

The vascular epiphytes of a lowland forest in Panama— species composition and spatial structure

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Abstract We conducted a comprehensive census of the vascular epiphytes in a lowland forest in Panama by means of a canopy crane. In 0.4 ha of ca. 40-m tall forest, 103 species of vascular epiphytes with 13,099 individuals were found. The orchids were the most important family both in species and individual numbers, accounting alone for >40% of all species and >50% of all individuals. There was a clear vertical segregation of species with a concentration at intermediate heights: more than 50% of all individuals were found between 15 m and 25 m above ground. Tree species identity, tree size and the position of a tree in the forest (“space”) all influenced species composition. However, none of the two environmental variables nor space alone explained more than 10% of the total variation in epiphyte assemblages in several canonical correspondence analyses. By far the largest proportion of the observed variation remained unexplained and is arguably due to mere chance. In the future, our results will be used as a baseline

data-set for the direct observation of the long-term dynamics in a diverse epiphyte community.

Keywords Biodiversity · Bromeliaceae · Orchidaceae · Tropical forests · San Lorenzo crane site · Patchiness

Introduction

The control of alpha diversity, i.e. the number of species coexisting at a small spatial scale, remains a central question of community ecology, particularly for hyper-diverse tropical rain forests. While enormous progress has been made in understanding the mechanisms underlying the diversity of trees in tropical forests (Harms et al. 2000; Hubbell et al. 1999; Volkov et al. 2005) this is much less true for other life forms. Considering that “non-trees” generally form by far the larger portion of tropical phytodiversity (Galeano et al. 1999; Gentry and Dodson 1987) there is a clear need for descriptive and experimental data on community composition and community dynamics of the co-occurring groups of epiphytes, hemiepiphytes, lianas and vines, shrubs and forbs. Vascular epiphytes frequently represent the most species-rich life form in tropical forests (Benzing 1990; Gentry and Dodson 1987). Although their contribution to local species richness is generally greater in montane forests (Kelly et al. 2004), they still account for at least 10–20% of all vascular

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species in most lowland forests (Balslev et al. 1998; Benavides et al. 2005; Bordenave et al. 1998; Croat 1978; Whitmore et al. 1985).

Here we present a complete inventory of the vascular epiphytes found in 0.4 ha of lowland forest on the Caribbean slope of Panama and provide detailed data on their spatial distribution. A tower crane allowed repeated access to the forest canopy and facilitated a comprehensive sampling of the epiphytes growing on almost 1,400 trees. The paper describes the current composition of the epiphyte community comprising >13,000 individuals, analyses vertical and horizontal distribution patterns, and studies the effect of tree size and tree species on the composition of epiphyte assemblages. Future descriptive census work will determine whether the current patterns in this species-rich epiphyte community are rather stable in time and space, while on-going experiments explore the underlying mechanisms of these distributions.

Materials and methods

Field site and census work

This study was conducted at the San Lorenzo Canopy Crane site, which is 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 estimated to be around 3500 mm. Canopy height of this primary rain forest is quite variable and reaches 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 was inspected for the occurrence of vascular epiphytes. While the census included woody hemi-epiphytes of the genera *Ficus*, *Coussapoa*, *Clusia* and *Havetiopsis* and abundant climbing aroids such as *Philodendron schottianum*, the analysis of this paper is limited to holo-epiphytes. There are a number of species in the Araceae, which may grow either as an epiphyte or as secondary hemiepiphyte (Croat 1978). In this study, both life forms were observed in individuals of *Philodendron radiatum* and *P. sagittifolium*. Again, only truly epiphytic individuals are included in the analysis.

The following data were collected for each individual: height of attachment (minimum and maximum in creeping species), leaf/frond number, leaf length, stem length and/or number of shoots

(depending on species). The delimitation of individual plants is often difficult in vascular epiphytes, and we followed Sanford's (1968) definition of an "individual": a group of rhizomes and leaves belonging to one species, which forms a clearly delimited stand. With the exception of small seedlings, which could frequently not be identified to species, all plant sizes were included in the census.

Species names of flowering plants follow the Flora of Panama Checklist and Index (D'Arcy 1987), authorities for ferns are according to Lellinger (1989) and Croat (1978), for filmy ferns compare also Zotz and Büche (2000). *Encyclia aemula* (= *Prosthechea aemula*) was treated as a separate species following Dressler (1993). Voucher specimens are deposited in the herbarium of the Smithsonian Tropical Research Institute, Panama (Tupper Center).

Data analysis

The spatial structure and the influence of host tree characteristics (tree identity and tree size (dbh = diameter at breast height)) on the composition of epiphyte assemblages (= epiphytes on a single host tree) were explored with ordination techniques using CANOCO 4.5 (Lepš and Šmilauer 2003). With canonical correspondence analysis (CCA) one can partition the variation in community composition among different environmental variables, allowing also for the inclusion of a spatial component (Borcard et al. 1992). We could, however, not include all three explanatory variables (i.e. tree species, tree size, and spatial component) in a single analysis for a number of reasons (see below), but rather performed one series of analyses focusing on the spatial component and another one focusing on the role of tree species identity. To reduce heteroscedasticity, species abundance data were log-transformed before analysis.

The distances between trees could only be assessed reliably for the subset of epiphytes growing on trunks and the branches close to the trunk. Moreover, considering the usual vertical stratification in epiphyte distributions (Nieder et al. 2000; Pittendrigh 1948; Zotz 2007) a meaningful analysis of a spatial component can only be accomplished by restricting the vertical extension within the forest: we confined our analysis to epiphytes growing in the lowermost 10 m above the ground and only to those trees with, respectively, at least two or three species

in this region. The spatial coordinates and the dbh data for this analysis were obtained from unpublished plot data (Rick Condit, STRI, unpubl.). A first CCA included 2181 epiphytes on 201 trees belonging to 71 species of epiphytes, another analysis encompassed 129 assemblages with 1934 epiphytes of 70 species. Most of the, respectively, 68 and 52 tree species of the two data sets as environmental variables were rare (e.g. 33 of the 68 species were singletons), so tree species identity was not included in the analyses and variance was only partitioned between dbh and a spatial component. The matrix of geographical coordinates (x and y) was completed by adding all terms of a cubic trend surface regression using the software package SpaceMaker2 (Borcard and Legendre 2004). To avoid an artificial increase of the explained variation by chance, the nine terms of the resulting equation were reduced to seven by applying the CANOCO procedure of “manual forward selection of explanatory variables”.

