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Neither Host-specific nor Random: Vascular Epiphytes on Three Tree Species in a Panamanian Lowland Forest

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• *Background and Aims* A possible role of host tree identity in the structuring of vascular epiphyte communities has attracted scientific attention for decades. Specifically, it has been suggested that each host tree species has a specific subset of the local species pool according to its own set of properties, e.g. physicochemical characteristics of the bark, tree architecture, or leaf phenology patterns.
• *Methods* A novel, quantitative approach to this question is presented, taking advantage of a complete census of the vascular epiphyte community in 0·4 ha of undisturbed lowland forest in Panama. For three locally common host-tree species (*Socratea exorrhiza, Marila laxiflora, Perebea xanthochyma*) null models were created of the expected epiphyte assemblages assuming that epiphyte colonization reflected random distribution of epiphytes in the forest.
• *Key Results* In all three tree species, abundances of the majority of epiphyte species (69–81 %) were indistinguishable from random, while the remaining species were about equally over- or under-represented compared with their occurrence in the entire forest plot. Permutations based on the number of colonized trees (reflecting observed spatial patchiness) yielded similar results. Finally, a third analysis (canonical correspondence analysis) also confirmed host-specific differences in epiphyte assemblages. In spite of pronounced preferences of some epiphytes for particular host trees, no epiphyte species was restricted to a single host.
• *Conclusions* The epiphytes on a given tree species are not simply a random sample of the local species pool, but there are no indications of host specificity either.

Key words: Epiphytes, community assembly, null model, host preference, colonization, Panama, Orchidaceae, Bromeliaceae, Araceae.

INTRODUCTION

Vascular epiphytes, i.e. non-parasitic plants using trees only as structural support, comprise a major proportion of tropical phytodiversity. While rarely exceeding 15 % of the vascular flora in lowland rainforests (e.g. Croat, 1978), their contribution may exceed 50 % in some montane forests with >120 species in 1·5 ha (Kelly *et al.*, 2004). Individual trees may have >80 species growing on them (Kreft *et al.*, 2004; Krömer *et al.*, 2005). Many hypotheses have been put forward to account for the local co-existence of such a hyper-diverse group of plants, for example, frequent disturbance (bark defoliation, detached branches, tree falls) that prevents competitive exclusion (Benzing, 1981), vertical niche diversification (Johansson, 1974; Gentry and Dodson, 1987) or host tree specificity (Went, 1940).

Subsequent observational and descriptive studies have provided quantitative evidence for niche assembly along vertical abiotic gradients as well as for the importance of disturbance for epiphyte population and community processes (Griffiths and Smith, 1983; Hietz, 1997; Hietz and Briones, 1998; Zotz *et al.*, 2005), while there is little support for the notion of strict host-specificity in vascular epiphytes (Benzing, 1990; Zimmerman and Olmsted, 1992). However, failure to find a one-to-one match between particular species pairs of host trees and epiphytes is not equivalent to 'neutrality' of host tree species identity in respect to the structuring of epiphyte communities. Went (1940) came close to the concept of species-specificity by proposing that the occurrence of certain epiphyte species was solely linked to host-tree identity since he could not explain their distribution with physical factors characterizing the host trees (e.g. bark roughness, age of host tree, humus accumulation and light availability). Rather than tree identity, the fact that each potential host tree species offers a different set of architectural traits (e.g. branch angles, diameters, etc.), chemical and morphological bark characteristics, phenological patterns, or microclimatic regimes suggests that there could be rather unique epiphyte assemblages on each host tree species: Zotz *et al.* (1999) called these assemblages 'phorophyte-specific epiphyte spectra'. The existence of such spectra, in turn, would directly link the local tree diversity to local epiphyte diversity, albeit probably in a rather diffuse way. Comments on differences of tree species in their suitability for vascular epiphytes, either in general or for particular epiphyte taxa, abound in the literature, although most are rather anecdotal (e.g. Mesler, 1975; Cribb *et al.*, 2002; Moran and Russell, 2004). Quantitative and experimental approaches, on the other hand, are rare (e.g. Benzing, 1978; Callaway *et al.*, 2002), and all these studies tested either the preference of only one or two epiphyte species for a set of host trees (Benzing, 1978; Ackerman *et al.*, 1989; Callaway *et al.*, 2002) or host specificity in the strict sense (Zimmerman

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and Olmsted, 1992; Migenis and Ackerman, 1993). This paper presents a novel approach that constitutes a critical test of the notion of phorophyte-specific epiphyte spectra. In it the null hypothesis that the species assemblage found on a particular host tree species in a forest is just a random subset of the local species pool of epiphytes is examined. This was done taking advantage of a complete inventory of the vascular epiphytes in 0·4 ha of a tropical lowland forest in Panama (Zotz, 2004). A study on host specificity of vascular epiphytes in a tropical rainforest faces the prominent problem that tree species as well as epiphyte species are frequently very rare. In the study plot at San Lorenzo, only the three tree species *Socratea exorrhiza*, *Marila laxiflora* and *Perebea xanthochyma* were sufficiently common and frequently used by epiphytes to warrant their inclusion in this study allowing for appropriate statistical power.

MATERIALS AND METHODS

Study site and species

The data for this study were collected at the San Lorenzo Canopy Crane Site that is located near the Atlantic coast of the Republic of Panama. The forest around this facility has not experienced any severe human disturbance for at least 200 years (Condit *et al.*, 2004). Average annual rainfall is approx. 3100 mm (Wright *et al.*, 2003). A 52-m-tall construction crane covers approx. 9000 m^2 of forest with its jib of 54 m. A small gondola allowed easy access to the vascular epiphytes in this area, although the use of binoculars was necessary in rare cases. Briefly, between mid-1999 and early 2002 each individual epiphyte in an area of 0·4 ha on all trees with a diameter at breast height of >1 cm was registered with species name, plant size and location on the tree (Zotz, 2004; G. Zotz, unpubl. res.). The census included 1358 trees, 389 of which had epiphytes growing on them. Although both species richness and individual abundance correlated with tree size (Laube and Zotz, 2006; G. Zotz, unpubl. res.), epiphytes were occasionally found on trees with even the smallest diameter at breast height. Plant names of angiosperms follow the Flora of Panama checklist (D'Arcy, 1987), while fern names are according to Lellinger (1989).

The first tree species included in the analysis was *Socratea exorrhiza* (Mart.) H. Wendl. (Arecaceae). This stilt-root palm, which occurs from Nicaragua to northern South America, reaches up to 30 m (Croat, 1978). Unlike most other palms its trunk diameter increases with height (Schatz *et al.*, 1985). There were 31 individuals in the study plot. *Marila laxiflora* Rusby (Clusiaceae), which is known only from wetter forests in Panama and occurred with 40 individuals at San Lorenzo, reaches similar heights (Croat, 1978). The 38 individuals of the third species, *Perebea xanthochyma* H. Karst. (Moraceae), reached up to 35 m. The species occurs from Costa Rica to Peru.

