

# Long-term changes of the vascular epiphyte assemblage on the palm *Socratea exorrhiza* in a lowland forest in Panama

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## Abstract

**Question:** What are the qualitative and quantitative long-term changes in the vascular epiphyte assemblage on a particular host tree species?

**Location:** Lowland rain forest of the San Lorenzo Crane Plot, Republic of Panama.

**Methods:** We followed the fate of the vascular epiphyte assemblage on 99 individuals of the palm *Socratea exorrhiza* by three censuses over the course of five years.

**Results:** The composition of the epiphyte assemblage changed little during the course of the study. While the similarity of epiphyte vegetation decreased on individual palms through time, the similarity analysed over all palms increased. Even well established epiphyte individuals experienced high mortality with only 46% of the originally mapped individuals surviving the following five years. We found a positive correlation between host tree size and epiphyte richness and detected higher colonization rates of epiphytes per surface area on larger trees.

**Conclusions:** Epiphyte assemblages on individual *S. exorrhiza* trees were highly dynamic while the overall composition of the epiphyte vegetation on the host tree species in the study plot was stable. We suggest that higher recruitment rates, due to localized seed dispersal by already established epiphytes, on larger palms promote the colonization of epiphytes on larger palms. Given the known growth rates and mortality rates of the host tree species, the maximum time available for colonization and reproduction of epiphytes on a given tree is estimated to be ca. 60 years. This time frame will probably be too short to allow assemblages to be ever saturated.

**Keywords:** Community stability; Dispersal limitation; Host tree; Mortality.

**Nomenclature:** Angiosperms: D'Arcy (1987); Ferns: Lellinger (1989).

## Introduction

Our current understanding of the dynamics of vascular epiphyte assemblages is largely derived from observations of the epiphytes on individual trees or forests differing in age (Dudgeon 1923; Catling et al. 1986; Ibisch 1996; Zotz & Vollrath 2003). Although data obtained with such 'space-for-time' substitutions (Pickett 1989) allow some inferences on the speed and direction of dynamic community processes, they obviously cannot replace direct observations (Rees et al. 2001). There are some more recent papers that document the dynamics of epiphyte populations over up to seven years (Hietz 1997; Zotz 1998; Zotz et al. 2005), but to our knowledge not a single publication reports direct observations of long-term changes in the composition of an epiphyte assemblage.

Knowledge of the dynamics at this scale is vital for at least two reasons: (1) to analyse the mechanisms behind the frequently stunning  $\alpha$ -diversity of tropical epiphyte communities we have to know how stable these are in time and space, and (2) information on the 'natural' situation in undisturbed forests is important for conservation efforts because it can be used as a reference for the interpretation of epiphyte community dynamics in secondary forests, which will most likely be the common type of tropical vegetation in future decades (Wright & Muller-Landau 2006).

The dynamics of vascular epiphyte assemblages is expected to differ from that of soil rooted plants in a number of ways, mostly because of the dynamics of the supporting trees (Hietz 1997; Zotz et al. 2005). Trees provide new substratum on trunks and branches by continuous growth, but also introduce a high degree of disturbance due to the turnover of branches and twigs. Unless epiphyte colonization of individual trees is fast, it will inevitably be truncated because of the limited longevity of individual supports (Benzing 1990). Vertical tree growth creates new colonization opportunities for epiphyte species in certain strata in the vertical

profile of the forest (Zotz & Vollrath 2003). Additional, age related changes in bark structure and humus accumulation in the canopy create further diversification of the arboreal habitat (Nadkarni 2000). Inherently slow growth (Schmidt & Zotz 2002) and restricted dispersal ability (Murren & Ellison 1998) can explain the usually observed low individual densities and the pronounced patchiness in epiphyte assemblages in lowland forests (Bennett 1986; Zotz & Vollrath 2003; Benavides et al. 2005), which in turn would make true succession, i.e. the competitive displacement of one set of plant species by another (Crawley 1997), rather unlikely. Indeed, a detailed analysis on more than 1000 *Annona* trees of different size (Zotz et al. 1999) did not find any indication for subsequent replacement of early colonizers by later arrivals.

The present publication is part of an ongoing research effort to document the long-term dynamics of the species-rich epiphyte vegetation in a lowland forest near the Caribbean coast of Panama (Zotz 2004a). Here, we report the changes in species composition and abundance of the vascular epiphytes growing on one particular host tree species, the stilt-root palm *Socratea exorrhiza* over a period of five years.