A second series of CCAs focused on the potential influence of tree species identity on epiphyte assemblages. Since precise spatial positions of epiphytes were only available for those growing on trunks, this analysis ignored a spatial component. The following requirements had to be met by a tree species to be included in this analysis: (1) it occurred with at least three individuals in the study plot, and (2) each tree was colonized by at least two epiphyte species. These conditions were fulfilled by 11 species with 91 trees, which were inhabited by a total of 71 epiphyte species. Including tree species identity as dummy variables, differences in the epiphyte assemblages among species were analysed using Monte Carlo permutation tests (with manual forward selection). Ordinations were optimized by species, and rare species were down-weighted. CCAs were performed with abundance data and with binary (presence-absence) data. In the resulting ordination diagrams, which express both the variation in species composition and the principal relationships between epiphyte species and environmental variables (=tree species), species with low weight in the ordination (<5% of the species with the highest weight in the data set) are not shown for reasons of clarity. Other statistical analyses were done with STATISTICA software (Version 5.1, Statsoft, Tulsa, OK, USA).

Taxonomic differences in the degree of species patchiness were further analysed by using the ratio of

the number of colonized trees and the total abundance of each species as an index (PI) in an analysis of covariance. Only taxonomic groups (families with the exception of “ferns”) with at least 3 species and ≥ 10 individuals each were included. Data were again log-transformed before analysis to reduce heteroscedasticity.

Results

In the forest plot of 0.4 ha, we inspected a total of 1373 trees with a diameter at breast height (dbh) ≥ 1 cm. Fewer than 30%, or 389 trees, hosted at least one vascular epiphyte, while 934 trees lacked epiphytes. Trees with epiphytes had a significantly greater dbh than those without (t -test $t = 12.5$, $P < 0.001$). There were, however, a few larger trees without epiphytes in the study plot, e.g. a *Vochysia ferruginea* with 37 cm dbh and a *Marila laxiflora* with 26 cm dbh. Among epiphyte-bearing trees we found the expected correlations between tree size (dbh) and epiphyte occurrence (dbh and abundance: $r = 0.59$, $P < 0.05$; dbh and species number: $r = 0.72$, $P < 0.01$), respectively. In the plot there were 126 species of trees. Epiphytes were found on 90 (=71%) of these tree species. Only 194 trees belonging to 56 species exceeded a dbh of 10 cm: 161 (83%) of these were used by vascular epiphytes as substrate.

The 13,099 individuals of holopiphytes (Appendix 1) in the 0.4 ha plot, which belonged to 103 species, were very unevenly distributed among the 389 host trees—a full 15% of the total (1978 individuals) were found on a single large individual of *Brosimum utile* (dbh: 85 cm); the 10 largest trees together hosted almost 50% of all individuals (6136 of 13099). An even higher importance of large trees was indicated at the species level: the highest number of species was found on a large *Poulsenia armata* tree (dbh: 55 cm) that hosted 50 species (almost 50% of the total), while a total of 83 species of vascular epiphytes were found on the largest ten trees (>80%).

In addition to the 103 species of holopiphytes we found 14 species of primary and secondary hemiepiphytes in the 0.4 ha plot (Appendix 1). A thorough search for additional species in the remaining 0.5 ha of forest accessible by crane yielded an additional 6 species of holopiphytes (all orchids with a single or very few individuals) and 2 species of primary hemiepiphytes (also in low abundance).

Accidental epiphytes, i.e. taxa normally growing as terrestrials, were very rare, the exceptions being two large individuals of *Dieffenbachia longispatha* (Araceae) that were near the tree base of two trees and an unidentified tree seedling growing in rotten material in a crotch in ca. 15 m.

Systematic composition and relative species abundances

The orchids were by far the most species-rich group with 45 species (44%), followed by ferns and fern-allies with ca. 28% (Appendix 1). The remaining 29 species belonged to five different families (Araceae, Bromeliaceae, Cactaceae, Gesneriaceae, Piperaceae). The orchids were also dominant in terms of individual numbers, representing >50% of all plants. Seven of the 10 most common species were orchids, with the two most abundant orchids (*Scaphyglottis longicaulis* and *S. behrii*) accounting for almost a fourth of the total number of epiphytes. At the other extreme of the distribution of relative species abundances, orchids were only slightly over-represented: 8 of the 15 species with only 1 or 2 individuals were orchids.

Vertical distribution of epiphytes

More than half of all individual epiphytes were found at 15–25 m above the ground (Table 1). A remarkably high proportion of individuals (9.2%) occurred in the lowermost 5 m, while very few were growing in the

uppermost 5–10 m of the forest. Variation in species richness along the vertical axis was more or less consistent with this pattern, although the mode was slightly lower. The lower strata were dominated by ferns (e.g. *Trichomanes* spp., *Dicranoglossum panamense*), the medium and upper strata by orchids, in particular *Scaphyglottis longicaulis*, *S. behrii* and *Maxillaria uncata*. The vertical distribution of individual species was only analysed for those with at least 50 individuals. Not surprisingly, species abundance was significantly correlated with vertical range ($P < 0.01$, Pearson Product Moment correlation on log-transformed data), although species abundance explained <19% of the variation. The extent of vertical stratification of individual species is illustrated for four common bromeliads in Fig. 1.