Data analysis

The local epiphyte species pool (hemi-epiphytes were excluded) consisted of 103 species with 13 099 individuals. The species pool on *Socratea exorrhiza* comprised 39 epiphyte species with 354 individuals, *Marila laxiflora* hosted 47 species with 496 individuals and *Perebea xanthochyma* 32 species with 227 individuals. Null models of the epiphyte assemblage on a given host tree species were created with R (Version 2.2.1; R Development Core Team, 2005) as follows. To create, for example, the null model for *Socratea exorrhiza*, 354 individuals were randomly selected from the complete list of epiphyte individuals in the local species pool. Individuals were drawn from the list with replacement. This process was repeated 1000 times and 95 % confidence intervals were obtained for each species by discarding the 25 highest and the 25 lowest values. Ranges expected by chance were then compared with the actual species abundances for each species separately. Accordingly, null models were created for the epiphyte assemblages on *Marila laxiflora* and *Perebea xanthochyma*.

Similarly, null models were created for the epiphyte distributions on the tree species as a random sample based on the number of host trees a given epiphyte species inhabited in the study plot. For a given epiphyte species that was growing on a tree species, the number of trees that were inhabited by epiphytes was randomly selected from the complete list of trees found in the study plot. For example, the epiphytic orchid, *Scaphyglottis longicaulis*, was found on 44 trees, but was absent on 1314 trees. To create a null model for the distribution on *Socratea exorrhiza*, 31 trees, i.e. the number of *Socratea exorrhiza* trees in the plot, were randomly selected from this complete tree list with replacement. This process was repeated 1000 times and 95 % confidence intervals were obtained as described above. Accordingly, tree-based null models were created for the epiphyte species on the 40 *Marila laxiflora* and 38 *Perebea xanthochyma* trees growing in the study plot.

Also a completely different method was used to analyse epiphyte species preferences, i.e. canonical correspondence analysis (CCA) with CANOCO software (Version 4.5; ter Braak and Šmilauer, 1997). This ordination technique is designed to detect the variation in species composition that can be explained best by environmental variables (host tree identity in the present case), which is achieved by combining aspects of regular ordination and regression (ter Braak, 1995). The resulting ordination diagrams express both the variation in species composition and the principal relationships between species and environmental variables. 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). Two separate CCAs were run, one with abundance data, another with binary (presence/absence) data. The data sets used in these analyses were not completely identical to the ones described above. First, infrequent epiphyte species were excluded, reducing the species number to, respectively, 43 (abundance data) and 39 (binary data) and, secondly, only trees with at least three epiphyte individuals were included, leaving 70 trees of three tree species. Ordinations were optimized by species and Monte Carlo permutation tests run 499 times.

RESULTS

If epiphyte species showed no preference for particular host tree species, their relative abundances on a tree should simply reflect their relative abundance in the forest as a whole. In slightly more than half of all cases (57·3 %) the null hypothesis of a random sample could indeed not be rejected. However, almost 43 % of the epiphyte species in the study plot showed a higher or lower abundance, respectively, on at least one of the focal tree species than expected by chance (Table 1). Three epiphyte species (*Dicranoglossum panamense*, *Trichomanes angustifrons* and *Tillandsia anceps*) were more frequent than expected by chance on all three tree species, while five epiphyte species (*Pleurothallis brighamii*, *Trichosalpinx orbicularis*, *Trichomanes nummularium*, *Maxillaria uncata* and *Scaphyglottis graminifolia*) were invariably less frequent than expected by chance.

Socratea exorrhiza

The abundance of the majority of epiphyte species (77·7 %) on *Socratea exorrhiza* could not be distinguished from random (Fig. 1A). A significantly higher abundance than expected was observed in 11·6 % of all cases, significantly lower abundance in 10·7 %. The most pronounced preference for *Socratea exorrhiza* was found in the bromeliad *Guzmania subcorymbosa*: 26 individuals inhabited the palm in the study plot whereas a maximum of only five individuals was expected by chance (Appendix 1). Substantial deviations from the expected abundances were also found in the aroid *Anthurium clavigerum* (17 individuals, 0–4 plants expected by chance), the gesneroid *Columnea billbergiana* (8 individuals, 0–2 expected) or the fern *Ananthacorus angustifolius* (51 individuals, 9–24 expected). On the other hand, otherwise locally rather common orchids were conspicuously absent (e.g. *Scaphyglottis graminifolia*, *Maxillaria uncata* and *Trichosalpinx orbicularis*). By chance alone, these species were expected to occur with up to 53 individuals on this palm.

Marila laxiflora

On *Marila laxiflora* about two-thirds of the epiphyte species (68·9 %) showed an abundance indistinguishable from random (Fig. 1A). A portion of 18·5 % of the species that occurred in the San Lorenzo plot were significantly more abundant on this tree species than in the remaining plot, while 12·6 % showed a significantly lower abundance than expected. The strongest preference for this host tree was found in some ferns and aroids: *Trichomanes angustifrons* (13 individuals, 0–2 expected, Appendix 2), *Dicranoglossum panamense* (123 individuals, 13–30 expected) or *Anthurium acutangulum* (24 individuals, 1–8 expected). Among locally common orchid species only *Pleurothallis brighamii* was completely absent (20–40 individuals expected).

Perebea xanthochyma

The epiphyte assemblage of *Perebea xanthochyma* showed the smallest deviation from random among the

TABLE 1. *Overview on the occurrence of epiphyte species on three host tree species in 0·4 ha of the San Lorenzo crane plot in relation to a null assemblage deduced from the local epiphyte pool*

Species	Family	*Socratea*	*Marila*	*Perebea*
Aechmea tillandsioides	Bromeliaceae	0	+	+
Ananthacorus angustifolius	Vittariaceae	+	0	+
Anthurium acutangulum	Araceae	0	+	0
Anthurium clavigerum	Araceae	+	+	0
Anthurium friedrichsthalii	Araceae	0	+	0
Anthurium hacumense	Araceae	0	+	0
Asplenium juglandifolium	Aspleniaceae	–	–	0
Asplenium serratum	Aspleniaceae	+	0	0
Campylocentrum micranthum	Orchidaceae	0	+	+
Campyloneurum occultum	Polypodiaceae	–	0	0
Catasetum viridiflavum	Orchidaceae	0	+	0
Codonanthe macradenia	Gesneriaceae	0	+	+
Columnea billbergiana	Gesneriaceae	+	0	0
Dichaea panamensis	Orchidaceae	–	+	0
Dicranoglossum panamense	Polypodiaceae	+	+	+
Elaphoglossum herminieri	Lomariopsidaceae	–	–	0
Elaphoglossum latifolium	Lomariopsidaceae	0	–	0
Elaphoglossum sporadolepis	Lomariopsidaceae	–	0	–
Encyclia fragrans	Orchidaceae	+	0	0
Epidendrum imatophyllum	Orchidaceae	0	+	0
Epidendrum nocturnum	Orchidaceae	+	0	0
Gongora quinquenervis	Orchidaceae	0	+	+
Guzmania subcorymbosa	Bromeliaceae	+	0	0
Maxillaria uncata	Orchidaceae	–	–	–
Microgramma lycopodioides	Polypodiaceae	0	+	0
Microgramma reptans	Polypodiaceae	0	+	0
Niphidium crassifolium	Polypodiaceae	0	–	–
Ornithocephalus bicornis	Orchidaceae	0	+	0
Peperomia rotundifolia	Piperaceae	0	+	0
Pleurothallis brighamii	Orchidaceae	–	–	–
Polypodium percussum	Polypodiaceae	0	–	0
Scaphyglottis graminifolia	Orchidaceae	–	–	–
Scaphyglottis longicaulis	Orchidaceae	0	–	–
Scaphyglottis prolifera	Orchidaceae	–	0	–
Sobralia fragrans	Orchidaceae	+	0	0
Stelis crescentiicola	Orchidaceae	0	–	0
Tillandsia anceps	Bromeliaceae	+	+	+
Tillandsia bulbosa	Bromeliaceae	0	–	0
Trichomanes angustifrons	Hymenophyllaceae	+	+	+
Trichomanes ekmannii	Hymenophyllaceae	0	+	+
Trichomanes nummularium	Hymenophyllaceae	–	–	–
Trichomanes ovale	Hymenophyllaceae	0	0	+
Trichosalpinx orbicularis	Orchidaceae	–	–	–
Vriesea gladioliflora	Bromeliaceae	+	0	+

