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Long-term changes of vascular epiphyte assemblages in the tropical lowlands of Panama

by

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List of papers

This thesis is based on the following papers:

Paper I: Laube, S. and G. Zotz (2006) “Long-term changes of the vascular epiphyte assemblage on the palm *Socratea exorrhiza* in a lowland forest in Panama.” Journal of Vegetation Science 17: 307-314

Paper II: Laube, S. and G. Zotz (2006) “Neither host specific nor random: vascular epiphytes on three tree species in a Panamanian rainforest.” Annals of Botany 97: 1103-1114

Paper III: Laube, S. and G. Zotz, “A metapopulation approach to the analysis of long-term changes in the epiphyte vegetation of *Annona glabra*.” (manuscript)

My contribution to the papers

Paper I:	We used data collected for another research project (Zotz and Vollrath, 2003). I collected the data of the 2004 epiphyte census. Further I conducted all analyses and wrote the text. Zotz provided helpful comments and discussion on the text.
Paper II:	I am responsible for the idea, conducting most of the analyses and writing the text. Zotz provided the data from an earlier work (Zotz and Vollrath, 2003), performed the Canonical Correspondence Analysis, and made helpful comments on the text.
Paper III:	This study builds on a previous study by Zotz et al. (1999). Zotz suggested the study and provided helpful comments on the text. I conducted the data sampling. Further, I suggested the analysis approach, conducted the analyses and wrote the text.

Contents

Abstract

The study provides insights into the dynamic processes of vascular epiphyte vegetation in two host tree species of lowland forest in Panama. Further, a novel approach is presented to examine the possible role of host tree identity in the structuring of vascular epiphyte communities: For three locally common host tree species (*Socratea exorrhiza, Marila laxiflora, Perebea xanthochyma*) we created null models of the expected epiphyte assemblages assuming that epiphyte colonization reflected random distribution of epiphytes in the forest. 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 underrepresented compared to their occurrence in the entire forest plot. Permutations based on the number of colonized trees (reflecting observed spatial patchiness) yielded similar results. Finally, a 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. We conclude that 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.

To determine the qualitative and quantitative long-term changes in the vascular epiphyte assemblage of the host tree *Socratea exorrhiza*, in the lowland forest of the San Lorenzo Crane Plot, we followed the fate of the vascular epiphyte assemblage on 99 individuals of this palm species, in three censuses over the course of five years. The composition of the epiphyte assemblage changed little during the course of the study. While the similarity of epiphyte vegetation decreased on single palm individuals through time, the similarity analyzed 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. Epiphyte assemblages on single *Socratea exorrhiza* trees were highly dynamic while the overall composition of the epiphyte vegetation on the host tree species in the study plot was rather 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 *Socratea exorrhiza* tree is estimated to be about 60 years.

Changes in the epiphyte vegetation of c. 1000 individuals of the host tree species *Annona glabra* at Barro Colorado Island over the course of eight year were documented by means of repeated censuses. Considerable increase in the abundance of the dominating epiphyte species and ongoing colonization of the host tree species suggests that the epiphyte vegetation has not reached a steady state in the maximal 80 years since the establishment of the host tree. Epiphyte species composition as a whole was rather stable. We disentangled the relationship between epiphyte colonization and tree size/available time for colonization with the finding that tree size explained only a low proportion of colonization while other factors like connectivity to dispersal source and time explain may explain a larger part. Epiphyte populations are patchily distributed and examined species exhibit properties of a metapopulation with asynchronous local population growth, high local population turnover, a positive relationship between regional occurrence and patch population size, and negatively correlated relationship between extinction and patch occupancy. The documented metapopulation processes highlight the importance of not colonized suitable habitat for the conservation of epiphytes.

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List of Abbreviations

%	percent
°	arc degree
’	arc minute
°C	degree Celsius
λ	population growth rate
A	Area
a.s.l.	above sea level
ANOVA	Analysis of variance
A_{TS}	trunk surface area
BCI	Barro Colorado Island
C	constant used for calculating the species area curve (when $A = 1$)
c	circumference
c.	“circa” (Lat.); ‘about’
CCA	Canonical Correspondence Analysis
cf.	“confer” (Lat.); ‘compare’
C_H	crown height
cm	centimeter
C_V	crown volume
C_W	crown width
DBH	diameter at breast height
e.g.	“exempli gratia” (Lat.); ‘example given’ or ‘for example’
et al.	“et alii” (Lat.); ‘and others’
etc.	“et cetera” (Lat.); ‘and so on’
F	F-value, statistical value used by ANOVA
Fig.	figure
h	height
ha	hectare
hc	height class
i.e.	“id est” (Lat.); ‘that is’
km	kilometer
m	meter

m^2	square meter
mm	millimeter
n	sample size
N	North
P	probability
R	coefficient of correlation
R^2	coefficient of regression
rh	relative humidity
S	South, or species richness
SD	standard deviation
W	West
z	z-value, statistical value used by Mann-Whitney U-test, or gradient value of species area curve

Chapter 1

Introduction

Dynamics in plant communities

The study of vegetation change is one of the fundamental components of research in the history of vegetation science. Probably the earliest study created with permanent plots that is still running now dates back 150 years (Johnston, 1991). Since then, most studies have focused on succession, defined generally as the directional change of species composition at a site over time. The different patterns of succession have been thoroughly described by many authors (Clements, 1916; West et al., 1981; Burrows, 1990). Recently, the focus of research has broadened from descriptive studies of successional patterns to an approach to analyze the mechanisms of plant community dynamics (Connell and Slayter, 1977; Tilman, 1988; Agnew et al., 1993).

Long-term studies are indispensable in answering fundamental questions about the structure and dynamics of vegetation: How species rich is a plant community? Why are some species common and others rare? Is the species assemblage stable? If not, what are the rates of change in species composition? And what are the factors that appear to drive this change? In addition to space-for-time substitutions they serve as a reliable instrument for a deeper understanding of successional change (Pickett, 1989). Many studies in vegetation dynamics have focused on annuals and short lived perennials, because it was thought that trees were so long-lived that there was no prospect of obtaining important insights into the community dynamics of forests (Rees et al., 2001). This perspective has changed fundamentally with the establishment of permanent forest plots in tropical countries (Hubbell and Foster, 1983; Manokaran et al., 1992; Condit, 1998). Today, most of the knowledge on plant dynamics and underlying processes in tropical forests has been inferred from locally detailed studies of trees and shrubs (e.g. Crow, 1980; Condit et al., 1992; Whitmore and Burslem, 1998; Hubbell et al., 1999; Wills et al., 2006). The large dataset accumulating for trees and shrubs is in sharp contrast to the situation in tropical herbaceous plant communities. Although much of the high total diversity of vascular plants in rain forests is a result of the many species of epiphytic plants (Gentry and Dodson, 1987a), studies on the dynamics of epiphyte communities are lacking. Moreover, because epiphytes live in an environment that is very different from the environment experienced by trees on which they live, they can be expected to have different patterns of diversity than trees and to exist under very different conditions of growth rates and disturbance (Huston, 1994). Thus, mechanisms maintaining diversity that have been derived from the study of trees might not be directly applicable to epiphytes.