Horizontal distribution

We conducted two canonical correspondence analyses (CCAs) to assess the spatial structure of the epiphyte assemblages on individual trees. One CCA included all assemblages with at least 2 species of epiphytes on the lowermost 10 m (201 trees), another one included only those with at least 3 species of epiphytes in that region (129 trees): tree size (dbh) and “space” together explained a rather small, but significant portion of the variation in the species matrix, about 10% in both analyses (Table 2).

We also found preferences of epiphyte species for particular species of host trees. For example, the 6

Table 1 Occurrence of vascular epiphytes in the vertical profile of the San Lorenzo Forest

Height above ground (m)	Species number	Individuals	Species (% total)	Individuals (% total)	Typical species (>10% of total height class)
>35	15	158	14.6	1.2	PLBR MAX ELA
30–35	30	319	29.1	2.4	MAX PLBR
25–30	47	1408	45.6	10.7	SB MAX PLBR ELA SP
20–25	62	3072	60.2	23.4	SB ELA MAX SL PLBR
15–20	74	3570	71.8	27.2	SL ELA SB
10–15	75	2137	72.8	16.3	SL
5–10	63	1246	61.2	9.5	DICRA
0–5	56	1209	54.4	9.2	TRIA DICRA TREK

Given are the numbers of individuals and species, and the percentages of the total found in 5 m height classes from the forest floor to the top of the canopy. Also given are those species which accounted for more than 10% of the total in each height class

Species abbreviations; DICRA: *Dicranoglossum panamense*; ELA: *Elaphoglossum sporadolepis*; MAX: *Maxillaria uncata*; PLBR: *Pleurothallis brighamii*; SB: *Scaphyglottis behrii*; SL: *Scaphyglottis longicaulis*; SP: *Scaphyglottis prolifera*; TREK: *Trichomanes ekmanii*; TRIA: *Trichomanes angustifrons*

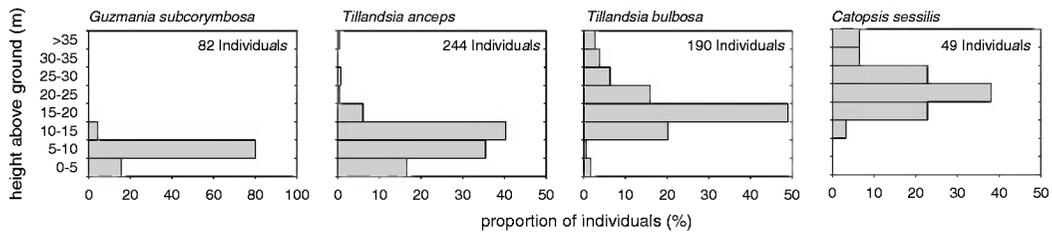


Fig. 1 Vertical distribution of four epiphytic bromeliads. Given are the proportions of each species found in 5 m height classes. Note that the x-axis in the leftmost plot differs from the other plots

Table 2 Percentages of variation in epiphyte assemblages explained by tree size (dbh) and “space”

Factor	Analysis 1	Analysis 2
“space”	7.7	6.3
Dbh	1.9	1.5
“space” and dbh	0.1	5.0
unexplained	90.3	87.2

The first analysis included 201 trees with at least 2 species of epiphytes per tree, the second 129 trees with at least 3 species of epiphytes. Monte Carlo tests revealed significance of all canonical axes ($P < 0.05$)

Poulsenia armata trees in this census hosted 90% of all *Lockhartia acuta* (53 of 58 individuals), the 12 *Brosimum utile* trees 69% of all *Tillandsia bulbosa* (129 of 187 individuals). Likewise, although the palm species *Socratea exorrhiza* represented only 8% of all trees with epiphytes, it hosted almost 40% of all *Guzmania subcorymbosa* individuals. Two CCAs with Monte Carlo permutation tests revealed that the assemblages on different tree species were indeed different: five of the 11 analysed tree species showed significant marginal effects ($P < 0.05$). Including these five species, about 13% of the variation in the epiphyte species abundance data was explained by tree species identity (Fig. 2). Analysing binary (presence-absence) data yielded similar results, indicating that the apparent preferences were not an artefact of highly patchy distributions of individual species. Subsequently, we included tree size (dbh) as an additional environmental variable. Variance partitioning showed that tree size was less important than tree species: dbh alone explained about 2%, compared to about 9% in the case of tree species identity alone.

The abundance of a species (number of individuals) and its point distribution (number of colonized trees) were closely correlated ($r = 0.84$, Fig. 3) Using the ratio of the abundance of an epiphyte species/the number of

colonized trees as an indicator of patchiness (PI), we could identify a considerable variability in aggregation (Appendix 1). At one extreme there were highly dispersed species like *Polypodium triseriale* (PI = 1.1), in which 11 individuals were found on 10 different trees, or *Anthurium acutangulum* (PI = 1.6) with 98 individuals on 63 trees, at the other extreme highly clumped species like *Pleurothallis brighamii* (PI = 89), where 800 Individuals were found on only nine trees. Overall, PI varied significantly between different taxonomic groups. Although many orchids occurred with few individuals on any colonized tree, others were so abundant on individual trees that Orchidaceae were identified as the family with the highest PI. The lowest PI, with little variation among species, was observed in the aroids, which often featured large and massive individuals (Table 3).