## Material and Methods

This study was conducted at the San Lorenzo Canopy Crane site that is located near the Atlantic coast of the Republic of Panama (Wright et al. 2003). The facility at 130 m a.s.l. is situated in a forest that has not experienced any severe human disturbance for at least 200 a (Condit et al. 2004). Mean annual rainfall is ca. 3100 mm, with a pronounced dry season in the first months of the year: February and March each receive only ca. 45 mm of rain. A 52 m tall construction crane covers ca. 1 ha of forest with its jib of 54 m. A small gondola allowed easy access to the epiphytes on the focal trees of this study, *Socratea exorrhiza* (Arecaceae), although the use of binoculars was necessary in rare cases. This palm reached up to 28 m in a few cases, but the mean tree height in this study was below 10 m. The epiphyte assemblage growing on this palm was first studied in the late 1999 dry season. Epiphytes were not labelled individually, but the attachment site of each individual was recorded with its azimuth and the distance to the ground determined with a measuring tape (Zotz & Vollrath 2003). To investigate the subsequent fate of these epiphytes, the census was repeated in 2002 and 2004, always at the same time of the year. A few palms that could not be relocated during subsequent censuses, and individuals < 1 m in height, are not included in the present study. Both palm height and

trunk surface area could be estimated using the allometric relationships established by Zotz & Vollrath (2003).

This report investigates the temporal changes in the composition of vascular epiphyte assemblages growing on a cohort of 99 palm trees. In each census, we determined the trunk diameter above the stilt roots base (DBH, to the nearest mm), and examined both trunk and stilt roots for the presence of vascular epiphytes. Throughout the study we used DBH as a measure of size. Each individual epiphyte was registered with species name, size and location on the tree (height, cardinal direction). Hemi-epiphytes were also registered, whether or not they had contact with the soil. Vines and lianas were ignored. Depending on the species, either stem height/length or the length of the longest leaf were used as a measure of size. With few exceptions we were able to identify each individual to species level, even in the case of juveniles (only tiny seedlings were ignored). Estimates of the maximum size of each species were available from Zotz (2004b) who examined more than 13 000 individuals of 103 species in 0.4 ha of the study plot. In this report, 'individual' is used *sensu* Sanford (1968), i.e. as 'group of stems'. Voucher specimens are deposited at the herbarium of the Smithsonian Tropical Research Institute, Panama.

Two commonly used diversity indices were calculated for the epiphyte assemblages on individual host trees: Simpson's diversity Index and the Shannon-Wiener Index (Krebs 1989).

The similarity of epiphytic assemblages between tree individuals and within an individual in time were assessed using the Chao-Sørensen abundance based similarity Index (Chao et al. 2005). To compare the similarity of epiphyte assemblages on individual palms within and among census years we applied a bootstrap to Chao-Sørensen Index values of every palm individual. With the bootstrapping procedure we are estimating the sampling distribution of the Chao-Sørensen Index values by resampling with replacement from the original sample. For example, for calculating the similarity of epiphytic assemblages on 56 palms in 1999 we first determined the similarity of the epiphyte assemblage on a given palm with all other palms by calculating Chao-Sørensen Index values. We then randomly took 56 of these indices from the dataset while replacing every taken sample before choosing the next sample. This was repeated 600 times. By discarding the 15 highest and the 15 lowest values we obtained 95% confidence intervals. The resulting values were used for further analysis. Statistical analysis was carried out with STATISTICA (Anon. 1998) and EstimateS (Colwell 2005).

## Results

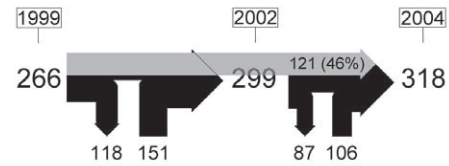
### Host trees

Three years after the initial census of 1999, ten of the original 99 trees had died. One of these was a small juvenile (DBH: 55 mm), the remaining individuals ranged from 118 mm to 157 mm DBH. During the next two years only two additional large palms (110 mm and 150 mm DBH) died. Excluding the single juvenile palm, the DBH at death ranged from 110 mm to 157 mm, which corresponds to an age of 40-120 a according to Zotz & Vollrath (2003); the mean age estimate being  $79 \pm 29$  (mean  $\pm$  SD,  $n = 11$ ). The mean DBH increase during the study was  $6.6 \pm 10.8$  mm (mean  $\pm$  SD,  $n = 82$ ) which corresponds to an increase in palm height of ca. 0.6 m in five years.

