphyte individuals (b) and the number of epiphyte species (c) and host tree size (dbh; in mm), respectively. The estimated tree age (y) is also given (compare Figure 1). Each symbol is a different tree (n = 118). The lines are best-fit polynomial regressions: bryophyte cover (%) = 0.52 –0.03 dbh + 0.004 dbh^2 + 8.7 × 10^{-7} dbh^3, r^2 = 0.22; individuals = 1.23 –0.03 dbh – 0.0006 dbh^2 + 1.2 × 10^{-5} dbh^3, r^2 = 0.34; and species number = 0.21 – 0.01 dbh + 3.6 × 10^{-6} dbh^2 + 2.6 × 10^{-6} dbh^3, r^2 = 0.47.

within a small area of lowland forest: we observed a maximum of 16 species on a single large tree (Figure 3c), and distinguished a total of 66 taxa on the 57 trees with epiphytes. This represents about half of all epiphyte taxa in the 0.9-ha plot (Zotz & Schultz, unpubl. data). Species were clearly segregated vertically (Figure 2). Several species occupied a rather limited range, but others like *Ananthacorus angustifolius* could be found over almost the entire trunk. Competition seems an unlikely explanation for this pattern, considering the low densities of epiphytes (less than 1 individual m^{-2}). Alternatively, we assume that differences in light and humidity requirements may explain much of the observed segregation. Unfortunately, there is little information on the ecophysiology of most of the component species to test this suggestion.

Although overall diversity of epiphytes on *Socratea exorrhiza* was high, colonization was probably very slow. The youngest palms with vascular epiphytes (two species of ferns; Figures 3b,c) were estimated to be about 20 y old. Dudgeon (1923) described a very similar picture in his classic study in a Himalayan forest: it took vascular epiphytes about two decades to get established on *Quercus incana* trees. A somewhat faster development was reported from a montane forest in the Bolivian Andes (Ibisch 1996). There, 10-y-old *Alnus acuminata* trees hosted a larger number of epiphyte species, amounting to about half of the maximum diversity found on 'mature' trees. Finally, Catling *et al.* (1986) found an average number of three species per tree in a 13-y-old grapefruit orchard in Belize, while 30-y-old plantations averaged eight species per tree. Thus, colonization of trees by vascular epiphytes seems to be rather slow in general, but mostly faster than in the palm tree of this study.

At the time of the initial colonization by vascular epiphytes, *Socratea* trees had grown to about 5 m height (Figure 1), i.e. probably still did not offer suitable substrate for those species restricted to higher strata (e.g.

Table 1. Correlation between plant size, estimated as length of longest leaf (L) or shoot (S), and host tree dbh for the 13 most common epiphyte species. Shown are the results of separate Spearman rank order correlation analyses with sample size (n), correlation coefficient (Spearman R), t-value and P level. Significance is indicated by asterisks.

Species	Size	Abbreviation	n	Spearman R	$t_{(n-2)}$	P
Ananthacorus angustifolius	L	Aa	76	–0.16	–1.4	0.17
Anthurium clavigerum	L	Ac	21	0.52	2.63	0.017*
Asplenium serratum	L	As	18	0.05	0.2	0.84
Dichaea panamensis	S	Dp	16	0.45	1.91	0.07
Dicranoglossum panamense	L	Dcp	56	–0.13	–0.93	0.36
Elaphoglossum sporadolepis	L	Es	70	0.15	1.27	0.21
Guzmania subcorymbosa	L	Gs	40	0.48	3.34	0.002*
Niphidium crassifolium	L	Nc	24	0.67	4.15	0.000*
Philodendron schottianum	L	Ps	49	–0.05	–0.33	0.74
Scaphyglottis graminifolia	S	Sg	34	0.17	0.97	0.34
Scaphyglottis longicaulis	S	Sl	51	–0.15	–1.05	0.30
Sobralia fragrans	S	Sf	31	–0.04	–0.19	0.85
Tillandsia anceps	L	Ta	23	0.03	0.13	0.9

Table 2. Correlation between the per cent occurrence of the 13 most common epiphyte species and the total number of taxa per tree. For each species we give the % occurrence in the 57 epiphyte assemblages, correlation coefficient (Spearman R), t-value and P level. Significance is indicated by asterisks.