Discussion

A comparison of the number of species and individuals in the San Lorenzo area with other reports indicate that this epiphyte community (103 species in 0.4 ha and ca. 110 species in 0.9 ha; Appendix 1) is not exceptional compared to other undisturbed Neotropical lowland forests. For example, Benavides et al. (2005) describe 188 species of epiphytes with 3569 individuals in 0.75 ha of lowland forest in Colombia, and a similar diversity is reported for 1 ha by Balslev et al. (1998) for the Amazonian lowlands of Ecuador. In two 0.4 ha plots in the Chocó region of Colombia, Galeano et al. (1999) found 111 and 174 species, respectively. On the other hand, Nieder et al. (2000) found only 37 species of holo-epiphytes with about 600 individuals in 1.5 ha of a lowland forest in Venezuela. A similar picture emerges when the maximum point diversity of this study, i.e. 50

Fig. 2 Biplot of a canonical correspondence analysis for epiphytes on 11 host tree species. The plot is based on epiphyte abundance data, binary (presence/absence) data yielded similar results (not shown). Tree species with significant marginal effects are: *Apeiba membranacea* (Am), *Brosimum utile* (Bu), *Marila laxiflora* (MI), *Perebea xanthochyma* (Px), *Poulsenia armata* (Pa). Centroid scores for the dummy variables are shown as filled circles

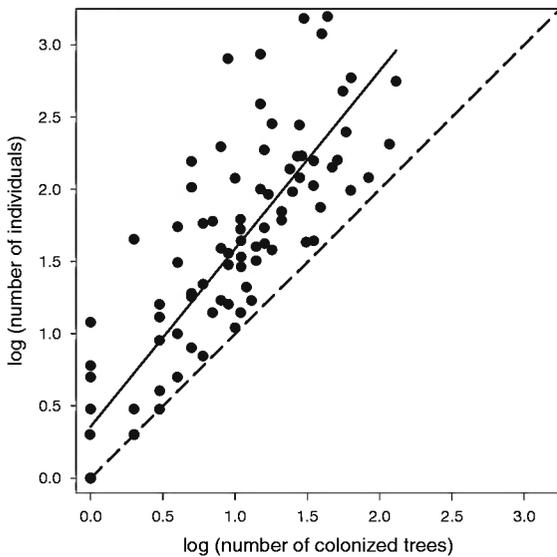
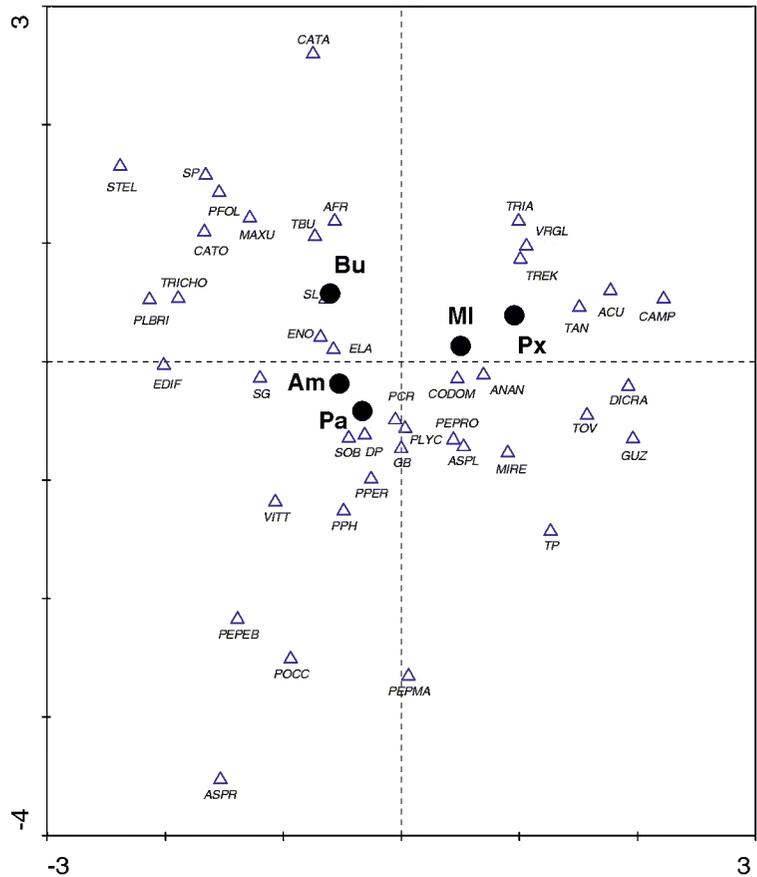


Fig. 3 Relationship between the number of colonized trees and the total number of epiphyte individuals in 0.4 ha of lowland forest. Each dot stands for a different species. The regression (solid line) is highly significant ($P < 0.001$, $r^2 = 0.71$). The dashed line represents the 1:1 match

Table 3 Differences in the point abundances of the most important epiphyte groups

Plant group	Individuals per tree	Number of species
Araceae	2.3	10 ^{ad}
Bromeliaceae	4.7	6 ^a
Ferns	4.6	23 ^{ac}
Orchidaceae	7.7	28 ^{ab}
Piperaceae	5.3	3 ^a

Different letters indicate significant differences (LSD test, $P < 0.05$). ANCOVA (abundance as covariate) on log-transformed data: $F_{4,64} = 2.91$, $P = 0.028$. For reasons of clarity the shown means were calculated by inverse transformation

epiphyte species on a single *Poulsenia* tree, is compared with other lowland sites. Freiberg (1999) registered 74 epiphytes on a single *Virola michelii* tree in French Guyana (45 m a.s.l.), Kreft et al. (2004) report 81 species in Ecuadorian Amazonia at 230 m a.s.l., while only up to 12 species were found in a Amazonian lowland forest in Venezuela (Nieder et al.

2000). Finally, our finding that a large proportion of the trees do not host epiphytes is also in accord with earlier reports (Richards 1996), and suggests that even in undisturbed primary forests in the lowlands, the epiphyte vegetation is far from being saturated.

Taxonomically, the epiphyte vegetation at San Lorenzo was dominated by orchids (Appendix 1), again similar to most other sites in the Neotropics (Freiberg 1996; Krömer et al. 2005; Wolf and Flamenco 2003; Zotz et al. 1999). In some Amazonian rainforests, in contrast, aroids are the most speciose family (e.g. Rudas and Prieto 1998; Benavides et al. 2005, but see Nieder et al. 2000).