### Epiphyte vegetation

During this study, we observed a total of 65 species of vascular epiphytes growing on *Socratea exorrhiza* (Table 1, next page). Nine were found only in the first census, four species were found only in 2002 and two species were found only in 2004. All of them were rare taxa (Table 1). While the total epiphyte species number decreased by nine (-16%) in five years (Table 2), the total number of individuals increased by 194 (+20%) from 763 individuals in 1999 to 957 in 2004. However, when accounting for the decreasing number of palms due to mortality, both species richness and abundance per inhabited palm increased by 5% and 29%, respectively. These increases were not accompanied by an increase in diversity indices: the median Simpson Index was 0.78 in 1999 and 0.77 in 2004, the respective numbers for the Shannon-Wiener Index were 0.22 and 0.24.

This gross increase in epiphyte abundance was achieved in spite of considerable mortality. Our analysis of net turnover rates did not include small epiphyte individuals because these could not be tracked reliably



**Fig. 1.** Net-turnover of epiphyte individuals from 1999 to 2004 on 99 *Socratea exorrhiza* palms. Note that only plants > 50% of maximum size of a given species are considered. Large figures are the individual numbers in the three census years, vertical arrows indicate recruitment and mortality and the grey arrow represents the proportion of plants originally found in 1999 and still present in 2004.

in time without individual tagging. Restricting the analysis to larger individuals (> 50% maximum size of a given species = 'well-established' plants) revealed surprisingly high temporal changes (Fig. 1). Consistent with the increase in abundance with time in plants of all sizes (Table 2), the number of larger individuals also increased during the first three years by ca. 11%: 118 individuals died and 151 were recruited from smaller size classes. Even when excluding epiphyte extinction events due to tree mortality only around two thirds of all larger individuals originally found in 1999 were still present three years later, and only about half after five years (data not shown). This analysis did not consider losses due to tree mortality. Including these additional losses reduced the percentage of survivors to 46% (Fig. 1). Since 50% maximum size is an arbitrary cut-off, we explored the effect of the choice of cut-off on the result, finding consistent results. For example, analysing net-turnover rates for plants of > 20% of maximum plant size yielded a survival rate of 37% after five years, including losses due to tree mortality. Numbers of individuals increased only slightly (4% in five years) but this low number was due to tree mortality. When excluding losses due to tree mortality the number of individuals in this size class increased by 12% during the first three years: 221 died and 299 were recruited from smaller size classes (data not shown).

**Table 2.** Characteristics of *Socratea exorrhiza* host trees and their epiphytes. Data are from three censuses between 1999 and 2004. Colonization events are defined as the occurrence of epiphytes on formerly uninhabited trees in a subsequent census. Extinction events represent the loss of all epiphytes on a given palm.

	1999	2002	2004
Number of palms	99	89	87
Mean annual palm mortality in %	-	3.4	1.1
Number of palms with epiphytes	58 (58.6%)	54 (60.7%)	52 (59.8%)
Epiphyte individuals per palm: means $\pm$ SD (range)	$7.6 \pm 16.3$ (1-99)	$9.4 \pm 18.2$ (1-90)	$10.8 \pm 21.2$ (1-85)
Epiphyte species per palm: means $\pm$ SD (range)	$2.7 \pm 3.8$ (1-16)	$2.6 \pm 3.6$ (1-16)	$2.8 \pm 4.2$ (1-20)
Species density: individuals/m <sup>2</sup> ; means $\pm$ SD; maximum	$1.3 \pm 1.1$ ; 5.1	$1.1 \pm 0.9$ ; 4.0	$1.3 \pm 1.1$ ; 4.2
Individual density: individuals/m <sup>2</sup> ; means $\pm$ SD; maximum	$3.0 \pm 3.2$ ; 14.1	$3.5 \pm 4.7$ ; 27.4	$4.3 \pm 3.2$ ; 14.3
Colonization events	-	7	4
Extinction events	-	6	4
Total number of epiphyte species	56	49	47
Total number of epiphyte individuals	763	899	957

**Table 1.** Vascular epiphytes and hemi-epiphytes occurring on *Socratea exorrhiza* in three census years. Species are ranked by decreasing abundance in the first census. Hemi-epiphytes are marked with an asterisk. Wind-dispersed seeds are typical of all the *Bromeliaceae*, *Orchidaceae* and ferns of this study, with one exception (*Aechmea tillandsioides*).