Species more frequent on a given host tree species than expected by random distribution are indicated with '+'; species less frequent are indicated with '–'; species occurring in a frequency as expected by random distribution are indicated with '0'. Excluded are the 59 species occurring in all three focal tree species in a frequency as expected by random distribution.

For a detailed analysis of host preference compare Appendices 1–3.

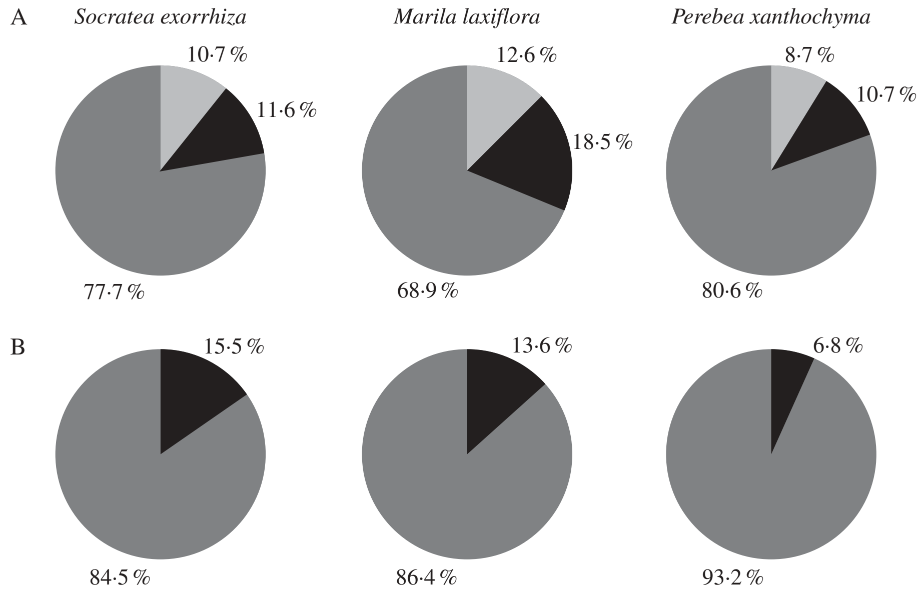

FIG. 1. Distribution of epiphyte species in the San Lorenzo forest plot according to (A) individual-based comparisons of the occurrence on host trees of a given species with that of a null model (white, species found with fewer individuals on a host tree species than expected by chance; black, species found with more individuals than expected by chance; grey, species found in a frequency indistinguishable from that expected by chance); (B) tree-based occurrence on host trees of a given species (black, species found on more trees than expected by chance; dark grey, species found on a number of trees indistinguishable from that expected by chance).

three focal tree species: 80·6 % of all species showed an abundance indistinguishable from random (Fig. 1A). About equal proportions were more abundant (10·7 %) or less abundant (8·7 %) than expected. The strongest preference for this tree was observed in the fern *Trichomanes angustifrons* (24 individuals, 0–2 expected, Appendix 3) followed by the bromeliad *Aechmea tillandsioides* (12 individuals, 0–2 expected), and the orchid *Campylocentrum micranthum* (10 individuals, 0–2 expected). The orchids *Scaphyglottis graminifolia, Pleurothallis brighamii* and *Trichosalpinx orbicularis* were conspicuously absent. Under random distribution these species were expected to occur with up to 37 individuals.

Spatial patchiness

This first analysis has an obvious shortcoming because the null assemblages implicitly assume that individuals of a given epiphyte species are distributed evenly in the forest plot. As this is clearly not the case, a second series of null models that account for the patchiness of epiphyte spatial distributions was created: the number of trees for a given tree species, that an epiphyte species should inhabit, was determined based on the number of trees this species actually inhabited in the study plot as described in Materials and methods. The overall results were quite consistent with the first analysis. With few exceptions, species that were more common than expected by chance in the first analysis were also more common in the second (Table 2). Unambiguous exceptions were *Vriesea gladioliflora* (*Socratea exorrhiza*), *Microgramma lycopodioides* (*Marila laxiflora*) and *Codonanthe macradenia* (*Perebea xanthochyma*), while the tree-based occurrences of *Tillandsia anceps* and *Trichomanes ovale* on *Perebea xanthochyma* were marginally higher than expected. No species, however, could be shown to be less abundant than expected by chance in this tree-based analysis since the lower boundary of the null distribution almost always included zero (Fig. 1B).

Ordination

The ordination approach yielded similarly significant differences of epiphyte assemblages between tree species in the analyses of both the abundance data (Fig. 2) and the binary data (not shown). The explained variance, however, was very low in either case: only 5·4 % for abundance data and 4·7 % for binary data. Consistent with the very high proportion of species occurrences indistinguishable from random expectations in *Perebea xanthochyma* (approx. 80 %, Fig. 1A), the marginal effects of this species were not significant (Monte-Carlo permutation, $P > 0{\cdot}2$), in contrast to the significant effects of the other two species ($P < 0{\cdot}05$).

DISCUSSION

A preference of particular epiphyte species for particular host tree species has been reported repeatedly in the literature (Oliver, 1930; Mesler, 1975; Benzing, 1990; Male and Roberts, 2005). However, no study to date has tried to link the composition of the entire epiphyte assemblage occurring on a particular tree species to the local species pool in the quantitative manner of the present study. A majority of species (approx. 69–81 %, individual-based; approx. 85–93 %, tree-based) showed no bias in

TABLE 2. *Numbers of trees a given epiphyte species inhabited in 0·4 ha of the San Lorenzo Crane Plot (light and bold numbers) and generated numbers of a random distribution based on the distribution of a given species on all forest trees in the plot for the three host tree species* Socratea exorrhiza, Marila laxiflora *and* Perebea xanthochyma