Current knowledge

Vascular epiphytes came into the focus of scientific interest with Schimper's (1888) monograph on the epiphyte vegetation in the neotropics. Extensive studies in other rainforests of the world followed (Oliver, 1930; Went, 1940; Johansson, 1974). Soon, researchers became interested in the remarkable morphological and physiological adaptations that are responses to the epiphytes' rather extreme habitat (e.g. Nabokich, 1899; Renner, 1933; Gessner, 1956). With the introduction of alpine climbing techniques (Perry, 1978) about three decades ago, and the establishing of more permanent observation facilities (e.g. canopy cranes: Parker, 1992; or canopy walkways: Inoue et al., 1995), researchers were able to conduct studies of a more quantitative manner. The new access provided the great advantage of observing and sampling their study organisms *in situ*. As a consequence studies on diversity, spatial distribution, and ecology of vascular epiphytes increased rapidly. Thorough observations of the canopy soon revealed that epiphytes contribute a substantial proportion to the total plant species richness of a rainforest. Single trees can host more than 100 vascular epiphyte species (Valdivia, 1977; Nowicki, 1998) and epiphyte communities represent up to 35 % (Gentry and Dodson, 1987b) and even 50 % (Kelly et al., 2004) of all vascular plants in a local flora. It was then recognized that on a global scale epiphytes constitute about 10 % of the vascular plant diversity (Kress, 1986).

The distribution of vascular epiphytes is almost exclusively restricted to the tropics and subtropics with few species occurring in warmer temperate regions like New Zealand (Dickinson et al., 1993), Chile (Muñoz et al., 2003) or North-West America (Sillett and Van Pelt, 2000). This restriction is believed to be caused by their intolerance to frost and drought (Benzing, 1990), although experimental evidence is lacking and exceptions have been found (Zotz, 2002). Among tropical regions most vascular epiphytes occur in the neotropics (Madison, 1977) where the vast majority of species can be found in montane rain forests. Epiphyte diversity reaches its peak in mid-elevations of 1500 - 2500 m a.s.l. (Gentry and Dodson, 1987a; Nieder et al., 2001). Factors that have been suggested to explain this pattern include environmental gradients (Wolf and Flamenco-S., 2003; Krömer et al., 2005), topography (Kreft et al., 2004) and the mid-domain effect (Cardelus et al., 2006).

Epiphyte vegetation plays an important role in the rainforest ecosystem. Epiphytes intercept and store water and nutrients (Veneklaas and Van Ek, 1990; Coxson and Nadkarni, 1995; Clark et al., 1998) and contribute considerably to primary productivity, litterfall and nutrient cycling (Putz, 1983; Nadkarni, 1986). Further, they provide a habitat for arthropods and even some vertebrates (Frank, 1983; Wake, 1987; Davidson and Epstein, 1989) and serve as food sources for different groups of animals (Nadkarni and Matelson, 1989; Benzing, 1990). With the growing concern for conservation issues, such as biodiversity, global climate change, and preservation of rain forests, the forest canopy has been recognized as a region of great ecological importance and several studies suggest that epiphytes can serve as indicators for environmental changes (Brighigna et al., 1997; Hietz, 1998; Barthlott et al., 2001).

Epiphytes use trees as structural support and different factors have been identified that influence the diversity and coexistence of this hyper-diverse group of plants such as frequent disturbance due to the dynamic substrate (Benzing, 1981a), vertical niche diversification (Johansson, 1974) or host tree identity (Went, 1940). The latter is the summation of different properties that may vary with each host species (e.g. tree size, bark morphology and bark chemistry, architectural traits and leaf phenology patterns). The frequent finding that tree size influences epiphyte occurrence, i.e. large trees host more epiphytes than smaller conspecifics (Catling and Lefkovitch, 1989; Hietz and Hietz-Seifert, 1995; Zotz and Vollrath, 2003), can be ascribed to at least two factors. First, larger trees depict a larger target area for colonizing epiphyte seeds. Finally, larger trees are usually older than smaller conspecifics and therefore have been available longer for colonization. Although tree size - epiphyte richness relationships have been known for a long time (Went, 1940), an analysis that separates tree size from time has not yet been conducted. The direct effect of tree size on epiphyte colonization can only be measured by excluding the factor time. This can not be inferred from a single observation but only from repeated observations of different sized conspecific trees in time.

High host specificity, i.e. the exclusive association of an epiphyte species with one or a few particular tree species, has rarely been found (Sulit, 1950; 1953) and is not considered to be a general trend among epiphytes (Ackerman et al., 1989). On the other end of the continuum stands the random occupation of host trees by epiphytes, an assumption that is rather hypothetical given the different requirements of epiphyte species for germination and growth. Ecological studies show that the real situation in most epiphyte species lies somewhere between both extremes and it has been suggested that each host tree species has a specific subset of the local epiphyte species pool according to its own set of properties (Zotz et al., 1999). There is no published study that examines the notion of host-specific epiphyte spectra in particular host tree species based on the entire epiphyte species pool in an area.

In the past, information on dynamic processes in vascular epiphyte vegetation were mainly deduced from time replacing side-by-side observations (Johansson, 1974; Madison, 1979; Catling et al., 1986; Catling and Lefkovitch, 1989) or were of rather short duration (Bennett, 1986). Long-term observations, although highly desirable (Benzing, 1990), have been conducted only recently and focused on the population dynamics of only one or a few species (Larson, 1992; Hietz, 1997; Zotz et al., 2005; Tremblay et al., 2006). So far, a single attempt has been made that documented the changes of the complete epiphyte vegetation on host trees over several years (Schmit-Neuerburg, 2002).

In this thesis I focus on the epiphyte assemblage of the two host tree species *Annona glabra* L. (Annonaceae) and *Socratea exorrhiza* (Mart.) H. Wendl. (Arecaceae). The first host tree species has a population not older than 88 years and the latter one is growing in an intact forest that has not experienced severe disturbance for several centuries. More than 1000 individuals of *Annona glabra* were observed for epiphyte occurrence in two census events over the course of eight years. *Annona glabra* was chosen because it offers a unique combination of features (Zotz et al., 1999): (1) *Annona glabra* is used as a support by many epiphyte species; (2) it is comparatively small allowing sampling of all epiphytes growing on it; (3) it grows exclusively in swampy areas (in this case along the shore line) thus allowing access to the entire population of the host tree.

The fate of the epiphyte vegetation on the second host tree species, S*ocratea exorrhiza*, was examined with a dataset comprising three census events over the course of five years. Here, direct access to the host trees and their epiphytes was obtained by means of a canopy crane. Reasons for choosing this particular host tree species were: (1) Limitation to a single host tree with a large number of sampled individuals allowed us to distinguish the effect of host tree identity and tree size on the epiphyte assemblage over the entire size range of this tree species. (2) Knowledge of average host tree growth rates made it possible to roughly estimate tree age. (3) The simple architecture of this palm allowed the quantification of the substrate area available for epiphyte colonization, which has rarely been tried before for obvious reasons.

Aims

The general aim of this thesis was to increase our knowledge of the dynamics in vascular epiphyte assemblages. The information not only increases our knowledge of how stable these communities are in time and space in order to explain the high diversity of this plant group. Such information from undisturbed forests is also required for conservation efforts because it can be used as a reference for the interpretation of epiphyte community dynamics in secondary forests.

More specifically, the aims were to

- investigate the turnover of epiphytes in an undisturbed forest and the importance of local factors such as tree properties and dispersal on the distribution pattern and colonization of vascular epiphytes on host trees (Chapter 3)

- investigate the role of host tree identity in the structuring of a vascular epiphyte assemblage by analysing the specific epiphyte spectra of host tree species in a forest (Chapter 4)

- investigate the dynamics of vascular epiphyte populations and their distribution and colonization pattern at the scale of several square kilometres (Chapter 5)

Chapter 2

General Methods and Study Sites

The field-work for this thesis was conducted in two distinct areas located in the Republic of Panama, namely, at the San Lorenzo Crane site (Chapter 3 and 4) and on Barro Colorado Island (Chapter 5).