A detailed analysis of the distributional patterns within individual host trees is published elsewhere (Zotz 2007b). The largest proportion of epiphyte individuals and species was found at intermediate heights in the forest (Table 1, Fig. 1), which is consistent with the common observation in tree-based studies that most species grow in the inner and mid-crown of individual trees (Johansson 1974). This spatial pattern is usually explained by vertical gradients in abiotic conditions (Benzing 1990; Johansson 1974; Ter Steege and Cornelissen 1989), primarily water and light, but without data on the spatial distribution of available substrate it is impossible to exclude a much more parsimonious explanation, i.e. that the pattern reflects at least partly spatial differences in colonizable substrate. One of the few direct comparisons of substrate availability and substrate use in a small tree, *Annona glabra*, indicates that epiphytes were indeed much more common in the central part of tree crowns than expected (Zotz 1997), but without further quantitative studies we cannot determine whether this is generally true.

Differences in spatial distribution among species were in part related to taxonomy. Consistent with previous findings (Hietz and Hietz-Seifert 1995), orchids showed stronger clustering than other groups. This seems puzzling in view of the dust-like orchid seeds. One possible explanation is related to the dependence of orchids on symbiotic fungi in the early stages of their ontogeny (Hietz and Hietz-Seifert 1995): seeds may rarely find the appropriate fungus on branches where no orchid is already present. In contrast, the much more dispersed spatial pattern observed in aroids is probably a consequence of prevailing zoochory.

There is a long-standing debate on the influence of the host tree on the composition of epiphyte

assemblages. Almost invariably tree size is reported to affect both species richness and abundance (Flores-Palacios and García-Franco 2006; Zotz and Vollrath 2003), but it remains unclear whether size is not simply a proxy for the time available for colonization. A recent study based on repeated censuses (Laube and Zotz 2007), showed that larger trees were more heavily colonized by new species than smaller ones in the same period of time, which is evidence that size as such is important, probably mostly via increased habitat diversity. Apart from host tree size, the role of host tree identity is also a recurring issue in epiphyte ecology (Benzing 1990). True host specificity as originally advocated by Went (1940) is certainly rare if it occurs at all, while the other extreme, complete randomness in host tree selection, is unlikely as well: a particular host tree species offers a specific combination of phenological patterns, architectural traits (e.g. branch angles, diameters etc.), and morphological and chemical bark characteristics. Consistent with recent studies on host preferences in epiphytes (Bernal et al. 2005; Laube and Zotz 2006b), we found a significant influence of host tree identity on the composition of epiphytes assemblages (Fig. 2), although the explained variance was rather low with about 13%. Noteworthy, since rarer epiphyte species with but a few individuals were not included in the present analysis, the possibility remains that some of the rare species have specific requirements that are only met by few or—in the extreme case—a single local tree species. This possibility, which is highly relevant in the context of the conservation of rare epiphyte species, can only be addressed at a much larger spatial scale and/or experimentally. A second set of analyses revealed a significant spatial structure explaining the variation among epiphyte assemblages to a similarly low degree, about 10% (Table 2). We do not know how strongly “space” may be confounded by tree species identity, but the large number of rare tree species in these analyses indicates a genuine role of “space”, which is also consistent with the high patchiness at a smaller spatial scale, i.e. individual trees, which is clearly due to dispersal limitation (Table 3). Taken together, our data suggest significant influences of tree size, tree species and space on the epiphyte assemblages in this lowland forest, but by far most of the variation seems to be due to mere chance.

A common weakness of the present and most other community level studies with epiphytes is that they

ignore the factor time, which does not allow us to answer a number of central questions of community ecology: for example, how stable is the current community composition in time, or how consistent are the observed vertical stratifications (Fig. 1). There are a number of recent studies that directly address temporal community dynamics over a few years (Laube and Zotz 2006a, 2007; Schmit-Neuerburg 2002), but considering the slow growth of vascular epiphytes (Hietz et al. 2002; Schmidt and Zotz 2002) this may be too short to cover the relevant periods necessary to detect many dynamic processes. The canopy crane at our study site will allow us to conduct repeated censuses over prolonged periods of time and also allow an independent test of many strongly debated issues in community ecology that were mostly developed from studies with ground-rooted trees (Harms et al. 2001; Hubbell 2001; Wills et al. 2006).

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Appendix

Appendix 1 Species list of the holoeiphytes and hemieiphytes occurring at the San Lorenzo Crane site

Species—Family	Abundance	Colonized trees
1—Holoepiphytes		
Araceae		
<i>Anthurium acutangulum</i> Engl.	98	63
<i>Anthurium bakeri</i> Hook. f.	1	1
<i>Anthurium brownii</i> Mast.	32	14
<i>Anthurium clavigerum</i> Poepp.	44	35
<i>Anthurium durandii</i> Engl.	40	14
<i>Anthurium friedrichsthali</i> Schott	159	51

Appendix 1 continued

Species—Family	Abundance	Colonized trees
<i>Anthurium hacumense</i> Engl.	75	39
<i>Anthurium scandens</i> (Aubl.) Engl.	34	11
<i>Philodendron radiatum</i> Schott	21	12a
<i>Philodendron sagittifolium</i> Liebm.	42	16a
<i>Stenospermation angustifolium</i> Hemsl.	22	6
Aspleniaceae		
<i>Asplenium juglandifolium</i> Lam.	156	5
<i>Asplenium serratum</i> L.	142	47
Bromeliaceae		
<i>Aechmea tillandsioides</i> (Mart.) Baker var. <i>kienastii</i>	19	5
<i>Catopsis sessiliflora</i> (R. & P.) Mez	92	17
<i>Guzmania musaica</i> (Linden & Andre) Mez in DC.	3	1
<i>Guzmania subcorymbosa</i> L.B. Sm.	70	21
<i>Tillandsia anceps</i> Lodd.	248	59
<i>Tillandsia bulbosa</i> Hook.	187	16
<i>Vriesea gladioliflora</i> (Wendl.) Ant.	106	35
<i>Vriesea sanguinolenta</i> Cogn. & Marchal	1	1
Cactaceae		
<i>Epiphyllum phyllanthus</i> L.	13	10
<i>Hylocereus monacanthus</i> (Lem.) Britt. & Rose.	19	6
Gesneriaceae		
<i>Codonanthe macradenia</i> J.D. Sm.	239	55
<i>Columnnea billbergiana</i> Beurl.	12	4
<i>Drymonia serrulata</i> (Jacq.) Mart.	1	1
Hymenophyllaceae		
<i>Hymenophyllum brevifrons</i> Kunze	1	1
<i>Trichomanes anadromum</i> Rosenstr.	2	2
<i>Trichomanes angustifrons</i> W.Boer	205	117
<i>Trichomanes ekmannii</i> W.Boer	120	84
<i>Trichomanes godmanii</i> Hook	3	3
<i>Trichomanes nummularium</i> C.Chr.	2	2
<i>Trichomanes ovale</i> W.Boer	43	31
<i>Trichomanes punctatum</i> W.Boer	17	13
Lomariopsidaceae		
<i>Elaphoglossum</i> sp.	103	5
<i>Elaphoglossum herminieri</i> (Bory & Fee) Moore	197	8
<i>Elaphoglossum sporadolepis</i> (Kunze) Moore	1187	40