Species	*Socratea exorrhiza*	*Marila laxiflora*	*Perebea xanthochyma*
Ananthacorus angustifolius	**11** (0; 4)	5 (0; 5)	**7** (0; 5)
Anthrophyum lanceolatum	0 (0; 2)	1 (0; 2)	1 (0; 2)
Anthurium acutangulum	2 (0; 4)	**10** (0; 5)	3 (0; 5)
Anthurium clavigerum	**12** (0; 3)	**8** (0; 4)	0 (0; 3)
Anthurium friedrichsthallii	1 (0; 3)	**8** (0; 4)	1 (0; 4)
Anthurium hacumense	1 (0; 3)	**7** (0; 3)	0 (0; 3)
Asplenium serratum	**5** (0; 3)	4 (0; 4)	0 (0; 4)
Campyloneurum occultum	0 (0; 2)	3 (0; 3)	1 (0; 3)
Campyloneurum phylliditis	**4** (0; 3)	3 (0; 3)	1 (0; 3)
Catasetum viridiflavum	0 (0; 2)	**5** (0; 2)	0 (0; 2)
Codonanthe macradenia	4 (0; 4)	**8** (0; 4)	1 (0; 4)
Dichaea panamensis	0 (0; 3)	**5** (0; 3)	1 (0; 3)
Dicranoglossum panamense	**8** (0; 6)	**17** (1; 8)	**17** (1; 7)
Elaphoglossum sporadolepis	**8** (0; 3)	3 (0; 3)	1 (0; 3)
Epidendrum nocturnum	**3** (0; 2)	1 (0; 2)	0 (0; 2)
Guzmania subcorymbosa	**3** (0; 2)	2 (0; 3)	1 (0; 2)
Microgramma lycopodioides	**3** (0; 2)	1 (0; 3)	1 (0; 3)
Niphidium crassifolium	**5** (0; 4)	**7** (0; 4)	1 (0; 4)
Peperomia rotundifolia	2 (0; 3)	**4** (0; 3)	2 (0; 3)
Polypodium percussum	3 (0; 3)	1 (0; 3)	1 (0; 3)
Scaphyglottis graminifolia	0 (0; 3)	2 (0; 3)	0 (0; 3)
Scaphyglottis longicaulis	**4** (0; 3)	2 (0; 4)	1 (0; 4)
Scaphyglottis prolifera	0 (0; 2)	2 (0; 2)	0 (0; 2)
Sobralia fragrans	**6** (0; 2)	1 (0; 3)	0 (0; 3)
Tillandsia anceps	**10** (0; 4)	**8** (0; 4)	4 (0; 4)
Trichomanes angustifrons	5 (0; 5)	**10** (0; 6)	**16** (0; 5)
Trichomanes ekmannii	3 (0; 3)	**10** (0; 3)	**8** (0; 3)
Trichomanes ovale	2 (0; 2)	1 (0; 3)	3 (0; 3)
Vriesea gladioliflora	2 (0; 3)	2 (0; 3)	**5** (0; 3)

Numbers in brackets indicate the lower and upper boundary of the random generated tree numbers. Only species occurring on ⩾5% of the host trees in the plot are shown. Bold numbers indicate species occurring on a higher number of trees than expected by random distribution.

respect to the focal tree species (Fig. 1), their occurrence is thus consistent with the notion of a random assembly: individual trees are just redundant colonization opportunities for epiphytes irrespective of tree species identity. The remaining taxa were about equally over- or under-represented in abundance. This conclusion would change if the present analysis were confined to the more common species. If considering, for example, only the ten most common epiphyte species, the proportion of taxa deviating from a random sample would be much higher (cf. Appendices 1–3). However, as we were interested in the entire community and see no basis to distinguish unambiguously 'common' and 'rare' species, all species were included in the analysis.

The low proportion of taxa that were under-represented in abundance came as a surprise at least in the case of *Socratea exorrhiza*. A bias *against* a large proportion of species had been mostly expected considering the simple architecture of this palm that lacks features generally assumed to facilitate epiphyte establishment (Benzing, 1990), e.g. crotches, humus accumulations (Andrade and Nobel, 1996) or rough bark with a high water-holding capacity (Callaway *et al.*, 2002). In addition, in contrast to other palm species that feature suitable horizontal growing sites for epiphytes in accumulated debris in persistent leaf bases (e.g. *Copernicia tectorum*; Holbrook and Putz, 1996), *Socratea exorrhiza* offers only vertical growing sites, which again is believed to hinder establishment (Benzing, 1990).

Among those taxa that were found more frequently than expected on *Perebea xanthochyma*, both in respect to the number of individuals and the number of inhabited trees, were filmy ferns of the genus *Trichomanes*, with the species *T. ekmannii* found on *Perebea xanthochyma* accounting for more than one-quarter of the entire plot population (Appendix 3; Zotz, 2004). Similarly, *Socratea exorrhiza* appeared to be a good host for all larger tank bromeliads growing in the study plot, the extreme case being *Guzmania subcorymbosa*, which was very rare on any other tree species. Individuals of rare epiphyte species that inhabited only one of the focal tree species were invariably found on other trees in the forest plot as well. Thus, no epiphyte species was restricted to a certain host tree species.

Due to an almost complete lack of information on the biology of most epiphytes it can only be speculated why particular epiphyte taxa may prefer a given tree species. The reasons why some species are *not* found on a palm, on the other hand, are less obscure. For example, there are a number of substrate specialists in the local epiphyte flora, for which particular requirements are known; there are so-called twig epiphytes such as *Catopsis sessiliflora* (Bromeliaceae; Zotz and Laube, 2005) or *Notylia albida* (Orchidaceae; Chase, 1987), or dead wood specialists such as *Catasetum viridiflavum* (Orchidaceae). In contrast to the crowns of larger dicotyledonous trees, which feature branches and twigs and frequently a large proportion of dead wood (Schulz and Wagner, 2002), these microhabitats do not exist on living palms and, not surprisingly, all these specialists were never observed there (Appendix 1). It is much less obvious, however, why *Catopsis sessiliflora*, for example, was not observed at all on the other two tree species either. Similar to the conspicuous absence of many locally common orchid species from *Socratea exorrhiza*, this absence may be more related to patchy species distributions than to real positive or negative substrate preferences. This is indicated, for example, by the regular occurrence of many (missing) orchids such as *Scaphyglottis graminifolia* or *Dichaea panamensis* on *Socratea exorrhiza* trees (compare Appendix 1) outside the study plot. Severe dispersal limitation in general, which probably causes this patchiness, is also suggested by the observation that orchids such as *Maxillaria uncata* (857 individuals in the 0·4 ha plot) and *Trichosalpinx orbicularis* (390 individuals; compare Zotz, 2004), although very abundant in individual numbers, are found only on a few trees in the plot (3·9 % of trees; G. Zotz, unpubl. res.). Finally, some of the positive and negative associations between host tree species and epiphyte species are likely to be false, considering the statistical methods used in the