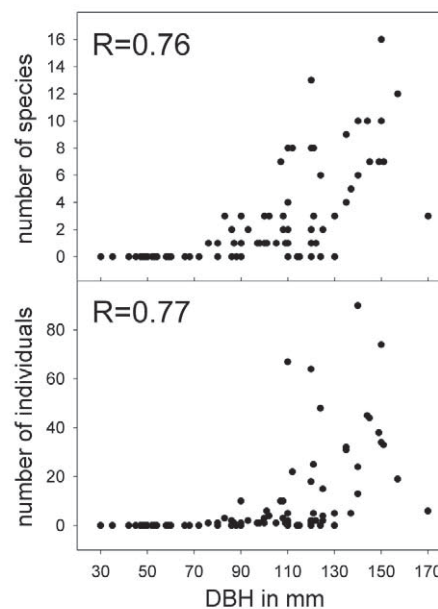
Species	Family	1999		2002		2004	
		Individuals	Rank	Individuals	Rank	Individuals	Rank
<i>Guzmania subcorymbosa</i>	<i>Bromeliaceae</i>	95	1	110	2	109	2
<i>Ananthacorus angustifolius</i>	<i>Vittariaceae</i>	76	2	73	4	105	3
<i>Elaphoglossum sporadolepis</i>	<i>Lomariopsidaceae</i>	71	3	128	1	151	1
<i>Dicranoglossum panamense</i>	<i>Polypodiaceae</i>	56	4	60	5	27	10
<i>Philodendron fragrantissimum</i> *	<i>Araceae</i>	54	5	42	8	82	4
<i>Scaphyglottis longicaulis</i>	<i>Orchidaceae</i>	51	6	76	3	57	7
<i>Scaphyglottis graminifolia</i>	<i>Orchidaceae</i>	35	7	44	7	37	8
<i>Sobralia fragrans</i>	<i>Orchidaceae</i>	30	8	25	11	11	16
<i>Tillandsia anceps</i>	<i>Bromeliaceae</i>	25	9	22	12	28	9
<i>Nipidium crassifolium</i>	<i>Polypodiaceae</i>	25	9	30	9	65	6
<i>Anthurium clavigerum</i> *	<i>Araceae</i>	22	11	12	19	15	14
<i>Asplenium serratum</i>	<i>Aspleniaceae</i>	17	12	18	13	23	12
<i>Dichaea panamensis</i>	<i>Orchidaceae</i>	16	13	5	24	9	18
<i>Vriesea gladioliflora</i>	<i>Bromeliaceae</i>	15	14	16	15	25	11
<i>Epidendrum nocturnum</i>	<i>Orchidaceae</i>	13	15	15	16	13	15
<i>Polybotrya villosula</i> *	<i>Dryopteridaceae</i>	12	16	15	16	18	13
<i>Epidendrum difforme</i>	<i>Orchidaceae</i>	11	17	3	32	3	31
<i>Anthurium friedrichsthallii</i>	<i>Araceae</i>	10	18	10	20	9	18
<i>Trichomanes angustifrons</i>	<i>Hymenophyllaceae</i>	8	19	0		3	31
<i>Columnnea billbergiana</i>	<i>Gesneriaceae</i>	8	19	0		0	
<i>Codonanthe macradenia</i>	<i>Gesneriaceae</i>	7	21	3	32	4	26
<i>Campyloneurum phylliditis</i>	<i>Polypodiaceae</i>	7	21	13	18	10	17
<i>Syngonium podophyllum</i> *	<i>Araceae</i>	6	23	7	22	5	24
<i>Trichomanes ovale</i>	<i>Hymenophyllaceae</i>	5	24	0		1	41
<i>Trichomanes ekmanii</i>	<i>Hymenophyllaceae</i>	5	24	2	37	4	26
<i>Peperomia rotundifolia</i>	<i>Piperaceae</i>	5	24	17	14	4	26
<i>Anthurium acutangulum</i>	<i>Araceae</i>	5	24	5	24	6	22
Unidentified juveniles	<i>Polypodiaceae</i>	4	28	49	6	0	
<i>Topobea praecox</i> *	<i>Melastomataceae</i>	4	28	3	32	2	35
<i>Tillandsia bulbosa</i>	<i>Bromeliaceae</i>	4	28	0		1	41
<i>Scaphyglottis prolifera</i>	<i>Orchidaceae</i>	4	28	3	32	3	31
<i>Polypodium percussum</i>	<i>Polypodiaceae</i>	4	28	4	28	3	31