Species	% Occurrence	Spearman R	$t_{(n-2)}$	P
Anthurium clavigerum	26	0.75	2.75	0.03*
Ananthacorus angustifolius	32	0.85	3.90	0.01*
Asplenium serratum	14	0.29	0.76	0.48
Dichaea panamensis	5	0.37	0.98	0.37
Dicranoglossum panamense	21	0.92	5.84	0.001*
Elaphoglossum sporadolepis	26	0.85	4.02	0.01*
Guzmania subcorymbosa	9	0.87	4.38	0.004*
Niphidium crassifolium	12	0.87	4.24	0.01*
Philodendron schottianum	42	–0.22	–0.54	0.61
Scaphyglottis graminifolia	11	0.63	1.97	0.10
Scaphyglottis longicaulis	12	0.80	3.32	0.02*
Sobralia fragrans	16	0.85	3.95	0.007*
Tillandsia anceps	23	0.68	2.29	0.06

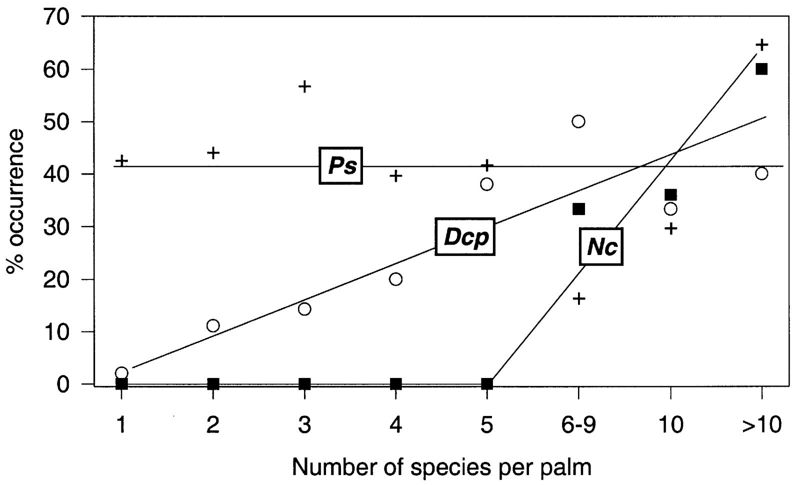

Figure 4. The per cent occurrence of the most common epiphyte species in communities differing in species number from 1 to 16. The lines were drawn by hand. *Dcp = Dicranoglossum panamense* (open circles), *Nc = Niphidium crassifolium* (closed squares), *Ps = Philodendron schottianum* (crosses).

Table 3. The identity of nearest neighbours of the six most common epiphytes. For each species the observed occurrence of species pairs and the limits of 95% confidence intervals of random distributions (in parentheses) are given. Bold numbers indicate species pairs, which were observed more commonly than expected; numbers in italics are combinations less common than expected. Note that the matrix is asymmetric because the fact that individual A is nearest neighbour to individual B does not imply that B is nearest neighbour to A.

	Aa	Es	Dcp	Sl	Ps	Gs
Ananthacorus angustifolius (Aa)	**28**	3	**20**	2	2	1
	(2;16)	(3;13)	(2;10)	(2;10)	(1;9)	(1;8)
Elaphoglossum sporadolepis (Es)	3	**38**	2	3	*0*	2
	(3;13)	(2;12)	(2;9)	(1;9)	(1;9)	(1;8)
Dicranoglossum panamense (Dcp)	**12**	5	**26**	*0*	*0*	*0*
	(2;11)	(1;10)	(1;9)	(1;8)	(1;7)	(1;6)
Scaphyglottis longicaulis (Sl)	1	3	0	**36**	*0*	0
	(0;10)	(1;9)	(0;8)	(0;9)	(1;7)	(0;6)
Philodendron schottianum (Ps)	2	1	*0*	1	**23**	2
	(2;9)	(1;9)	(1;7)	(1;7)	(0;8)	(0;6)
Guzmania subcorymbosa (Gs)	1	2	1	0	0	**25**
	(1;8)	(1;8)	(0;7)	(0;6)	(0;6)	(0;7)

Table 4. Association of 13 species of vascular epiphytes with bryophyte mats. Given are the observed and the expected frequencies (assuming similar proportions for all species) for individuals growing in bryophytes (bryophyte +) or on bare bark (bryophyte –). Bold numbers indicate significant differences between observed and expected frequencies (χ^2, P < 0.05). For species abbreviations see Table 1.