Appendix 1 continued

<i>Species</i> — <i>Family</i>	Abundance	Colonized trees
Orchidaceae		
<i>Aspasia principissa</i> Reichb.f.	53	11
<i>Campylocentrum micranthum</i> (Lindl.) Maury	30	9
<i>Catasetum viridiflavum</i> Hook.	70	21
<i>Caularthron bilamellatum</i> (Reichb.f.) Schult.	1	1
<i>Cochleanthes lipscombiae</i> (Rolfe) Garay	3	2
<i>Cryptarrhena guatemalensis</i> Schltr.	<5	b
<i>Dichaea panamensis</i> Lindl.	279	28
<i>Dimerandra emarginata</i> (G. Meyer) Hoehne	16	3
<i>Elleanthus longibracteatus</i> (Lindl. ex Griseb.) Fawc.	4	3
<i>Encyclia chacaoensis</i> (Reichb.f.) Dressl.	16	9c
<i>Encyclia aemula</i> (Lindl.) Cam. & Ram.		c
<i>Encyclia chimborazoensis</i> (Schlechter) Dressl.		c
<i>Epidendrum coronatum</i> R. & P.	<5	b
<i>Epidendrum difforme</i> Jacq.	36	9
<i>Epidendrum imatophyllum</i> Lindl.	4	3
<i>Epidendrum nocturnum</i> Jacq.	38	18
<i>Epidendrum rousseauae</i> Schltr.	1	b
<i>Epidendrum schlechterianum</i> Ames	5	4
<i>Gongora quinquenervis</i> R. & P.	10	4
<i>Jacquinella pedunculata</i> Dressler	2	2
<i>Jacquinella</i> sp.	1	1
<i>Kefersteinia</i> sp.	1	1
<i>Lockhartia acuta</i> (Lindl.) Reichb.f.	58	6
<i>Lockhartia pittieri</i> Schltr.	2	2
<i>Macradenia brassavolae</i> Rchb. f.	1	b
<i>Masdevallia livinstoneana</i> Rchb. f.	45	2
<i>Maxillaria crassifolia</i> (Lindl.) Rchb.	2	1
<i>Maxillaria discolor</i> Rchb. f.	55	4
<i>Maxillaria uncata</i> Lindl.	857	15
<i>Maxillaria variabilis</i> Batem. ex Lindl.	1	1
<i>Maxillaria</i> sp.	<5	b
<i>Mormodes powellii</i> Schltr.	14	11
<i>Notylia albida</i> Klotsch	18	5
<i>Oncidium ampliatum</i> Lindl.	14	7
<i>Oncidium stenotis</i> Rchb. f.	<5	b

Appendix 1 continued

<i>Species</i> — <i>Family</i>	Abundance	Colonized trees
<i>Ornithocephalus bicornis</i> Lindl. in Benth.	17	8c
<i>Ornithocephalus powellii</i> Schlechter		c
<i>Pleurothallis brighamii</i> S. Wats.	800	9
<i>Pleurothallis grobyi</i> Lindl.	2	1
<i>Pleurothallis verecunda</i> Schlechter	7	6
<i>Polystachya foliosa</i> (Lindl.) Reichb.f.	62	11
<i>Scaphyglottis behrii</i> Hemsl.	1514	30
<i>Scaphyglottis longicaulis</i> S. Wats.	1568	44
<i>Scaphyglottis prolifera</i> Cogn.	284	18
<i>Sobralia fragans</i> Lindl.	169	27
<i>Sobralia fenzliana</i> Rchb.f.	9	3
<i>Stelis crescentiicola</i> Schlechter	119	10
<i>Trichocentrum capistratum</i> Rchb.f.	31	4
<i>Trichopilia maculata</i> Reichb.f.	12	1
<i>Trichosalpinx orbicularis</i> (Lindl.) Luer.	390	15
<i>Trigonidium egertonianum</i> Batem. ex Lindl.	60	7
Piperaceae		
<i>Peperomia cordulata</i> C. DC.	2	1
<i>Peperomia ebingeri</i> Yunck.	100	15
<i>Peperomia macrostachya</i> (Vahl) A. Dietr. in L.	39	8
<i>Peperomia obtusifolia</i> (L.) A.Dietr.	5	1
<i>Peperomia rotundifolia</i> (L.) H.B.K.	157	35
Polypodiaceae		
<i>Campyloneurum occultum</i> Gomez	137	24
<i>Campyloneurum phylliditis</i> (L.) K.Presl.	120	28
<i>Dicranoglossum panamense</i> (Christensen) Gómez	559	130
<i>Microgramma lycopodioides</i> (L.) Copel.	96	25
<i>Microgramma reptans</i> (Cav.) A.R. Sm.	44	11
<i>Niphidium crassifolium</i> (L.) Lellinger	478	56
<i>Pecluma pectinata</i> (L.) MG Price	29	11
<i>Polypodium costaricense</i> H.Christ	13	3
<i>Polypodium percussum</i> Cav.	170	29
<i>Polypodium triseriale</i> Sw.	11	10
Selaginellaceae		
<i>Huperzia dichotoma</i> (Jacq.) Trevis	6	1