<i>Peperomia ebingeri</i>	<i>Piperaceae</i>	4	28	5	24	5	24
<i>Clusia cf. uvitana</i> *	<i>Clusiaceae</i>	4	28	2	37	2	35
<i>Anthurium tetragonum</i>	<i>Araceae</i>	4	28	2	37	2	35
<i>Vittaria lineata</i>	<i>Vittariaceae</i>	3	36	6	23	0	
Unidentified juveniles	<i>Araceae</i>	3	36	4	28	9	18
<i>Philodendron sagittifolium</i> *	<i>Araceae</i>	3	36	0		2	35
<i>Microgramma lycopodioides</i>	<i>Polypodiaceae</i>	3	36	10	20	8	21
<i>Encyclia fragrans</i>	<i>Orchidaceae</i>	3	36	4	28	4	26
<i>Sobralia panamensis</i>	<i>Orchidaceae</i>	2	41	5	24	0	
<i>Polystachya foliosa</i>	<i>Orchidaceae</i>	2	41	3	32	4	26
<i>Polypodium triseriale</i>	<i>Polypodiaceae</i>	2	41	2	37	0	
<i>Pleopeltis panamensis</i>	<i>Polypodiaceae</i>	2	41	0		0	
<i>Philodendron radiatum</i> *	<i>Araceae</i>	2	41	1	42	1	41
<i>Guzmania mosaica</i>	<i>Bromeliaceae</i>	2	41	0		0	
<i>Campyloneurum occultum</i>	<i>Polypodiaceae</i>	2	41	30	9	72	5
Unidentified juveniles	<i>Orchidaceae</i>	1	48	0		0	
<i>Trichomanes punctatum</i>	<i>Hymenophyllaceae</i>	1	48	0		0	
<i>Stenospermation angustifolium</i>	<i>Araceae</i>	1	48	0		1	41
<i>Pleurothallis verecunda</i>	<i>Orchidaceae</i>	1	48	0		0	
<i>Peperomia macrostachya</i>	<i>Piperaceae</i>	1	48	1	42	2	35
<i>Ornithocephalus bicornis</i>	<i>Orchidaceae</i>	1	48	1	42	0	
<i>Monstera dilacerata</i>	<i>Araceae</i>	1	48	0		0	
<i>Elleanthus longibracteatus</i>	<i>Orchidaceae</i>	1	48	1	42	0	
<i>Drymonia serrulata</i>	<i>Gesneriaceae</i>	1	48	0		0	
<i>Dimerandra emarginata</i>	<i>Orchidaceae</i>	1	48	0		0	
<i>Anetium citrifolium</i>	<i>Vittariaceae</i>	1	48	1	42	6	22
<i>Aechmea tillandsioides</i>	<i>Bromeliaceae</i>	1	48	0		0	
<i>Trichosalpinx orbicularis</i>	<i>Orchidaceae</i>	0		4	28	0	
<i>Trichomanes spec.</i>	<i>Hymenophyllaceae</i>	0		0		1	41
<i>Pleurothallis brighamii</i>	<i>Orchidaceae</i>	0		0		1	41
<i>Philodendron tripartitum</i>	<i>Araceae</i>	0		1	42	1	41
<i>Hylocereus monacanthus</i>	<i>Cactaceae</i>	0		1	42	1	41
<i>Hecistopteris pumila</i>	<i>Vittariaceae</i>	0		2	37	2	35
<i>Anthurium hacumense</i>	<i>Araceae</i>	0		1	42	0	
<i>Anthurium brownii</i>	<i>Araceae</i>	0		1	42	0	
<i>Anthrophyum lanceolatum</i>	<i>Vittariaceae</i>	0		1	42	0	