San Lorenzo Crane site

The San Lorenzo Canopy Crane Site is located near Colón at the Caribbean coast of the Republic of Panama (9°17'N, 79°58'W, Fig. 2-1). The facility at 130 m a.s.l. is situated in a tropical wet evergreen forest that has not experienced any severe human disturbance for at least 200 years (Condit et al., 2004). The canopy height is quite variable, reaching maxima of c. 40 m. Average annual rainfall is c. 3100 mm with a pronounced dry season in the first months of the year: February and March each receive an average of only 45 mm of rain. The mean annual air temperature is 25.8 °C (Wright et al., 2003). A 52 m tall construction crane covers c. 9000 m^2 of forest with its jib that has a length of 54 m. A small cylindrical gondola allowed easy access to the vascular epiphytes in this area, although the use of binoculars was necessary in rare cases.

Study species

The study species *Socratea exorrhiza* (Mart.) H. Wendl. (Arecaceae) is a palm characterized by its prominent stilt roots. In the species the base of the trunk may be elevated more than a meter from the ground and is supported by an open cone of spiny stilt roots. This palm reaches up to 28 m in a few cases, but the average tree height in the study area was below 10 m. Different to most other palms this species exhibits a secondary growth when aging (Schatz et al., 1985). The species occurs from Nicaragua to northern South America.

Perebea xanthochyma Karst. (Moraceae) is a medium-sized tree of the forest understorey, in some cases reaching up to 35 m, typically with an irregular trunk and long, hanging branches. It is one of the dominant subcanopy trees of mature forest in the wetter parts of the Canal area. It occurs from Costa Rica to Peru.

The third host tree species *Marila laxiflora* Rusby (Clusiaceae) is known only from wetter forests in Panama. This shade-tolerant tree of the subcanopy is medium sized. It is common in evergreen lowland, riparian, and lower montane forests in the Neotropics from Mexico and the Antilles to Bolivia.

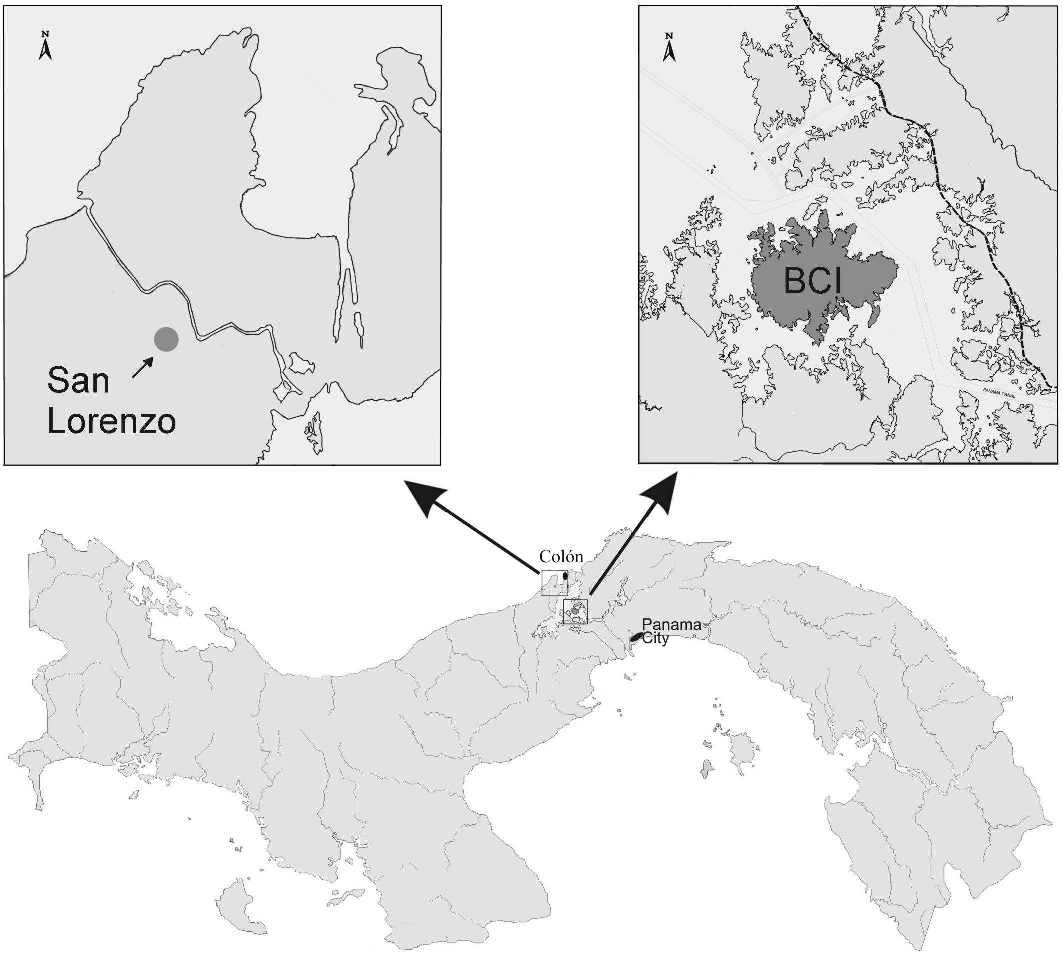

FIG. 2-1. Map of Panama and the two study sites Barro Colorado Island (BCI) and the San Lorenzo Crane Site.

Barro Colorado Island

The 1567 ha comprising Barro Colorado Island (BCI, 9°10'N, 79°51'W) is a biological reserve with a field station maintained by the Smitsonian Tropical Research Institute and is located in the Gatun Lake, Republic of Panama (Fig. 2-1). The island is part of the 5600 ha Barro Colorado Nature Monument. With the completion of the construction of the Panama Canal in 1914 the hill top Barro Colorado became an island due to the rising of the water level to create the main reservoir of water for the Panama Canal, Gatun Lake. Nine years later it was declared as a biological reserve. The vegetation is classified as tropical moist forest

(Holdridge et al., 1971) and covers the island almost completely. BCI receives an annual precipitation of c. 2600 mm. The climate of BCI is strongly seasonal with a pronounced dry season from late December to April during which only about 300 mm of rain fall occurs. The annual average temperature is 27 °C. A detailed description of vegetation, climate and ecology is provided by Leigh et al. (1982).

Study species

Annona glabra L. is a small, evergreen tree with a wide geographical distribution. In the New World it occurs from Florida to the Amazon, in the Old World in parts of Africa and has been introduced recently to Australia. In the canal region *Annona glabra* is restricted to the shore line of lakes and along small tributaries. This tree is multiple-stemmed in most cases and rarely exceeds 7 m in height (Croat and Busey, 1975). After the establishment of the BCI shore line the tree species *Annona glabra* started to colonize this new habitat (Fig. 2-2). Hence, none of the trees in the 2002 census were older than 88 years while the average age of trees is expected to be much lower. Considering that the trees had to grow a couple of years to reach a size that is suitable for epiphyte colonization we assume that epiphytes first established on the studied *Annona glabra* trees not more than 80 years ago. Accounts on tree architecture and bark characteristics can be found in Zotz (1997) and the effect of bark chemistry on the germination of epiphytes has been studied by Frei (1973). Air temperature and relative humidity (rh) were measured in the upper canopy of the forest and at the lake shore by Zotz and Winter (1994) and were shown to be quite similar, although rh tended to be slightly elevated close to the water. Thus, in spite of the small size of the host tree, epiphytes grow under conditions quite similar to the upper strata of the forest. Accumulations of humus are rarely found on *Annona glabra*, and almost all epiphytes grow directly attached to the bark.

FIG. 2-2. A multiple stemmed *Annona glabra* tree at the shore line of BCI. In the foreground, branches of another tree with the epiphytic orchids *Caularthron bilamellatum* and *Dimerandra emarginata*.

Notable exceptions in the study area are species associated with nests of ants or stingless bees such as *Codonanthe crassifolia* (Gesneriaceae) or *Peperomia cordulata* (Piperaceae).