	Species abbreviation												
	Aa	Ac	As	Dp	Dcp	Es	Gs	Nc	Ps	Sg	Sl	Sf	Ta
n	76	21	18	16	56	70	40	24	49	34	51	31	23
Observed frequencies													
Bryophyte +	**57**	**1**	3	3	**46**	**45**	**6**	8	**1**	16	**2**	13	4
Bryophyte –	**19**	**20**	15	13	**10**	**25**	**34**	16	**48**	18	**49**	18	19
Expected frequencies													
Bryophyte +	30	8	7	6	22	28	16	10	20	14	20	12	9
Bryophyte –	46	13	11	10	34	42	24	14	30	20	31	19	14

Scaphyglottis spp., cf. Figure 2). Further growth coincided with a strong increase in tree height and bryophyte cover (Figures 1, 3a). Both processes along with possible weathering of the bark (cf. Catling *et al.* 1986) should lead to habitat diversification and are expected to facilitate the colonization of palm trees by an increasing number of epiphytes. This expectation was only partly fulfilled. While we observed a substantially higher density, species numbers per unit surface area did not change with plant size.

Overall, the correlation between tree size and epiphyte load was quite weak (Figure 3), indicating that local idiosyncrasies such as proximity to sources of propagules, variation in microclimate (due to, for example, local differences in forest canopy height) or possible accidents caused by foraging arboreal animals (Perry 1978), falling palm fronds, or simply chance have a strong influence on the composition of the epiphyte community of a particular tree. The observation that many of the larger trees were devoid of epiphytes (Figure 3) in spite of their size and age (Figure 1) is not exceptional. For example, Johansson (1974) found that only 50% of all larger trees in an African rain forest carried epiphytes. However, in spite of the unpredictability of the resident epiphyte flora of any one tree and the dismissal of Went's (1940) concept of species specificity as a rare exception (Benzing 1990), we reiterate the suggestion of Zotz *et al.* (1999): each tree species in a given area of forest may host a specific *spectrum* of epiphyte taxa. Each tree species offers a unique set of architectural, morphological, chemical and phenological traits, which should give rise to a similarly unique subset of epiphytes from the local species pool, both in terms of species composition and, in particular, relative abundances. It was already pointed out by Went (1940) that accumulations of humus may mitigate possible effects of a host tree species. Hence, it is conceivable that differences in the epiphyte spectra between host trees are minor or absent in forests, where branches carry a dense cover of bryophytes, lichens and dead organic material, for example many montane forests.

Although vascular epiphytes were more commonly associated with patches of bryophytes than expected by chance, the majority of individuals, i.e. *c.* 60%, had colonized naked bark or crustose lichens. While there were obvious species-specific differences in the degree of the association with bryophytes (Table 4), none seemed to be dependent on bryophytes for establishment even on the smooth bark of a palm. This finding contrasts with other studies, in which the establishment of bryophytes was depicted as a *necessary* successional step in the development of epiphyte communities (Dudgeon 1923, Van Oye 1924). Our results are, however, consistent with the notion that mosses and liverworts strongly facilitate the establishment of seedlings of vascular epiphytes. Presently, our evidence is correlational: only experiments such as those by Laman (1995) can reveal the nature of this association. Although we emphasize the positive effects of cryptogams on vascular epiphytes, this interaction may have a negative outcome as well for seedlings. For example, Zotz & Andrade (2002) report the repeated observation of foliose lichen thalli over-growing and presumably killing the seedlings of epiphytic orchids.

The question whether there is true succession among vascular epiphytes is debated (Benzing 1990). While some studies (Catling *et al.* 1986, Catling & Lefkovitch 1989, Johansson 1974) describe the replacement and decline of early seral stages by later ones, others find no indication of such processes (Yeaton & Gladstone 1982, Zotz *et al.* 1999). Similar to these latter studies, most species in the present investigation increased in numbers in more complex epiphyte assemblages on older trees, none decreased in occurrence (Table 2). Figure 4 suggests three different groups of colonists. The hemi-epiphytic *Philodendron schottianum* and the epiphytic *Asplenium serratum* were frequent components of palms with epiphytes, irrespective of species numbers, i.e. may be called persistent pioneers. The majority of the remaining species showed a constant increase in frequencies with species number per tree, while a last group only occurred in more complex assemblages. Notably, the latter species, e.g. *Niphidium crassifolium* or *Scaphyglottis* spp., were those restricted to the upper part of the trunk (Figure 2, cf. Zotz & Winter 1994).