Of all palms 42% had no epiphytes growing on them (Table 2). In most cases (95% of all individuals) epiphytes grew on the stem, very few epiphytes were found on stilt roots. Among those trees with epiphytes, both the number of species and the number of individuals increased consistently with tree size in all census years (Fig. 2). The proportion of palms hosting epiphytes remained virtually constant during the study. This lack of a net change was the result of a number of successful colonizations of formerly uninhabited palms and the reverse process. Seven out of 41 palms (17%) found without epiphytes in 1999 were colonized by epiphytes in 2002. All of these palms were large palms with a DBH > 80 mm. In the subsequent period from 2002 to 2004 four out of 36 empty palms (11%) were colonized. On the other hand, six palms (DBH: 42 - 124 mm) lost all of their epiphytes during the first period (1999-2002), while four palms (DBH: 110 mm - 120 mm) did so during the second period. Almost all of these palms had only one or two epiphytes growing on them originally; the exceptional case being a palm with 45 juveniles of an unidentified fern species growing on it in 2002.

During the five-year study period, 32 palms were never inhabited by epiphytes, almost all of which were quite small in the initial census (DBH:  $66 \pm 31$  mm, mean  $\pm$  SD). The number of palms that hosted at least one epiphyte at one point in time was 67 (DBH = 115 mm  $\pm$  25 mm).

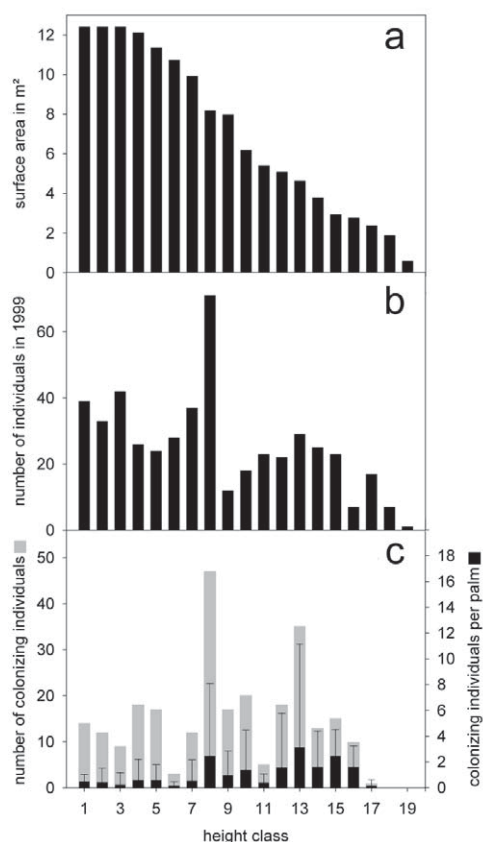
Palm size was important in respect to epiphyte numbers at a particular point in time, but also in respect to colonization patterns: we found significant correlations between the size of a host tree and the absolute numbers of epiphyte species and individuals that colonized it during the first period and established successfully, i.e. were still present in 2004 (Spearman  $R = 0.60$ ,  $p < 0.001$ ,  $n = 82$ , data not shown). If successful colonization by vascular epiphytes were only a function of substrate area, the number of new individuals per unit area should be independent of palm size. This was indeed the case for colonizing species (Spearman  $R = 0.14$ ,  $p = 0.29$ ,  $n = 57$ ), but not for new individuals (Spearman  $R = 0.31$ ,  $p < 0.05$ ,  $n = 57$ , data not shown). We analyzed palms with a DBH > 80 mm since smaller palms, with few exceptions, never hosted epiphytes (Fig. 2; Zotz & Vollrath 2003) and found that among these palms larger trees were colonized by more epiphyte individuals per bark surface area. While smaller palms (DBH = 80 mm - 100 mm) were colonized by less than one individual per m<sup>2</sup> in three years, this figure approximately doubled in the largest palms (140 - 160 mm). The maximum colonization of 24.1 individuals per m<sup>2</sup> in three years occurred on a palm (DBH = 110 mm) that was heavily colonized by juveniles of the fern species *Elaphoglossum sporadolepis*.



**Fig. 2.** Relationship between DBH of *Socratea exorrhiza* palms and inhabiting epiphyte species and individual numbers in the 2002 census. The relationships in 1999 and 2004 were very similar (Spearman Rank correlation,  $R \geq 0.76$ ,  $p < 0.001$ ,  $n = 88$ ).