The vascular epiphytes known from BCI are described in detail by Croat (1978, see also Zotz and Ziegler, 1997). Species names of flowering plants follow the Flora of Panama Checklist and Index (D'Arcy, 1987); authorities for ferns are according to Croat (1978). Voucher specimens of species are deposited in the BCI Herbarium, Panama.

Epiphyte census

The sampling protocol followed that of Zotz et al. (1999). The island with its 62 km shore line was divided into 120 sectors of 3° each starting with Sector 1 in the Laboratory Cove and proceeding clockwise (Fig. 2-3). Every other sector was entirely searched for occurring *Annona glabra* trees along the shore line.

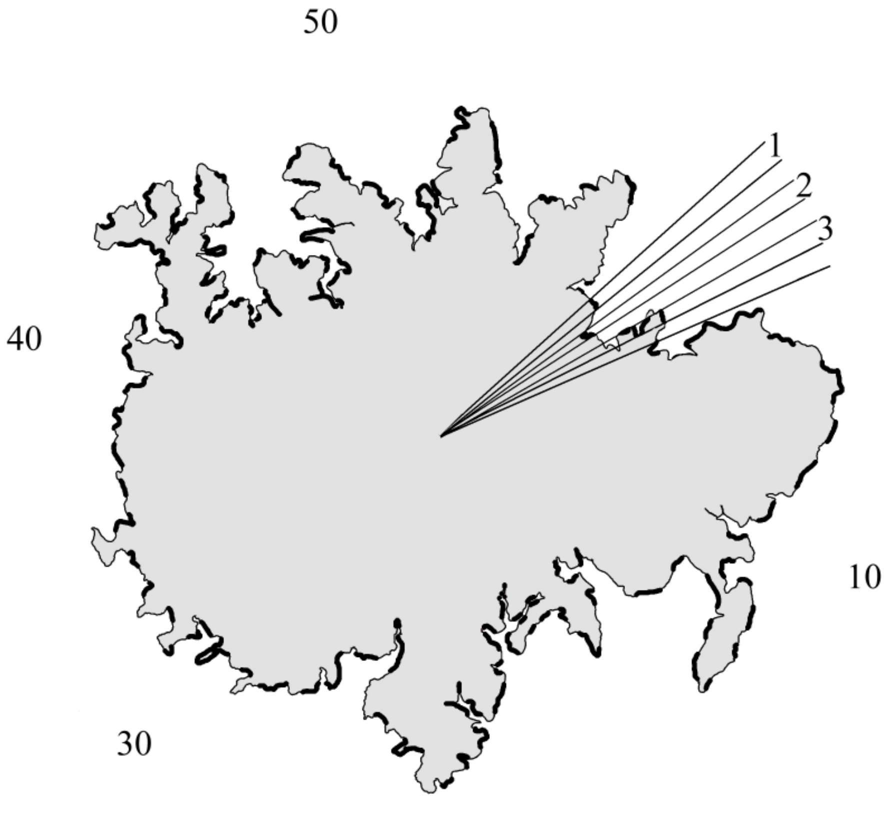

FIG. 2-3. Schematic map of BCI. Bold shore lines represent sector areas which alternate with intersector areas (hairline shores). Sectors are partly labelled by their respective numbers.

The following measurements for each encountered tree were recorded: number of stems, diameter at breast height (DBH) of every stem, height of the tallest stem, crown width (C_W) and crown height (C_H) and distance to the adjacent shore vegetation. Crown volume (C_V) was estimated as an ellipsoid (Bongers et al., 1988):

$$C_V = 0.167 \times \pi \times \left(\frac{C_W}{2} \right)^2 \times \frac{C_H}{2} .$$

Further, distance to the closest conspecifics was measured and trees were mapped. Each tree was carefully inspected for the occurrence of epiphytes. All epiphytes were counted and identified to species level, including both holo-epiphytes, i.e. genuinely epiphytic plants, and epiphytic hemi-epiphytes, i.e. plants with an epiphytic phase in the early or later stages of ontogeny (Putz and Holbrook, 1986). Conspecific epiphytes growing in close proximity were occasionally not distinguishable from each other. These “stands” were counted as one individual according to Sanford (1968).

Chapter 3

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

Introduction

Our current understanding of the dynamics of vascular epiphyte assemblages is almost completely derived from observations of the epiphytes on individual trees or forests differing in age (Dudgeon, 1923; Catling et al., 1986; Ibisch, 1996; Zotz and 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 can obviously not 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) in order to analyze the mechanisms behind the frequently stunning α-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 and 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 qualitatively new colonization opportunities for epiphyte species that prefer certain strata in the vertical profile of the forest (Zotz and 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 and Zotz, 2002) and restricted dispersal ability (Murren and Ellison, 1998) can explain the usually observed low individual densities and the pronounced patchiness in epiphyte assemblages in lowland forests (Bennett, 1986; Zotz and 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 glabra* 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 on-going 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

Study site and species

This study was conducted at the San Lorenzo Canopy Crane Site. For further detail on this study site see Chapter 2. A small gondola allowed easy access to the epiphytes on the focal tree of this study, *Socratea exorrhiza* (Mart.) H. Wendl. (Arecaceae) in this area, although the use of binoculars was necessary in rare cases. 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 as determined with a measuring tape (Zotz and 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. Therefore, 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). Throughout the study we used DBH as a measure of size. Both palm height and trunk surface area could be estimated using the allometric relationships established by Zotz and Vollrath (2003) where tree height (*h* in m) is calculated from DBH (in mm) as:

$$\log h = -0.25 + 0.01 \times DBH \ .$$

Trunk surface area (A_{TS}) was then calculated by treating the palm trunk as a cylinder,

$$A_{TS} = \pi \times DBH\left(\frac{DBH}{2} + h\right).$$

Both trunk and stilt roots were examined for the presence of vascular epiphytes. 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 out 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. Plant names of angiosperms follow the flora of Panama checklist (D'Arcy, 1987), while fern names are according to Lellinger (1989).

Data analysis

The similarity of epiphytic assemblages between tree individuals and within an individual in time were assessed using the Chao-Sørensen abundance based similarity index. This index differs from the classical Sørensen index in having a probability-based approach that reduces undersampling bias by estimating and compensating for the effects of unseen, shared species (Chao et al., 2005). Like the classical Sørensen index it varies between 0 and 1 with 0 for species assemblages that are completely different and 1 that are identical. To compare the similarity of epiphyte assemblages on individual palms within and among census years we applied a bootstrap to Chao-Sørensen indices of every palm individual. With the bootstrapping procedure we are estimating the sampling distribution of the Chao-Sørensen indices 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 indices. Then we 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. Two commonly used diversity indices were calculated for the epiphyte assemblages on individual host trees: Simpson’s diversity index and Shannon-Wiener index (Krebs, 1989). Statistical analysis was carried out with STATISTICA software (STATISTICA 6, Statsoft Inc., Tulsa, OK, USA) and EstimateS (Colwell, 2005).