Appendix 1 continued

Species—Family	Abundance	Colonized trees
Vittariaceae		
<i>Ananthacorus angustifolius</i> (Sw.) Und. & Max.	591	64
<i>Anetium citrifolium</i> (L.) Splitg.	8	5
<i>Anthrophyum lanceolatum</i> (L.) Kaulf.	61	21
<i>Hecistopteris pumila</i> (Spreng) J.Smith	10	4
<i>Vittaria lineata</i> (L.) J. Sm.	54	16
2—Hemiepiphytes		
Araceae		
<i>Monstera dilacerata</i> (K.Koch & Sello) K.Koch	1	1
<i>Philodendron fragrantissimum</i> (Hook) Kunth	159	115
<i>Philodendron tripartitum</i> (Jacq.) Schott	10	6
<i>Syngonium erythrophyllum</i> Birds. ex Bunting	1	1
<i>Syngonium podophyllum</i> Schott	29	25
Clusiaceae		
<i>Clusia</i> cf. <i>rosea</i> Jacq.	77	18
<i>Clusia</i> cf. <i>uvitana</i> Pitt.	3	2
<i>Havetiopsis flexilis</i> Spruce ex Planch.&Tr.	43	12
Dryopteridaceae		
<i>Polybotrya villosula</i> H.Christ	43	37
Lomariopsidaceae		
<i>Lomariopsis vestita</i> Fourn.	1	1
Melastomaceae		
<i>Topobea praecox</i> Gleason	24	14
Moraceae		
<i>Coussapoa magnifolia</i> Trecul.	<5	b
<i>Ficus</i> cf. <i>nymphaeaeifolia</i> Mill.	1	1
<i>Ficus</i> sp. 1	1	1
Rubiaceae		
<i>Cosmibuena skinneri</i> (Oerst.) Hemsl.	4	3
<i>Ravnia triflora</i> Oerst.	<5	b

For each species the number of individuals (abundance) and the number of colonized trees are given. The letters in the last column mean: (a) includes both holo- and hemi-epiphytic individuals; (b) occurs in the 0.9 ha crane plot, but not in the 0.4 ha epiphyte plot—abundances are estimates, (c) non-flowering individuals could not be distinguished consistently from congeners in the field

References

- Balslev H, Valencia R, Paz y Miño G, Christensen H, Nielsen I (1998) Species count of vascular plants in one hectare of humid lowland forest in Amazonian Ecuador. In: Dallmeier F, Comiskey JA (eds) Forest biodiversity in North, Central and South America, and the Caribbean. Man and the Biosphere 21. Parthenon Publishing Group, Paris, pp 585–594
- Benavides A-M, Duque AJ, Duivenvoorden JF, Vasco GA, Callejas R (2005) A first quantitative census of vascular epiphytes in rain forests of Colombian Amazonia. *Biodivers Conserv* 14:739–758
- Benzing DH (1990) Vascular epiphytes. General biology and related biota. Cambridge University Press, Cambridge
- Bernal R, Valverde T, Hernandez-Rosas L. (2005) Habitat preference of the epiphyte *Tillandsia recurvata* (Bromeliaceae) in a semi-desert environment in Central Mexico. *Can J Bot* 83:1238–1247
- Borcard D, Legendre P, Drapeau P (1992) Partialling out the spatial component of ecological variation. *Ecology* 73:1045–1055
- Borcard D, Legendre P (2004) SpaceMaker2 – User’s guide. Montreal, Université de Montréal, Département de sciences biologiques. Available from the web site <<http://www.fas.umontreal.ca/biol/legendre/>>
- Bordenave BG, de Granville J-J, Hoff M (1998) Measurements of species richness of vascular plants in a neotropical rain forest in French Guiana. In: Dallmeier F, Comiskey JA (eds) Forest biodiversity in North, Central and South America, and the Caribbean. Man and the Biosphere 21. Parthenon Publishing Group, Paris, pp 411–425
- Croat TB (1978) Flora of Barro Colorado Island. Stanford University Press, Stanford
- D’Arcy WG (1987) Flora of Panama: checklist and index. Missouri Botanical Garden, St Louis
- Dressler RL (1993) Field guide to the orchids of Costa Rica and Panama. Cornell University Press, Ithaca, NY
- Flores-Palacios A, García-Franco JG (2006) The relationship between tree size and epiphyte species richness: testing four different hypotheses. *J Biogeogr* 33:323–330
- Freiberg M (1996) Spatial distribution of vascular epiphytes on three emergent canopy trees in French Guiana. *Biotropica* 28:345–355
- Freiberg M (1999) The vascular epiphytes on a *Virola michelii* tree (Myristicaceae) in French Guiana. *Ecotropica* 5:75–81
- Galeano G, Suárez S, Balslev H (1999) Vascular plant species count in a wet forest in the Chocó area on the Pacific coast of Colombia. *Biodivers Conserv* 7:1563–1575
- Gentry AH, Dodson CH (1987) Contribution of non-trees to species richness of a tropical rain forest. *Biotropica* 19:149–156
- Harms KE, Condit R, Hubbell SP, Foster RB (2001) Habitat associations of trees and shrubs in a 50-ha neotropical forest plot. *J Ecol* 89:947
- Harms KE, Wright SJ, Calderón O, Hernandez A, Herre EA (2000) Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature* 404:493–495