The higher net colonization rate per unit area as observed in larger palms may be related to the higher number of already established epiphytes if successful recruitment were mostly restricted to the immediate vicinity of a seeding plant. To test this notion we compared the net colonization rates of all epiphyte species during the first census period on originally empty palms and palms that were already colonized by a given epiphyte species. A palm that already hosted a given wind-dispersed epiphyte species was indeed colonized significantly more often by conspecifics ( $2.0 \pm 1.8$  individuals in three years, mean  $\pm$  SD) than controls, i.e. trees lacking this species ( $0.1 \pm 0.2$  individuals,  $t$ -test,  $p < 0.001$ ,  $n = 21$  species). Additional, separate analyses with the two most important taxonomic groups of wind-dispersed species, the orchids and the ferns, yielded very similar numeric results (data not shown). There was no difference in palm DBH between groups ( $t$ -test;  $p = 0.71$ ;  $n_{\text{palms lacking species}} = 32$ ;  $n_{\text{palms hosting species}} = 18$ ). Animal-dispersed holo-epiphytes and hemi-epiphytes showed a similar trend, although differences were not significant: in general, already colonized palms were colonized by  $0.3 \pm 0.6$  individuals in three years, and empty palms by only  $0.04 \pm 0.06$  individuals ( $t$ -test,  $p = 0.21$ ,  $n = 13$  species).

Another possible explanation for the higher net colonization of larger palms is the creation of qualitatively different habitat patches along the tree trunk as the palm



**Fig. 3.** Vertical distribution of (a) substrate surface area; (b) epiphyte individuals found in 1999; (c) epiphyte colonization events (grey bars) on all *Socratea exorrhiza* considered and mean number of colonization events per palm (black bars, error bars = SD). We considered only 'successful' colonization, i.e. individuals colonizing a palm during the 1999/2002 period and found again in 2004. Hence, only the (33) palms included in (c) were included in graphs (a) and (b), resulting in 484 individuals in graph (b). Height classes (hc) are defined as: hc1: 0 m - 1 m above ground, hc2: 1.01 m - 2 m, etc.

grows. We tested this notion by quantifying the substrate area of palm trunks and colonization events as a function of height for all palms that were successfully colonized by epiphytes, i.e. epiphytes appearing after the first three years of the study and still present in 2004. Although the potential substrate area decreased considerably with height (Fig. 3a) most colonization events occurred in the upper sections of palm trunks with up to  $3.2 \pm 8.0$  newly established individuals (mean  $\pm$  SD; Fig. 3c) between 7 m - 8 m height. Only palms with at least 110 mm DBH exceed a height of 7 m (Zotz & Vollrath 2003). A direct comparison of the height of attachment of the original assemblage in 1999 and the new colonizers showed a significant shift towards the upper parts of the trunks (Mann-Whitney-*U*-Test,  $Z = 2.7$ ,  $p < 0.01$ , Fig. 3b, c).

Colonization and extinction events of individual species led to changes in the composition of the epiphyte assemblages on a given host tree. Comparing the epiphyte assemblages of a given palm between censuses yielded a significant decrease in similarity with time. The mean Chao-Sørensen abundance based similarity index for a palm individual that hosted at least one epiphyte individual was  $0.70 \pm 0.04$  between 1999 and 2002, but  $0.66 \pm 0.05$  between 1999 and 2004 (means  $\pm$  SD; *t*-test for dependent samples;  $p < 0.001$ ;  $n = 43$ ; data were bootstrapped). In contrast, the total epiphyte vegetation of all palms in the plot became more similar over time: the Chao-Sørensen abundance based similarity index increased from 0.15 in 1999 and 0.18 in 2002 to 0.21 in 2004 (one-factorial ANOVA,  $F = 5701$ ,  $p < 0.001$ ). After five years, there was only one exchange among the ten most abundant species based on the number of total individuals (*Sobralia fragrans*; *Orchidaceae*) dropped to rank 16 and *Campyloneurum occultum* (*Polypodiaceae*) rose to rank five), and only three exchanges among the 20 most abundant taxa.

## Discussion

Only 46% of all well established individuals originally found in 1999 on 99 *Socratea exorrhiza* palms were still alive in 2004 (Fig. 1), and the assemblages on individual palms showed decreased similarity through time. Analysed over all palm trees, however, the similarity increased and the species ranking changed very little (Table 1). This suggests that a stable subset of the local epiphyte species pool colonizes this palm species. Considering that the San Lorenzo Forest has not been disturbed for centuries (Condit et al. 2004), the epiphyte vegetation on *Socratea exorrhiza* may have reached a steady state. On the other hand, five years may still be too short a period for these slow growing plants (cf. Schmidt & Zotz 2002) to show possible long-term fluctuations, and only longer-term observations can provide unambiguous proof of the supposed stability in time.