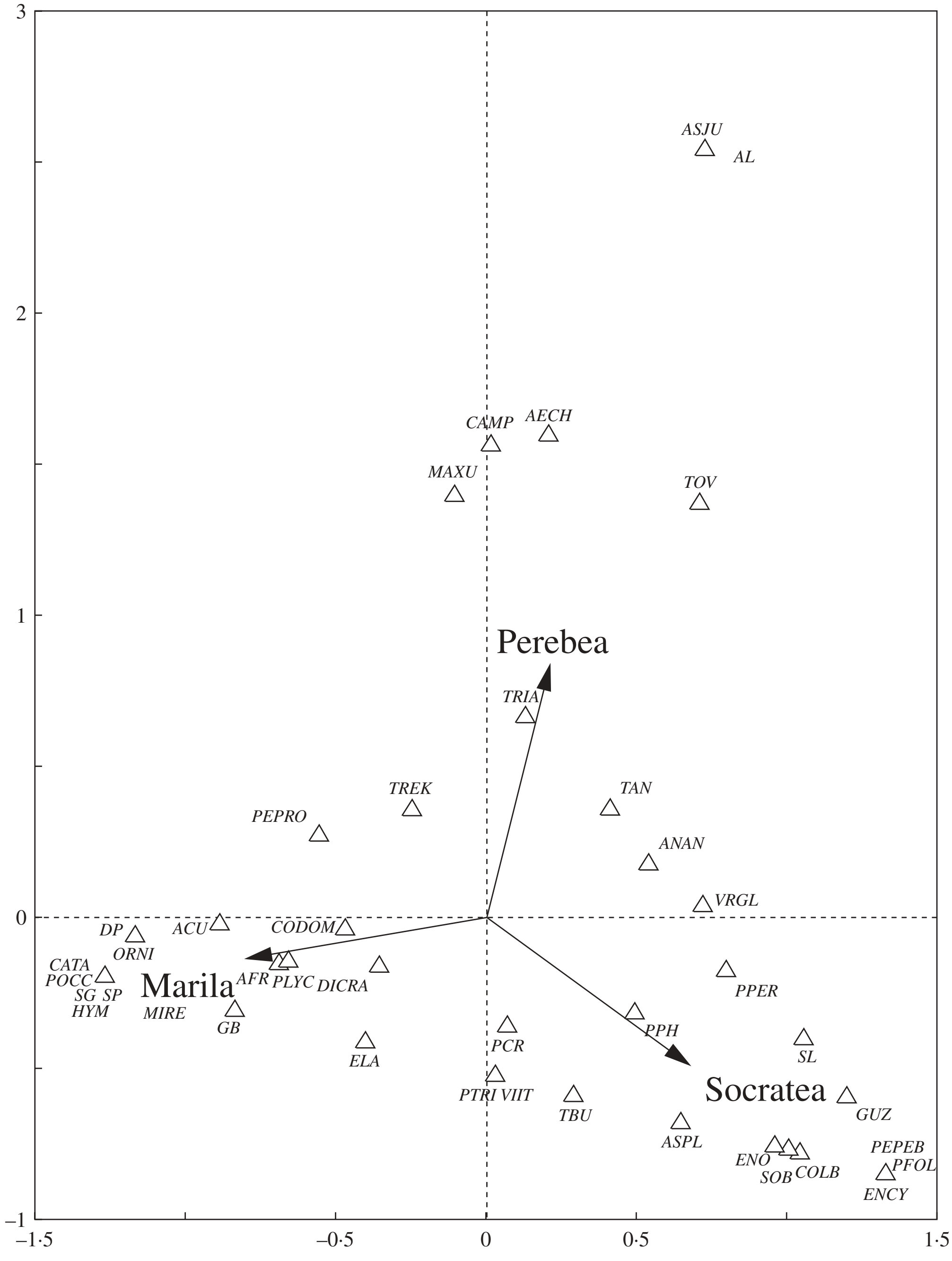

FIG. 2. Biplot of a canonical correspondence analysis for epiphytes on the three host tree species *Socratea exorrhiza*, *Marila laxiflora* and *Perebea xanthochyma*. The plot is based on epiphyte abundance data, binary (presence/absence) data yield very similar results (not shown).

present study. The conclusions are not expected to be affected substantially by such possible artefacts, however, because (*a*) there are a large number of positive and negative associations; (*b*) the observed abundances of many species are very far from random expectations; and (*c*) three different approaches yielded qualitatively consistent results (Figs 1 and 2). Nevertheless, it is essential that future studies use descriptive data like the ones presented here as the basis for manipulative experiments to identify the mechanisms behind the observed deviations from random expectations.

In summary, comparing the actual epiphyte assemblages on a particular host tree with the ones expected by null models, no evidence was found for strict host specificity in any epiphyte. However, a significant positive or negative bias of individual epiphyte species was found in a large proportion of the local species pool. While Went's (1940) concept of species-specificity in the strict sense can thus be rejected, the extreme alternative can be dismissed as well; the epiphytes on the three focal tree species are not just a random subset of the local epiphyte community.

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APPENDIX 1

Comparison of actual occurrence of epiphytes on *Socratea exorrhiza* and null assemblages created from the epiphyte pool in 0·4 ha of the San Lorenzo Crane Plot. The analysis is based on the individual number found on 31 *Socratea exorrhiza* trees. Shown are individual numbers of a given epiphyte species observed on *Socratea exorrhiza* and the expected range of individual numbers (lower and upper boundary of 95% confidence intervals). Bold names indicate species that were more common than expected; underlined names indicate species that are less common than expected.

Species	Family	Individuals on *Socratea*	Individuals of null assemblage		Rank	
			Lower boundary	Upper boundary	Null assemblage	*Socratea*
Scaphyglottis longicaulis	Orchidaceae	41	30	54	1	3
Scaphyglottis graminifolia	Orchidaceae	0	30	53	2	
Elaphoglossum sporadolepis	Lomariopsidaceae	17	22	43	3	6
Maxillaria uncata	Orchidaceae	0	15	33	4	
Pleurothallis brighamii	Orchidaceae	0	13	31	5	
Ananthacorus angustifolius	Vittariaceae	51	9	24	6	1
Dicranoglossum panamense	Polypodiaceae	49	9	23	7	2
Niphidium crassifolium	Polypodiaceae	9	7	20	8	11
Trichosalpinx orbicularis	Orchidaceae	0	4	17	9	
Scaphyglottis prolifera	Orchidaceae	0	3	13	10	
Dichaea panamensis	Orchidaceae	0	3	14	11	
Codonanthe macradenia	Gesneriaceae	4	2	12	12	16
Tillandsia anceps	Bromeliaceae	22	2	12	13	5
Trichomanes nummularium	Hymenophyllaceae	0	1	10	14	
Elaphoglossum herminieri	Lomariopsidaceae	0	1	10	15	
Tillandsia bulbosa	Bromeliaceae	3	2	10	16	20
Polypodium percussum	Polypodiaceae	4	1	9	17	16
Asplenium juglandifolium	Aspleniaceae	0	1	8	18	
Sobralia fragrans	Orchidaceae	14	1	9	19	8
Anthurium friedrichsthalii	Araceae	3	1	9	20	20
Peperomia rotundifolia	Piperaceae	3	1	9	21	20
Asplenium serratum	Aspleniaceae	14	0	8	22	8
Campyloneurum occultum	Polypodiaceae	0	1	8	23	
Campyloneurum phyllitidis	Polypodiaceae	6	0	7	24	14
Stelis crescentiicola	Orchidaceae	0	0	7	25	
Trichomanes ovale	Hymenophyllaceae	3	0	7	26	20
Elaphoglossum latifolium	Lomariopsidaceae	0	0	6	27	
Anthurium acutangulum	Araceae	2	0	6	28	26
Vriesea gladioliflora	Bromeliaceae	13	0	7	29	10
Peperomia ebingeri	Piperaceae	4	0	6	30	16
Microgramma lycopodioides	Polypodiaceae	3	0	6	31	20
Catopsis sessiliflora	Araceae	0	0	6	32	
Anthurium hacumense	Araceae	1	0	5	33	30
Guzmania subcorymbosa	Bromeliaceae	26	0	5	34	4
Catasetum viridiflavum	Orchidaceae	0	0	5	35	
Polystachya foliosa	Orchidaceae	2	0	4	36	26
Lockhartia acuta	Orchidaceae	0	0	4	37	
Anthrophyum lanceolatum	Vittariaceae	0	0	5	38	
Vittaria lineata	Vittariaceae	1	0	4	39	30
Trigonidium egertonianum	Orchidaceae	0	0	4	40	
Maxillaria discolor	Orchidaceae	0	0	5	41	
Aspasia principissa	Orchidaceae	0	0	4	42	
Microgramma reptans	Polypodiaceae	1	0	3	43	30
Masdevallia livingstoneana	Orchidaceae	0	0	4	44	
Epidendrum difforme	Orchidaceae	0	0	3	45	
Anthurium durandii	Araceae	0	0	3	46	
Anthurium clavigerum	Araceae	17	0	4	47	6
Trichomanes ekmannii	Hymenophyllaceae	4	0	4	48	16
Peperomia macrostachia	Piperaceae	1	0	4	49	30
Epidendrum nocturnum	Orchidaceae	6	0	3	50	14
Anthurium scandens	Araceae	0	0	3	51	
Anthurium brownii	Araceae	2	0	3	52	26
Campylocentrum micranthum	Orchidaceae	0	0	3	53	
Philodendron sagittifolium	Araceae	0	0	3	54	
Pecluma pectinata	Polypodiaceae	0	0	3	55	
Trichocentrum capistratum	Orchidaceae	0	0	3	56	
Hylocereus monacanthus	Cactaceae	0	0	2	57	
Stenospermation angustifolium	Araceae	0	0	2	58	
Aechmea tillandsioides	Bromeliaceae	1	0	2	59	30
Notylia albida	Orchidaceae	0	0	2	60	
Mormodes powellii	Orchidaceae	0	0	2	61	
Dimerandra emarginata	Orchidaceae	1	0	2	62	30
Polypodium triseriale	Polypodiaceae	2	0	2	63	26
Trichomanes angustifrons	Hymenophyllaceae	8	0	2	64	12
Trichopilia maculata	Orchidaceae	0	0	2	65	
Gongora quinquenervis	Orchidaceae	0	0	1	66	
Columnea billbergiana	Gesneriaceae	8	0	2	67	12
Oncidium ampliatum	Orchidaceae	0	0	2	68	
Philodendron radiatum	Araceae	0	0	2	69	