The observation that the number of individuals per species was considerably larger in more diverse species assemblages is consistent with the finding that long-distance dispersal is rare among vascular epiphytes (Murren & Ellison 1998). A predominance of short-distance dispersal would produce highly clumped distributions: consistent with this view, each species was most often its own nearest neighbour (Table 3; see also Hietz & Hietz-Seifert 1995*a*, Yeaton & Gladstone 1982). We suggest that most individuals on a given tree are the progeny of early arrivals, but work on the population genetics of a large number of epiphytic taxa is necessary to test this hypothesis more rigorously.

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Appendix 1. Vascular epiphytes and hemi-epiphytes occurring on *Socratea exhorriza*. Species are listed by decreasing abundance. Species names of flowering plants follow the Flora of Panama Checklist and Index (D'Arcy 1987), and Lellinger (1989). Hemi-epiphytes are marked with an asterisk.

Species	Family	Individuals
Ananthacorus angustifolius	Vittariaceae	76
Elaphoglossum sporadolepis	Lomariopsidaceae	70
Dicranoglossum panamense	Polypodiaceae	56
Scaphyglottis longicaulis	Orchidaceae	51
Philodendron schottianum *	Araceae	50
Guzmania subcorymbosa	Bromeliaceae	40
Scaphyglottis graminifolia	Orchidaceae	34
Sobralia fragans	Orchidaceae	31
Niphidium crassifolium	Polypodiaceae	24
Tillandsia anceps	Bromeliaceae	23
Anthurium clavigerum *	Araceae	21
Asplenium serratum	Aspleniaceae	18
Dichaea panamensis	Orchidaceae	16
Vriesea gladioliflora	Bromeliaceae	14
Epidendrum nocturnum	Orchidaceae	13
Epidendrum difforme	Orchidaceae	11
Polybotrya villosula	Dryopteridaceae	11
Anthurium friedrichsthalii	Araceae	11
Columnea billbergiana	Gesneriaceae	8
Campyloneurum phyllitidis	Polypodiaceae	7
Codonanthe macradenia	Gesneriaceae	7
Syngonium podophyllum *	Araceae	7
Campyloneurum occultum	Polypodiaceae	6
Trichomanes angustifrons	Hymenophyllaceae	6
unidentified juveniles	Polypodiaceae	5
Peperomia rotundifolia	Piperaceae	5
Anthurium cf. *acutangulum*	Araceae	5
unidentified juveniles	Araceae	5
Vittaria lineata	Vittariaceae	4
Peperomia ebingeri	Piperaceae	4
Scaphyglottis prolifera	Orchidaceae	4
Topobea praecox *	Melastomataceae	4
Trichomanes ekmanii	Hymenophyllaceae	4
Clusia cf. *uvitana* *	Clusiaceae	4
Tillandsia bulbosa	Bromeliaceae	4
Microgramma lycopodioides	Polypodiaceae	3
Pleopeltis percussa	Polypodiaceae	3
Encyclia chimborazoensis	Orchidaceae	3
Pleurothallis orbicularis	Orchidaceae	3
Trichomanes ovale	Hymenophyllaceae	3
Anthurium cf. *salviniae*	Araceae	3
Pleopeltis cf. *panamensis*	Polypodiaceae	2
Polypodium triseriale	Polypodiaceae	2
Polystachya foliosa	Orchidaceae	2
Sobralia panamensis	Orchidaceae	2
Guzmania mosaica	Bromeliaceae	2
Vriesea sanguinolenta	Bromeliaceae	2
Philodendron radiatum *	Araceae	2
Philodendron sp.	Araceae	2
Anetium citrifolium	Vittariaceae	1
Ravnia triflora *	Rubiaceae	1
Polypodium costaricense	Polypodiaceae	1
Peperomia macrostachya	Piperaceae	1
Dimerandra emarginata	Orchidaceae	1
Elleanthus longibracteatus	Orchidaceae	1
Ornithocephalus cf. *bicornis*	Orchidaceae	1
Pleurothallis verecunda	Orchidaceae	1
unidentified juvenile	Orchidaceae	1
Lomariopsis vestita	Lomariopsidaceae	1
Trichomanes godmanii	Hymenophyllaceae	1
Drymonia serrulata	Gesneriaceae	1
Epiphyllum phyllanthus	Cactaceae	1
Aechmea tillandsioides var. *kienastii*	Bromeliaceae	1
Monstera dilacerata	Araceae	1
Philodendron sagittifolium *	Araceae	1
Stenospermation angustifolium	Araceae	1