The suggested steady state certainly does not apply to the individual palm tree as the similarity decreases with time at this scale. The frequent colonization of formerly uninhabited palms and complete eradication of all epiphytes on a given palm (Table 2) also indicate otherwise. Arguing against the notion that a steady state is ever reached at the level of individual trees is the significant correlation of epiphyte species numbers and individuals with palm size with no obvious saturation (Fig. 2). Finally, the time available for colonization of *Socratea exorrhiza* may be short in comparison to the generation time of most epiphyte species. Zotz & Vollrath (2003) reported that epiphytes rarely establish on

*Socratea exorrhiza* trees with a DBH < 80 mm, i.e. on palms younger than 20 a, and our five-year observations confirm this. The larger palms that died during this study had a DBH of 110 mm to 157 mm. This corresponds to an age of ca. 80 a at death, leaving fewer than 60 a available for colonization. Epiphyte taxa preferring higher strata of the forest will not start colonizing *Socratea exorrhiza* until much later (Zotz & Vollrath 2003). Since it takes in the region of a decade between germination and first reproduction in most epiphytes studied (e.g. Benzing 1981; Hietz et al. 2002; Schmidt & Zotz 2002), this further reduces the time a palm is available for an epiphyte to complete its life cycle. The low density of epiphytes, even on large palms (Table 2), as a result of (1) low rates of successful colonization (as shown); (2) low growth rates (Schmidt & Zotz 2002) and (3) high mortality rates, even in the case of well-established individuals (Fig. 1) suggest that the life span of *Socratea exorrhiza* does not allow vascular epiphytes to colonize it completely. This time frame may be short in comparison to other tree species with greater life expectancies of individual trees, but such a comparison is only valid for epiphytes restricted to tree trunks. Individual branches of dicotyledonous trees with a more complicated architecture than palms may provide similarly short or even shorter colonization opportunities for dependent flora. Host-tree fall explained mortality of epiphytes only to some extent and drought is also an unlikely major cause of mortality: drought mostly affects smaller individuals (Zotz et al. 2001), while the present analysis only includes larger epiphytes, i.e. plants have passed the juvenile stage and are several years old. Thus, mortality must also be due to other causes. One possible reason is regularly falling palm leaves or branch fall of neighbouring trees (Gillman & Ogden 2005). Due to the palms monopodial architecture a falling branch or palm leaf that hits a palm and slides downwards the trunk could destroy many epiphyte individuals.

Similar to most studies on epiphyte-host tree relationships (e.g. Yeaton & Gladstone 1982; Hietz & Hietz-Seifert 1995; Zotz et al. 1999), we found a positive correlation between epiphyte richness and host size. The usual explanation invokes both the factors (1) greater time available for colonization and (2) greater bark area, i.e. a larger potential colonization surface for diaspores (Benzing 1990). Our finding that large palms have a higher colonization rate of epiphyte individuals per surface area than small palms implies that other factors change as the palm tree grows. Factors that could facilitate colonization are, e.g. a tree age related increase in bryophyte cover (Zotz & Vollrath 2003), weathering of the bark or increased light availability and associated changes of the microclimate as trunk height increases

that could allow the colonization by epiphyte species with higher light requirements: notably, a large proportion of all epiphytes is found preferentially at intermediate heights of the forest (Johansson 1974).

A different mechanism, that is not related to establishment conditions but to dispersal, may provide an additional explanation, and relates to the observed increase in large epiphyte individuals on larger/older palms (Zotz & Vollrath 2003). Although we did not directly study reproduction, we expect a higher number of sexually reproducing plants on larger palms, which produce offspring. The sexually derived progeny find a suitable habitat in the immediate vicinity, i.e. on the same palm trunk. Yeaton & Gladstone (1982) suggested that conspecifics as nearest neighbours may be common because the areas closest to a fruiting individual will be most heavily inundated with the wind-dispersed seeds. Our finding supports this explanation: *Socratea exorrhiza* palms, with established wind-dispersed epiphyte species, were colonized more frequently by conspecifics. The proposed, strong dispersal limitation is consistent with the findings of Trapnell et al. (2004) who reported that only conspecifics of the epiphytic orchid *Laelia rubescens* that occurred within a 45-cm range had a significant positive genetic structure.

In summary, we found that the epiphyte assemblages on single individuals of the host tree *S. exorrhiza* were highly dynamic while the overall composition of the epiphyte vegetation on *S. exorrhiza* in the study plot was stable over the course of five years. The high turnover was due to high mortality rates, even in well-established epiphytes, and the colonization of trees by new arrivals that was more pronounced in larger/older individuals of this host tree.

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