Species	Family	Individuals on *Socratea*	Individuals of null assemblage		Rank	
			Lower boundary	Upper boundary	Null assemblage	*Socratea*
Hecistopteris pumila	Vittariaceae	0	0	2	70	
Ornithocephalus powellii	Orchidaceae	0	0	1	71	
Sobralia panamensis	Orchidaceae	0	0	2	72	
Epiphyllum phyllanthus	Cactaceae	0	0	2	73	
Pleurothallis verecunda	Orchidaceae	1	0	1	74	30
Ornithocephalus bicornis	Orchidaceae	0	0	1	75	
Polypodium costaricense	Polypodiaceae	0	0	1	76	
Guzmania musaica	Bromeliaceae	0	0	1	77	
Elleanthus longibracteatus	Orchidaceae	1	0	1	78	30
Huperzia dichotoma	Selaginellaceae	0	0	1	79	
Epidendrum imatophyllum	Orchidaceae	0	0	1	80	
Anetium citrifolium	Vittariaceae	0	0	1	81	
Encyclia fragrans	Orchidaceae	3	0	1	82	20
Peperomia obtusifolia	Piperaceae	0	0	1	83	
Epidendrum schlechterianum	Orchidaceae	0	0	1	84	
Encyclia aemula	Orchidaceae	0	0	1	85	
Maxillaria crassifolia	Orchidaceae	0	0	1	86	
Cochleanthes lipscombiae	Orchidaceae	0	0	1	87	
Trichomanes punctatum	Hymenophyllaceae	1	0	1	88	30
Trichomanes godmanii	Hymenophyllaceae	0	0	1	89	
Encyclia chimborazoensis	Orchidaceae	0	0	1	90	
Anthurium bakeri	Araceae	0	0	1	91	
Trichomanes anadromum	Hymenophyllaceae	0	0	1	92	
Lockhartia pittieri	Orchidaceae	0	0	1	93	
Kefersteinia sp.	Orchidaceae	0	0	1	94	
Hymenophyllum brevifrons	Hymenophyllaceae	0	0	1	95	
Jacquiniella pedunculata	Orchidaceae	0	0	1	96	
Pleurothallis grobyi	Orchidaceae	0	0	1	97	
Caularthron bilamellatum	Orchidaceae	0	0	1	98	
Werauhia sanguinolenta	Bromeliaceae	0	0	1	99	
Peperomia cordulata	Piperaceae	0	0	1	100	
Jacquinella sp.	Orchidaceae	0	0	1	101	
Drymonia serrulata	Gesneriaceae	1	0	1	102	30
Maxillaria variabilis	Orchidaceae	0	0	1	103	

APPENDIX 2

Comparison of actual occurrence of epiphytes on *Marila laxiflora* and null assemblages created from the epiphyte pool in 0·4 ha of the San Lorenzo Crane Plot. The analysis is based on the individual number found on 40 *Marila laxiflora* trees. Shown are individual numbers of a given epiphyte species observed on *Marila laxiflora* and the expected range of individual numbers (lower and upper boundary of 95% confidence intervals). Bold names indicate species which were more common than expected; underlined names indicate species that are less common than expected.

Species	Family	Individuals on *Marila*	Individuals of null assemblage		Rank	
			Lower boundary	Upper boundary	Null assemblage	*Marila*
Scaphyglottis longicaulis	Orchidaceae	4	46	73	1	26
Scaphyglottis graminifolia	Orchidaceae	25	44	71	2	4
Elaphoglossum sporadolepis	Lomariopsidaceae	34	32	58	3	2
Maxillaria uncata	Orchidaceae	5	23	44	4	22
Pleurothallis brighamii	Orchidaceae	0	20	40	5	
Ananthacorus angustifolius	Vittariaceae	25	14	32	6	4
Dicranoglossum panamense	Polypodiaceae	123	13	30	7	1
Niphidium crassifolium	Polypodiaceae	10	11	27	8	16
Trichosalpinx orbicularis	Orchidaceae	1	8	22	9	37
Dichaea panamensis	Orchidaceae	19	5	17	10	7
Scaphyglottis prolifera	Orchidaceae	9	5	18	11	18
Tillandsia anceps	Bromeliaceae	16	4	15	12	9
Codonanthe macradenia	Gesneriaceae	28	4	16	13	3
Elaphoglossum herminieri	Lomariopsidaceae	0	3	13	14	
Trichomanes nummularium	Hymenophyllaceae	0	3	13	15	
Tillandsia bulbosa	Bromeliaceae	2	3	12	16	30
Polypodium percussum	Polypodiaceae	1	2	12	17	37