Results

Host trees

Three years after the initial census of 1999, 10 of the original 99 trees had died. One of them was a small juvenile (DBH: 55 mm), the remaining individuals ranged from 118 to 157 mm DBH. During the next two years only two additional large palms (110 and 150 mm DBH) died. Excluding the single juvenile palm, the DBH at death ranged from 110 to 157 mm, which corresponds to an age of 40 – 120 years according to Zotz and Vollrath (2003); the average age estimate being 79 years ± 29 (mean ± SD, n=11). The mean DBH increase during the study was 6.6 ± 10.8 mm (mean ± SD, n = 82) which corresponds to an increase in palm height of about 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* (Appendix 1). Nine of them were found only in the first census, four species were found only in 2002, and two species were found in 2004 only. All of them where rare taxa (cf. Appendix 1). While the total epiphyte species number decreased by nine (-16 %) in five years (Table 3-1), the total number of individuals increased by 194 (+20 %) from 763

TABLE 3-1. 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 unoccupied 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
average 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 ± SD (range)	7.6 ± 16.3 (1-99)	9.4 ± 18.2 (1-90)	10.8 ± 21.2 (1-85)
epiphyte species per palm: means ± SD (range)	2.7 ± 3.8 (1-16)	2.6 ± 3.6 (1-16)	2.8 ± 4.2 (1-20)
species density: individuals m^{-2}; means ± SD; maximum	1.3 ± 1.1; 5.1	1.1 ± 0.9; 4.0	1.3 ± 1.1; 4.2
individual density: individuals m^{-2}; means ± SD; maximum	3.0 ± 3.2; 14.1	3.5 ± 4.7; 27.4	4.3 ± 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

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 occupied 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 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. 3-1). Consistent with the increase in abundance with time in plants of all sizes (Table 3-1), the number of larger individuals also increased during the first three years by about 11 %: 118 individuals died and 151 were recruited from smaller size classes.

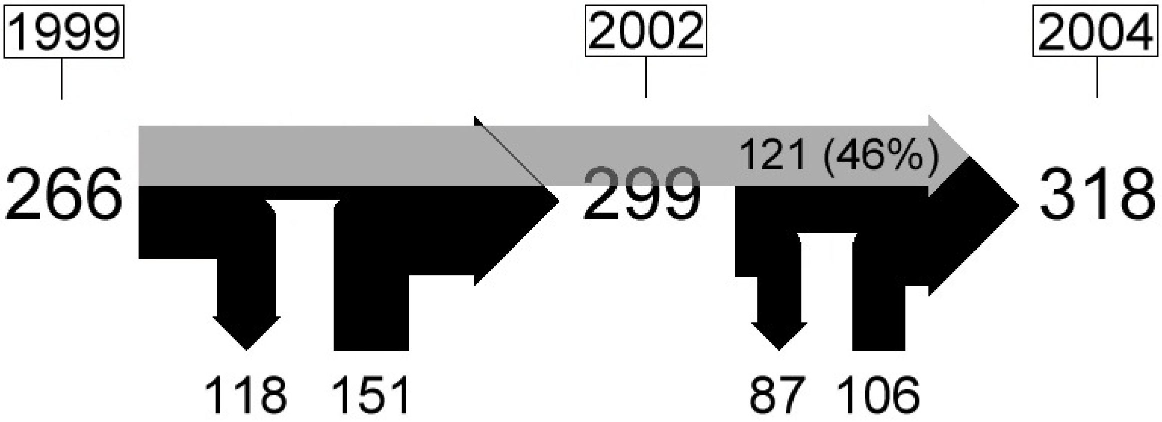

FIG. 3-1. Net-turnover of epiphyte individuals from 1999 to 2004 on 99 *Socratea exorrhiza* palms. Note, that only plants >50 % of maximum size of a given species are considered. Large figures are the individual numbers in the three census years, vertical arrows indicate recruitment and mortality, and the grey arrow represents the proportion of plants originally found in 1999 and still present in 2004.

Even when excluding epiphyte extinction events due to tree mortality only about two third 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.3-1). 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, analyzing 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).

Forty-two percent of all palms had no epiphytes growing on them (Table 3-1). 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. 3-2). 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 unoccupied palms and the reverse process. Seven out of 41 palms (17 %) found without epiphytes in 1999 were colonized by epiphytes by 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: 110-120 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.

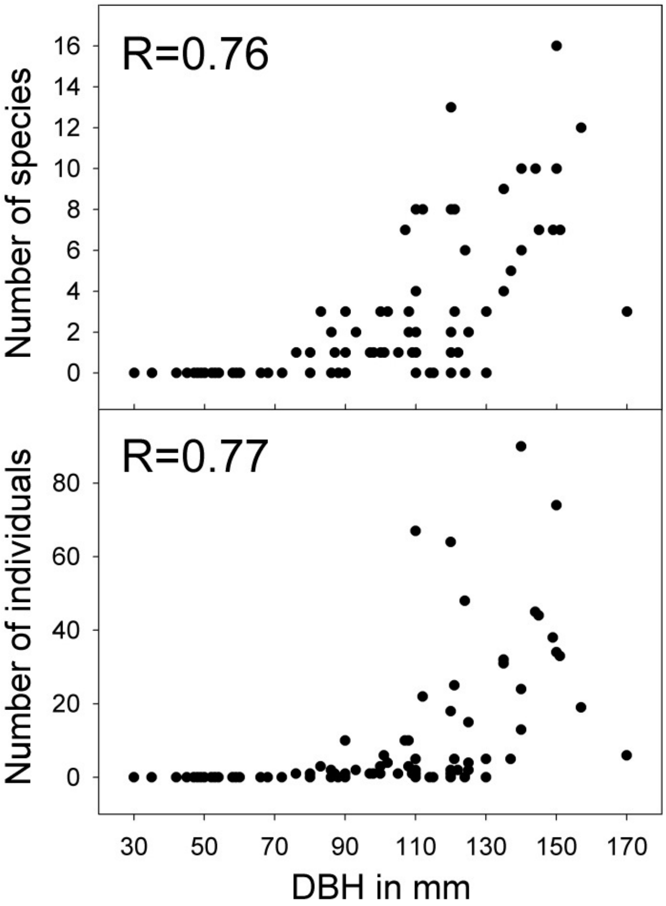

FIG. 3-2. Relationship between DBH of *Socratea exorrhiza* palms and occupying epiphyte species and individual numbers in the 2002 census. The relationships in 1999 and 2004 were very similar (Spearman Rank correlation, R≥0.76, P<0.001, n=88).

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

Palm size was not only 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 the 2004 census (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 included palms with a DBH ≥80 mm since smaller palms, with few exceptions, never hosted epiphytes (Fig. 3-2) and found that among these palms larger trees were colonized by more epiphyte individuals per bark surface area. While smaller palms (DBH = 80-100 mm) were colonized by less than one individual per m² in three years, this figure approximately doubled in the largest palms (140-160 mm). The maximum colonization of 24.1 individuals per m² in three years occurred on a palm (DBH = 110 mm) that was heavily colonized by juveniles of the fern species *Elaphoglossum sporadolepis*.

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 ± 1.8 individuals in three years, mean ± SD) than controls, i.e. trees lacking this species (0.1 ± 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 holoepiphytes and hemiepiphytes showed a similar trend, although differences were not significant: on average, already colonized palms were colonized by 0.3 ± 0.6 individuals in three years, and empty palms by only 0.04 ± 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 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. 3-3a) most colonization events occurred in the upper sections of palm trunks with up to 3.2 ± 8.0 newly established individuals (mean ± SD; Fig. 3-3c) between 7 – 8 m height. Only palms with at least 110 mm DBH exceed on average a height of 7 m (Zotz and 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. 3-3b and c).