- Hietz P, Ausserer J, Schindler G (2002) Growth, maturation and survival of epiphytic bromeliads in a Mexican humid montane forest. *J Trop Ecol* 18:177–191
- Hietz P, Hietz-Seifert U (1995) Intra- and interspecific relations within an epiphyte community in a Mexican humid montane forest. *Selbyana* 16:135–140
- Hubbell SP (2001) The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton
- Hubbell SP, Foster RB, O'Brien ST, Harms KE, Condit R, Wechsler B, Wright SJ, de Lao SL (1999) Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. *Science* 283:554–557
- Johansson D (1974) Ecology of vascular epiphytes in West African rain forest. *Acta Phytogeogr Suec* 59:1–136
- Kelly DL, O'Donovan G, Feehan J, Murphy S, Drangeid SO, Marcano-Berti L (2004) The epiphyte communities of a montane rain forest in the Andes of Venezuela: patterns in the distribution of the flora. *J Trop Ecol* 20:643–666
- Kreft H, Köster N, Küper W, Nieder J, Barthlott W (2004) Diversity and biogeography of vascular epiphytes in Western Amazonia, Yasuní, Ecuador. *J Biogeogr* 31:1463–1476
- Krömer T, Kessler M, Gradstein SR, Acebey A (2005) Diversity patterns of vascular epiphytes along an elevational gradient in the Andes. *J Biogeogr* 32:1799–1809
- Laube S, Zotz G (2006a) Long-term changes in the epiphyte vegetation of the palm, *Socratea exorrhiza*. *J Veg Sci* 17:307–314
- Laube S, Zotz G (2006b) Neither host-specific nor random: vascular epiphytes on three tree species in a Panamanian lowland forest. *Ann Bot* 97:1103–1114
- Laube S, Zotz G (2007) A metapopulation approach to the analysis of long-term changes in the epiphyte vegetation on the host tree *Annona glabra*. *J Veg Sci* 18 (in press)
- Lellinger DB (1989) The ferns and fern-allies of Costa Rica, Panama, and the Chocó (Part I: Psilotaceae through Dicksoniaceae). American Fern Society, Washington, DC
- Lepš J, Šmilauer P (2003) Multivariate analysis of ecological data using CANOCO. Cambridge University Press, Cambridge
- Nieder J, Engwald S, Klawun M, Barthlott W (2000) Spatial distribution of vascular epiphytes (including hemiepiphytes) in a lowland Amazonian rain forest (Surumoni Crane Plot) of Southern Venezuela. *Biotropica* 32:385–396
- Pittendrigh CS (1948) The Bromeliad-Anopheles-Malaria complex in Trinidad. I – The Bromeliad flora. *Evolution* 2:58–89
- Richards PW (1996) The tropical rain forest – an ecological study. Cambridge University Press, Cambridge
- Rudas-L A, Prieto-C A (1998) Floristic analysis of the Amacayacu National Park in the Mocoa Island, Amazon (Colombia). *Caldasia* 20:142–172
- Schmidt G, Zotz G (2002) Inherently slow growth in two Caribbean epiphytic species: A demographic approach. *J Veg Sci* 13:527–534
- Schmit-Neuerburg V (2002) Dynamics of vascular epiphyte vegetation in the Venezuelan lowland rain forest of the Surumoni Crane Project. PhD-thesis, Rheinische Friedrich-Wilhelm-Universität, Bonn
- Ter Steege H, Cornelissen JHC (1989) Distribution and ecology of vascular epiphytes in lowland rain forest of Guyana. *Biotropica* 21:331–339
- Volkov I, Banavar JR, He F, Hubbell SP, Maritan A (2005) Density dependence explains tree species abundance and diversity in tropical forests. *Nature* 438:658–661
- Went FW (1940) Soziologie der Epiphyten eines tropischen Regenwaldes. *Ann Jard Bot Buitenz* 50:1–98
- Whitmore TC, Peralta R, Brown K (1985) Total species count in a Costa Rican tropical rain forest. *J Trop Ecol* 1:375–378
- Wills C, Harms KE, Condit R, King D, Thompson J, He FL, Muller-Landau HC, Ashton P, Losos E, Comita L, Hubbell S, LaFrankie J, Bunyavejchewin S, Dattaraja HS, Davies S, Esufali S, Foster R, Gunatilleke N, Gunatilleke S, Hall P, Itoh A, John R, Kiratiprayoon S, de Lao SL, Massa M, Nath C, Noor MNS, Kassim AR, Sukumar R, Suresh HS, Sun IF, Tan S, Yamakura T, Zimmerman E (2006) Nonrandom processes maintain diversity in tropical forests. *Science* 311:527–531
- Wolf JHD, Flamenco-S A (2003) Patterns in species richness and distribution of vascular epiphytes in Chiapas, Mexico. *J Biogeogr* 30:1689–1707
- Wright SJ, Horlyck V, Basset Y, Barrios H, Bethancourt A, Bohlman SA, Gilbert GS, Goldstein G, Graham EA, Kitajima K, Lerdau MT, Meinzer FC, Ødegaard F, Reynolds DR, Roubik DW, Sakai S, Samaniego M, Sparks JP, Van Bael S, Winter K and Zotz G (2003) Tropical canopy biology program, Republic of Panama. In: Basset Y, Horlyck V and Wright SJ (eds) Studying forest canopies from above: the International Canopy Crane Network. United Nations Environmental Programme, Smithsonian Tropical Research Institute, New York, pp 137–155
- Zotz G (1997) Substrate use of three epiphytic bromeliads. *Ecography* 20:264–270
- Zotz G (2007) Johansson revisited: the spatial structure of epiphyte assemblages. *J Veg Sci* 18:123–130
- Zotz G, Bermejo P, Dietz H (1999) The epiphyte vegetation of *Annona glabra* on Barro Colorado Island, Panama. *J Biogeogr* 26:761–776
- Zotz G, Büche M (2000) The epiphytic filmy ferns of a tropical lowland forest – species occurrence and habitat preferences. *Ecotropica* 6:203–206
- Zotz G, Vollrath B (2003) The epiphyte vegetation of the palm, *Socratea exorrhiza* – correlations with tree size, tree age, and bryophyte cover. *J Trop Ecol* 19:81–90