			Individuals of null assemblage		Rank	
Species	Family	Individuals on *Marila*	Lower boundary	Upper boundary	Null assemblage	*Marila*
Sobralia fragrans	Orchidaceae	2	2	12	18	30
Anthurium friedrichsthalii	Araceae	14	2	11	19	10
Asplenium juglandifolium	Aspleniaceae	0	2	11	20	
Peperomia rotundifolia	Piperaceae	18	2	11	21	8
Asplenium serratum	Aspleniaceae	7	2	11	22	20
Campyloneurum occultum	Polypodiaceae	6	1	10	23	21
Stelis crescentiicola	Orchidaceae	0	1	9	24	
Campyloneurum phyllitidis	Polypodiaceae	3	1	9	25	28
Trichomanes ovale	Hymenophyllaceae	1	1	9	26	37
Vriesea gladioliflora	Bromeliaceae	4	1	8	27	26
Elaphoglossum latifolium	Lomariopsidaceae	0	1	8	28	
Peperomia ebingeri	Piperaceae	0	0	8	29	
Anthurium acutangulum	Araceae	24	1	8	30	6
Microgramma lycopodioides	Polypodiaceae	12	0	8	31	12
Catopsis sessiliflora	Araceae	0	0	7	32	
Anthurium hacumense	Araceae	10	0	7	33	16
Catasetum viridiflavum	Orchidaceae	11	0	6	34	15
Guzmania subcorymbosa	Bromeliaceae	2	0	6	35	30
Polystachya foliosa	Orchidaceae	0	0	6	36	
Anthrophyum lanceolatum	Vittariaceae	2	0	5	37	30
Lockhartia acuta	Orchidaceae	0	0	5	38	
Trigonidium egertonianum	Orchidaceae	0	0	6	39	
Aspasia principissa	Orchidaceae	0	0	5	40	
Maxillaria discolor	Orchidaceae	0	0	5	41	
Masdevallia livingstoneana	Orchidaceae	0	0	5	42	
Vittaria lineata	Vittariaceae	1	0	5	43	37
Trichomanes ekmannii	Hymenophyllaceae	12	0	4	44	12
Peperomia macrostachia	Piperaceae	0	0	4	45	
Anthurium clavigerum	Araceae	9	0	5	46	18
Microgramma reptans	Polypodiaceae	12	0	4	47	12
Anthurium durandii	Araceae	0	0	4	48	
Epidendrum nocturnum	Orchidaceae	1	0	4	49	37
Epidendrum difforme	Orchidaceae	0	0	4	50	
Anthurium scandens	Araceae	0	0	4	51	
Campylocentrum micranthum	Orchidaceae	5	0	3	52	22
Anthurium brownii	Araceae	1	0	4	53	37
Philodendron sagittifolium	Araceae	0	0	4	54	
Trichocentrum capistratum	Orchidaceae	0	0	4	55	
Pecluma pectinata	Polypodiaceae	0	0	4	56	
Notylia albida	Orchidaceae	1	0	3	57	37
Stenospermation angustifolium	Araceae	0	0	3	58	
Aechmea tillandsioides	Bromeliaceae	5	0	3	59	22
Oncidium ampliatum	Orchidaceae	0	0	2	60	
Hylocereus monacanthus	Cactaceae	0	0	3	61	
Trichomanes angustifrons	Hymenophyllaceae	13	0	2	62	11
Dimerandra emarginata	Orchidaceae	0	0	3	63	
Trichopilia maculata	Orchidaceae	0	0	2	64	
Columnea billbergiana	Gesneriaceae	1	0	2	65	37
Epiphyllum phyllanthus	Cactaceae	0	0	2	66	
Philodendron radiatum	Araceae	0	0	2	67	
Gongora quinquenervis	Orchidaceae	3	0	2	68	28
Mormodes powellii	Orchidaceae	0	0	2	69	
Hecistopteris pumila	Vittariaceae	0	0	2	70	
Polypodium triseriale	Polypodiaceae	2	0	2	71	30
Anetium citrifolium	Vittariaceae	0	0	2	72	
Ornithocephalus bicornis	Orchidaceae	5	0	2	73	22
Sobralia panamensis	Orchidaceae	1	0	2	74	37
Ornithocephalus powellii	Orchidaceae	0	0	2	75	
Pleurothallis verecunda	Orchidaceae	2	0	2	76	30
Epidendrum schlechterianum	Orchidaceae	1	0	1	77	37
Encyclia fragrans	Orchidaceae	0	0	1	78	
Polypodium costaricense	Polypodiaceae	0	0	1	79	
Epidendrum imatophyllum	Orchidaceae	2	0	1	80	30
Peperomia obtusifolia	Piperaceae	0	0	1	81	
Encyclia chimborazoensis	Orchidaceae	0	0	1	82	
Huperzia dichotoma	Selaginellaceae	0	0	1	83	
Elleanthus longibracteatus	Orchidaceae	0	0	1	84	
Encyclia aemula	Orchidaceae	0	0	1	85	
Guzmania musaica	Bromeliaceae	0	0	1	86	

Species	Family	Individuals on *Marila*	Individuals of null assemblage		Rank	
			Lower boundary	Upper boundary	Null assemblage	*Marila*
Trichomanes punctatum	Hymenophyllaceae	0	0	1	87	
Trichomanes anadromum	Hymenophyllaceae	1	0	1	88	37
Pleurothallis grobyi	Orchidaceae	0	0	1	89	
Cochleanthes lipscombiae	Orchidaceae	0	0	1	90	
Jacquinella sp.	Orchidaceae	0	0	1	91	
Jacquiniella pedunculata	Orchidaceae	0	0	1	92	
Trichomanes godmanii	Hymenophyllaceae	0	0	1	93	
Maxillaria variabilis	Orchidaceae	0	0	1	94	
Lockhartia pittieri	Orchidaceae	0	0	1	95	
Kefersteinia sp.	Orchidaceae	0	0	1	96	
Peperomia cordulata	Piperaceae	0	0	1	97	
Drymonia serrulata	Gesneriaceae	0	0	0	98	
Werauhia sanguinolenta	Bromeliaceae	0	0	1	99	
Maxillaria crassifolia	Orchidaceae	0	0	1	100	
Caularthron bilamellatum	Orchidaceae	0	0	1	101	
Hymenophyllum brevifrons	Hymenophyllaceae	0	0	1	102	
Anthurium bakeri	Araceae	0	0	1	103	

APPENDIX 3

Comparison of actual occurrence of epiphytes on *Perebea xanthochyma* and null assemblages created from the epiphyte pool in 0·4 ha of the San Lorenzo Crane Plot. The analysis is based on the individual number found on 38 *Perebea xanthochyma* trees. Shown are individual numbers of a given epiphyte species observed on *Perebea xanthochyma* and the expected range of individual numbers (lower and upper boundary of 95 % confidence intervals). Bold names indicate species which were more common than expected; underlined names indicate species that are less common than expected.