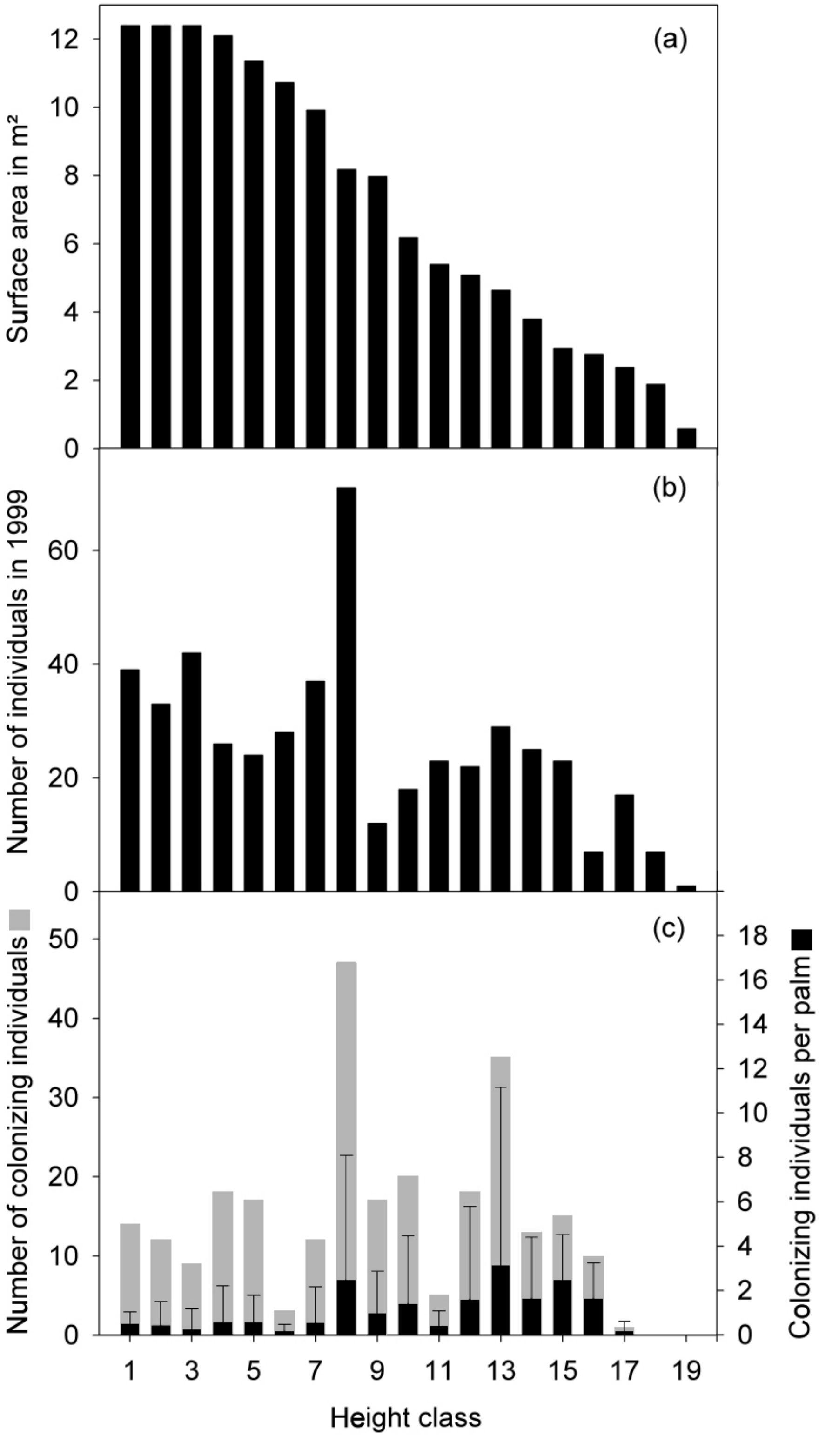

FIG. 3-3. Vertical distribution of (a) substrate surface area, (b) epiphyte individuals found in 1999 and (c) epiphyte colonization events (grey bars) on all *Socratea exorrhiza* palms considered and mean number of colonization events per palm (black bars, error bars = SD). We considered only "successful"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

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 average Chao-Sørensen abundance based similarity index for a palm individual that hosted at least one epiphyte individual was 0.70 ± 0.04 between 1999 and 2002, but 0.66 ± 0.05 between 1999 and 2004 (means ± 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 (Appendix 1).

Discussion

Only 46 % of all well-established individuals originally found in 1999 on 99 *Socratea exorrhiza* palms were still alive in 2004 (Fig. 3-1), and the assemblages on individual palms showed decreased similarity through time. Analyzed over all palm trees, however, the similarity increased and the species ranking changed very little (Appendix 1). This suggests that a rather 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 and 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 does certainly not apply to the individual palm tree as the similarity decreases with time at this scale. The frequent colonization of formerly unoccupied palms and complete eradication of all epiphytes on a given palm (Table 3-1) 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. 3-2). Finally, the time available for colonization of *Socratea exorrhiza* may be rather short in comparison to the average generation time of most epiphyte species. Zotz and Vollrath (2003) reported that epiphytes rarely get established on *Socratea exorrhiza* trees with a DBH <80 mm, i.e. on palms younger than 20 years, and our five-year observations confirm this. The larger palms that died during this study had a DBH of 110 to 157 mm. This corresponds to an average age of c. 80 years at death, leaving fewer than 60 years available for colonization. Epiphyte taxa preferring higher strata of the forest will not start colonizing *Socratea exorrhiza* until much later (Zotz and Vollrath, 2003). Since it takes on the order of a decade between germination and first reproduction in most epiphytes studied until today (Benzing, 1981b; Hietz et al., 2002; Schmidt and Zotz, 2002), this further narrows the time a palm is available for an epiphyte to complete its life cycle. The low density of epiphytes even on large palms (Table 3-1) as a result of (1) low rates of successful colonization, as shown, (2) low growth rates (Schmidt and Zotz, 2002) and (3) high mortality rates, even in the case of well-established individuals (Fig. 3-1) suggest that the lifespan of *Socratea exorrhiza* does not allow vascular epiphytes to colonize it completely. This time frame may be rather 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 and Ogden, 2005). Due to the palms monopodial architecture a falling branch or palm leaf that hits a palm and slides downwards the trunk could wipe out many epiphyte individuals.

Similar to most studies on epiphyte-host tree relationships (Yeaton and Gladstone, 1982; Hietz and 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 and ages. Factors that could facilitate colonization are, e.g. a tree age-related increase in bryophyte cover (Zotz and 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 a more parsimonious or an additional explanation, and relates to the observed increase in large epiphyte individuals on larger/older palms (Zotz and Vollrath, 2003). Although we did not directly study reproduction, we expect a higher number of sexually reproducing plants on larger palms, which produce offspring. This sexually derived progeny finds a suitable habitat in the immediate vicinity, i.e. on the same palm trunk. Yeaton and 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 an already 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 *Socratea exorrhiza* were highly dynamic while the overall composition of the epiphyte vegetation on *Socratea exorrhiza* in the study plot was rather 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.

Chapter 4

Neither host specific nor random: vascular epiphytes on three tree species in a Panamanian rainforest

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 (Croat, 1978), their contribution may exceed 50 % in some montane forests with more than 120 species in 1.5 ha (Kelly et al., 2004). Individual trees may have more than 80 species growing on them (Ingram and Nadkarni, 1993; 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, 1981a), vertical niche diversification (Johansson, 1974; Gentry and Dodson, 1987a), 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 and Olmsted, 1992; Migenis and Ackerman, 1993). Here, we present a novel approach that constitutes a critical test of the notion of phorophyte-specific epiphyte spectra: we examined 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. To do this, we took advantage of a complete inventory of the vascular epiphytes in 0.4 ha of a tropical lowland forest in Panama (Zotz, 2004b). 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* (Mart.) H. Wendl., *Marila laxiflora* Rusby and *Perebea xanthochyma* H. Karst. were sufficiently common and frequently used by epiphytes to warrant their inclusion in this study allowing for appropriate statistical power.

Material and Methods

Study site and species

The data for this study were collected at the San Lorenzo Canopy Crane Site. For further details on this facility see Chapter 2. 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 (DBH) of >1 cm was registered with species name, plant size, and location on the tree (Zotz, 2004b; 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 (Chapter 3, Zotz unpubl. res.), epiphytes were occasionally found on trees with even the smallest DBH. 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* (Arecaceae). This stilt-root palm, which occurs from Nicaragua to northern South America, reaches up to 28 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* (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* (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 13099 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 (R Development Core Team, 2005) as follows. To create, e.g., the null model for *Socratea exorrhiza*, we randomly selected 354 individuals 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, we created null models for the epiphyte assemblages on *Marila laxiflora* and *Perebea xanthochyma*. Similarly, we created null models for the epiphyte distributions on the tree species as a random sample based on the number of host trees a given epiphyte species occupied in the study plot. For a given epiphyte species that was growing on a tree species we randomly selected the number of trees that were occupied by epiphytes 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* we randomly selected 31 trees, i.e. the number of *Socratea exorrhiza* trees in the plot, from this complete tree list with replacement. We repeated this process 1000 times and obtained 95 % confidence intervals as described above. Accordingly, we created tree-based null models for the epiphyte species on the 40 *Marila laxiflora* and 38 *Perebea xanthochyma* trees growing in the study plot.

We also used a completely different method to analyze 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 our 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 relations between species and environmental variables. Including tree species identity as dummy variables, differences in the epiphyte assemblages among species were analyzed 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 optimised 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 4-1). Three epiphyte species (*Dicranoglossum panamense*, *Trichomanes angustifrons, Tillandsia anceps*) were more frequent than expected by chance in all three tree species, while five epiphyte species (*Pleurothallis brighamii*, *Trichosalpinx orbicularis*, *Trichomanes nummularium, Maxillaria uncata, 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. 4-1a). 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 occupied the palm in the study plot whereas a maximum of only 5 individuals was expected by chance (Appendix 2). 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.

TABLE 4-1. 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 more frequent on a given host tree species than expected by random distribution are indicated with “+”. Species less frequent are indicated with “-”, and 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 Appendix 2 to 4.

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	+

Marila laxiflora

On *Marila laxiflora* about two thirds of the epiphyte species (68.9 %) showed an abundance indistinguishable from random (Fig. 4-1a). 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 3), *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).

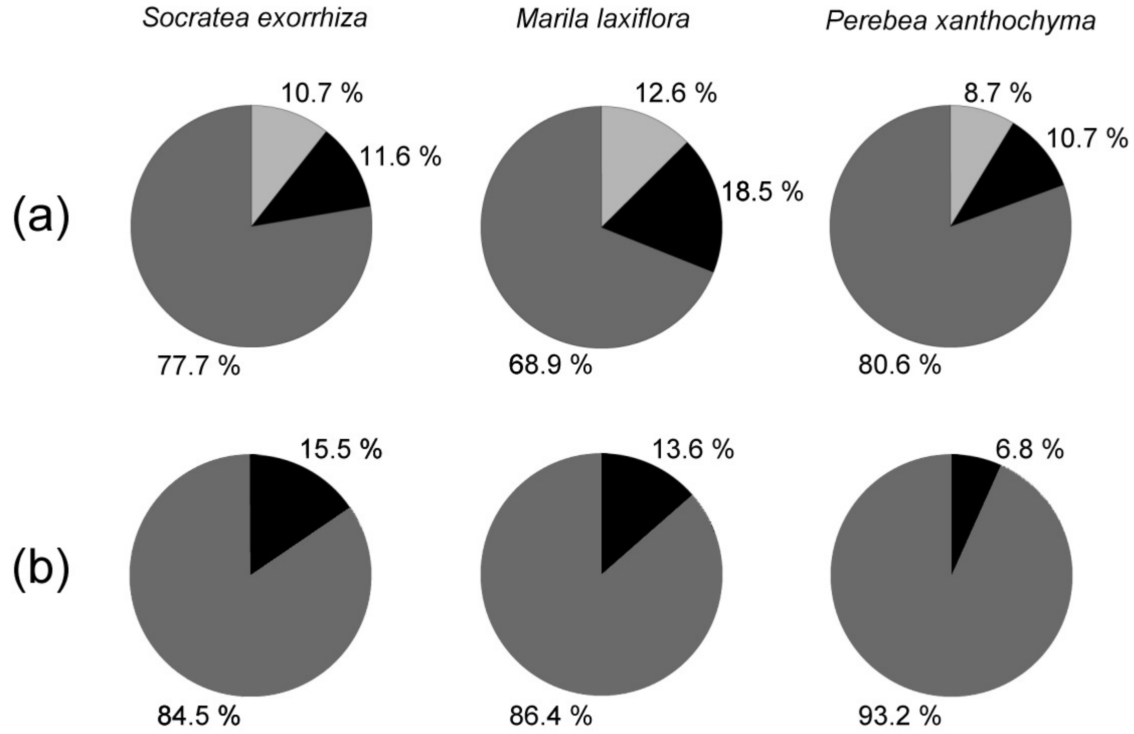

FIG. 4-1. Distribution of epiphyte species in the San Lorenzo forest plot according to (a) individual-based comparisons of the occurrence on host trees of a given species with that of a null model. Light grey: species found with fewer individuals on a host tree species than expected by chance, black: species found with more individuals than expected by chance, dark 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.

Perebea xanthochyma

The epiphyte assemblage of *Perebea xanthochyma* showed the smallest deviation from random among the three focal tree species: 80.6 % of all species showed an abundance indistinguishable from random (Fig. 4-1a). 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 4) 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, we created a second series of null models that account for the patchiness of epiphyte spatial distributions: we determined the number of trees for a given tree species, that an epiphyte species should occupy, based on the number of trees this species actually occupied 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 4-2). 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. 4-1b).

TABLE 4-2. Numbers of trees a given epiphyte species occupied in 0.4 ha of the San Lorenzo Crane Plot (plain 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*. 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.

Species	*Socratea exorrhiza*	*Marila laxiflora*	*Perebea xanthochyma*
Ananthacorus angustifolius	**11** (0;4)	5 (0;5)	**7** (0;5)
Anthurium hacumense	1 (0;3)	**7** (0;3)	0 (0;3)
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)
Asplenium serratum	**5** (0;3)	4 (0;4)	0 (0;4)
Campyloneurum occultum	0 (0;2)	3 (0;3)	1 (0;3)
Campyloneurum phyllitidis	**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)

Ordination

The ordination approach yielded similarly significant differences of epiphyte assemblages between tree species in the analyses of both the abundance data (Fig.4-2) 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* (c. 80 %, Fig. 4-1a), the marginal effects of this species were not significant (Monte-Carlo permutation, P>0.2), in contrast to the significant effects of the two other species (P<0.05).