Species	Family	Individuals on *Perebea*	Individuals of null assemblage		Rank	
			Lower boundary	Upper boundary	Null assemblage	*Perebea*
Scaphyglottis longicaulis	Orchidaceae	6	18	37	1	12
Scaphyglottis graminifolia	Orchidaceae	0	17	37	2	
Elaphoglossum sporadolepis	Lomariopsidaceae	1	13	30	3	18
Maxillaria uncata	Orchidaceae	7	8	23	4	11
Pleurothallis brighamii	Orchidaceae	0	7	20	5	
Dicranoglossum panamense	Polypodiaceae	43	4	16	6	1
Ananthacorus angustifolius	Vittariaceae	33	5	17	7	2
Niphidium crassifolium	Polypodiaceae	1	3	14	8	18
Trichosalpinx orbicularis	Orchidaceae	0	2	12	9	
Dichaea panamensis	Orchidaceae	1	1	9	10	18
Tillandsia anceps	Bromeliaceae	17	1	9	11	4
Scaphyglottis prolifera	Orchidaceae	0	1	9	12	
Trichomanes nummularium	Hymenophyllaceae	0	1	8	13	
Codonanthe macradenia	Gesneriaceae	11	1	9	14	7
Elaphoglossum herminieri	Lomariopsidaceae	0	0	7	15	
Tillandsia bulbosa	Bromeliaceae	0	0	7	16	
Sobralia fragrans	Orchidaceae	0	0	7	17	
Polypodium percussum	Polypodiaceae	1	0	7	18	18
Peperomia rotundifolia	Piperaceae	5	0	6	19	14
Anthurium friedrichsthalii	Araceae	1	0	6	20	18
Asplenium juglandifolium	Aspleniaceae	6	0	6	21	12
Asplenium serratum	Aspleniaceae	0	0	6	22	
Campyloneurum occultum	Polypodiaceae	1	0	6	23	18
Stelis crescentiicola	Orchidaceae	0	0	5	24	
Trichomanes ovale	Hymenophyllaceae	8	0	5	25	9
Campyloneurum phyllitidis	Polypodiaceae	1	0	5	26	18
Peperomia ebingeri	Piperaceae	1	0	5	27	18
Vriesea gladioliflora	Bromeliaceae	8	0	5	28	9
Elaphoglossum latifolium	Lomariopsidaceae	0	0	5	29	
Anthurium acutangulum	Araceae	4	0	5	30	15
Catopsis sessiliflora	Araceae	0	0	4	31	
Microgramma lycopodioides	Polypodiaceae	1	0	5	32	18
Polystachya foliosa	Orchidaceae	0	0	3	33	
Catasetum viridiflavum	Orchidaceae	0	0	4	34	

Species	Family	Individuals on *Perebea*	Individuals of null assemblage		Rank	
			Lower boundary	Upper boundary	Null assemblage	*Perebea*
Anthurium hacumense	Araceae	0	0	4	35	
Guzmania subcorymbosa	Bromeliaceae	2	0	4	36	16
Trigonidium egertonianum	Orchidaceae	0	0	3	37	
Lockhartia acuta	Orchidaceae	0	0	3	38	
Maxillaria discolor	Orchidaceae	0	0	3	39	
Anthrophyum lanceolatum	Vittariaceae	1	0	3	40	18
Aspasia principissa	Orchidaceae	0	0	3	41	
Anthurium clavigerum	Araceae	0	0	3	42	
Trichomanes ekmannii	Hymenophyllaceae	12	0	3	43	5
Vittaria lineata	Vittariaceae	0	0	3	44	
Masdevallia livingstoneana	Orchidaceae	0	0	3	45	
Epidendrum difforme	Orchidaceae	0	0	3	46	
Microgramma reptans	Polypodiaceae	0	0	3	47	
Epidendrum nocturnum	Orchidaceae	0	0	3	48	
Anthurium durandii	Araceae	1	0	3	49	18
Campylocentrum micranthum	Orchidaceae	10	0	2	50	8
Peperomia macrostachia	Piperaceae	0	0	3	51	
Anthurium scandens	Araceae	0	0	3	52	
Anthurium brownii	Araceae	0	0	2	53	
Philodendron sagittifolium	Araceae	0	0	2	54	
Pecluma pectinata	Polypodiaceae	0	0	2	55	
Trichocentrum capistratum	Orchidaceae	1	0	2	56	18
Aechmea tillandsioides	Bromeliaceae	12	0	2	57	5
Stenospermation angustifolium	Araceae	0	0	2	58	
Notylia albida	Orchidaceae	0	0	2	59	
Dimerandra emarginata	Orchidaceae	0	0	2	60	
Hylocereus monacanthus	Cactaceae	0	0	2	61	
Oncidium ampliatum	Orchidaceae	1	0	1	62	18
Trichomanes angustifrons	Hymenophyllaceae	24	0	2	63	3
Mormodes powellii	Orchidaceae	0	0	2	64	
Epiphyllum phyllanthus	Cactaceae	1	0	1	65	18
Columnea billbergiana	Gesneriaceae	0	0	1	66	
Trichopilia maculata	Orchidaceae	0	0	1	67	
Hecistopteris pumila	Vittariaceae	0	0	1	68	
Philodendron radiatum	Araceae	0	0	1	69	
Anetium citrifolium	Vittariaceae	0	0	1	70	
Ornithocephalus powellii	Orchidaceae	0	0	1	71	
Peperomia obtusifolia	Piperaceae	0	0	1	72	
Polypodium triseriale	Polypodiaceae	0	0	1	73	
Huperzia dichotoma	Selaginellaceae	0	0	1	74	
Encyclia fragrans	Orchidaceae	0	0	1	75	
Gongora quinquenervis	Orchidaceae	2	0	1	76	16
Pleurothallis verecunda	Orchidaceae	1	0	1	77	18
Guzmania musaica	Bromeliaceae	0	0	1	78	
Ornithocephalus bicornis	Orchidaceae	0	0	1	79	
Sobralia panamensis	Orchidaceae	0	0	1	80	
Epidendrum imatophyllum	Orchidaceae	0	0	1	81	
Trichomanes godmanii	Hymenophyllaceae	0	0	1	82	
Polypodium costaricense	Polypodiaceae	0	0	1	83	
Trichomanes punctatum	Hymenophyllaceae	0	0	1	84	
Elleanthus longibracteatus	Orchidaceae	0	0	1	85	
Encyclia chimborazoensis	Orchidaceae	0	0	1	86	
Pleurothallis grobyi	Orchidaceae	0	0	1	87	
Epidendrum schlechterianum	Orchidaceae	0	0	1	88	
Encyclia aemula	Orchidaceae	0	0	1	89	
Trichomanes anadromum	Hymenophyllaceae	0	0	1	90	
Cochleanthes lipscombiae	Orchidaceae	0	0	1	91	
Maxillaria crassifolia	Orchidaceae	0	0	1	92	
Jacquiniella pedunculata	Orchidaceae	0	0	1	93	
Caularthron bilamellatum	Orchidaceae	0	0	0	94	
Lockhartia pittieri	Orchidaceae	0	0	1	95	
Drymonia serrulata	Gesneriaceae	0	0	0	96	
Jacquinella sp.	Orchidaceae	0	0	0	97	
Kefersteinia sp.	Orchidaceae	0	0	0	98	
Hymenophyllum brevifrons	Hymenophyllaceae	0	0	0	99	
Peperomia cordulata	Piperaceae	0	0	1	100	
Maxillaria variabilis	Orchidaceae	0	0	0	101	
Werauhia sanguinolenta	Bromeliaceae	0	0	0	102	
Anthurium bakeri	Araceae	0	0	0	103	