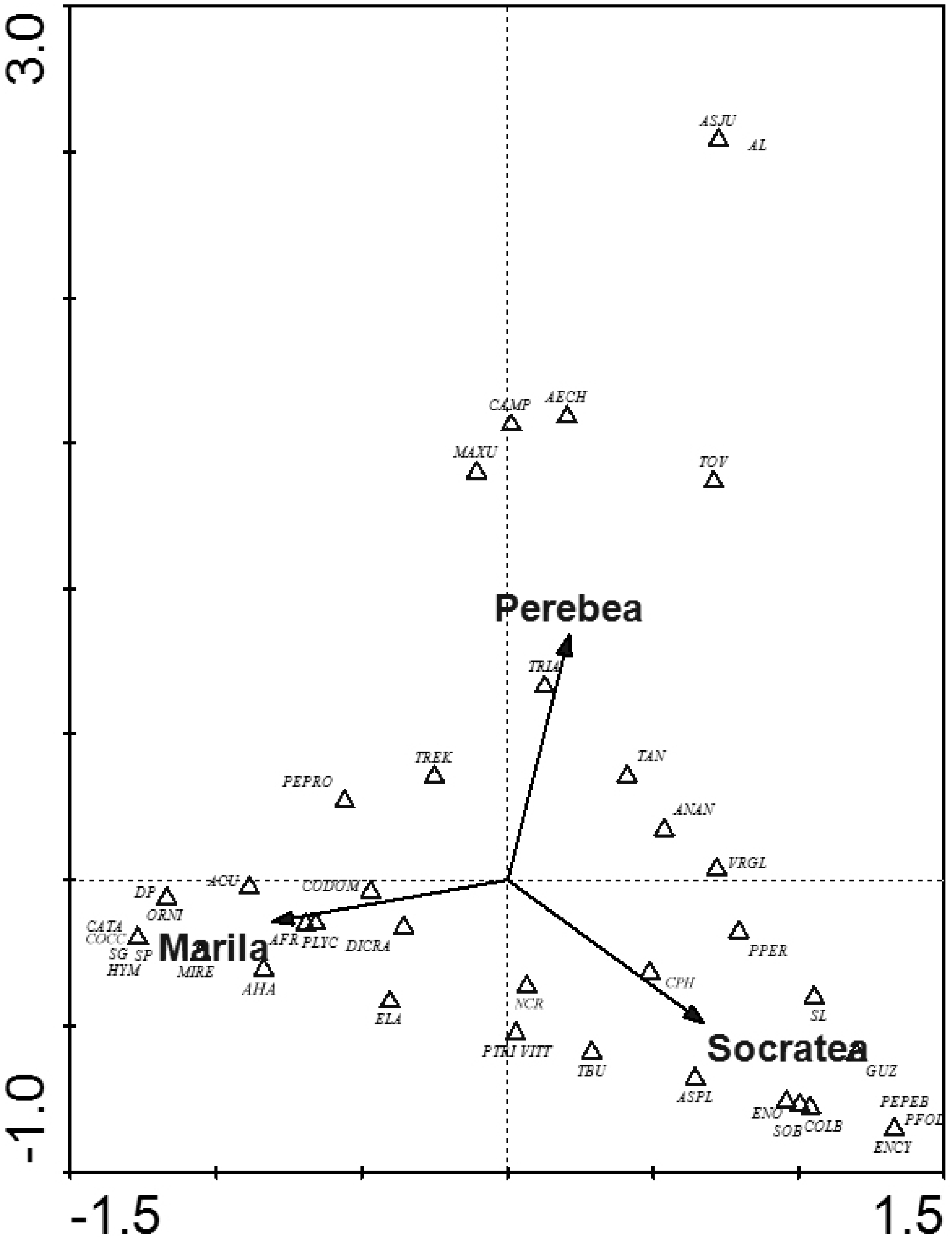

FIG. 4-2. Biplot of a canonical correspondence analysis for epiphytes on the three host tree species *Socratea exorrhiza*, *Marila laxiflora,* and *Perebea xanthochyma*. The plot is based on epiphyte abundance data, binary (presence/absence) data yield very similar results (not shown).

Species abbreviations refer to: *Anthurium acutangulum* (ACU), *Anthurium hacumense* (AHA), *Aechmea tillandsioides* (AECH), *Ananthacorus angustifolius* (ANAN), *Anthurium fragrantissimum* (AFR), *Asplenium serratum* (ASPL), *Campylocentrum micranthum* (CAMP), *Campyloneurum occultum* (COCC), *Campyloneurum phyllitidis* (CPH), *Catasetum viridiflavum* (CATA), *Codonanthe macradenia* (CODOM), *Columnea billbergiana* (COLB), *Dichaea panamensis* (DP), *Dicranoglossum panamense* (DICRA), *Elaphoglossum sporadolepis* (ELA), *Encyclia fragrans* (ENCY), *Epidendrum nocturnum* (ENO), *Guzmania subcorymbosa* (GUZ), *Hymenophyllum brevifrons* (HYM), *Maxillaria uncata* (MAXU), *Microgramma reptans* (MIRE), *Niphidium crassifolium* (NCR), *Ornithocephalus bicornis* (ORNI), *Peperomia ebingeri* (PEPEB), *Peperomia rotundifolia* (PEPRO), *Polypodium lycopodioides* (PLYC), *Polypodium percussum* (PPER), *Polypodium triseriale* (PTRI), *Polystachia foliosa* (PFOL), *Scaphyglottis graminifolia* (SG), *Scaphyglottis longicaulis* (SL), *Scaphyglottis prolifera* (SP), *Sobralia fragrans* (SOB), *Tillandsia anceps* (TAN), *Tillandsia bulbosa* (TBU),*Trichomanes angustifrons* (TRIA), *Trichomanes ekmannii* (TREK), *Trichomanes ovale* (TOV), *Vittaria lineata* (VITT), *Vriesea gladioliflora* (VRGL).

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 (c. 69 – 81 %: individual-based; c. 85 – 93 %: tree-based) showed no bias in respect to the focal tree species (Fig. 4-1), 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 underrepresented in abundance. This conclusion would change if we confined our analysis to the more common species. If considering, e.g., only the ten most common epiphyte species, the proportion of taxa deviating from a random sample would be much higher (cf. Appendices 2 to 4). However, as we were interested in the entire community and see no basis to distinguish unambiguously "common" and "rare" species, we included all species in the analysis.

The low proportion of taxa that were underrepresented in abundance came as a surprise at least in the case of *Socratea exorrhiza*. We had expected mostly a bias *against* a large proportion of species 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 occupied trees were filmy ferns of the genera *Trichomanes*, with the species *T. ekmannii* found on *Perebea xanthochyma* accounting for more than a quarter of the entire plot population (Appendix 4; Zotz, 2004b). 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 occupied 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 we can only speculate on the reasons why a given tree species may be preferred by particular epiphyte taxa. 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). Different from 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 2). 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 miss may be more related to patchy species distributions than to real positive or negative substrate preferences. This is indicated, e.g., by the regular occurrence of many (missing) orchids such as *Scaphyglottis graminifolia* or *Dichaea panamensis* on *Socratea exorrhiza* trees (compare Appendix 2) 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, 2004b), although very abundant in individual numbers, are only found on very few trees in the plot (3.9 % of trees; 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 present study. We do not expect our conclusions to be affected substantially by such possible artefacts, however, because (1) there are a large number of positive and negative associations, (2) the observed abundances of many species are very far from random expectations, and (3) three different approaches yielded qualitatively consistent results (Figs. 4-1, 4-2). Nevertheless, it is essential that future studies use descriptive data as 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 we found no evidence for strict host specificity in any epiphyte. We did find, however, a significant positive or negative bias of individual epiphyte species 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.

Chapter 5

A metapopulation approach to the analysis of long-term changes in the epiphyte vegetation on *Annona glabra*

Introduction

The spatial distribution of species has always been a question of evolutionary and ecological research (Grinnell, 1922; Wright, 1931; Krebs, 1978 and references therein). In ecology, the theory of island biogeography (MacArthur and Wilson, 1967) has made a major contribution to this field and has stimulated the development of the concept of the metapopulation (Levins, 1969; 1970). This is defined as an assemblage of populations where migration from one local population to other local populations is possible, resulting in a balance between extinction and colonization of these local populations. During the last decades, the metapopulation concept has become a widely recognized theory that is used to explain different ecological and evolutionary phenomena at large spatial scales, e.g. the geographical distribution of species, large-scale population dynamics, and maintenance of genetic variation. Moreover, the metapopulation concept has become an important tool to explain species persistence in fragmented landscapes with great implications for conservation biology (Nee and May, 1992; Tilman et al., 1994; Zartman and Shaw, 2006). The initial form of the metapopulation concept was derived from the study of animal populations and as of today the concept has been improved upon by numerous zoological studies (Hanski and Gilpin, 1997), while relatively few data are available for plants (for review see Eriksson, 1996; Husband and Barrett, 1996; Freckleton and Watkinson, 2002; Ouborg and Eriksson, 2004). This scarcity is thought to be due to methodological difficulties imposed by their biology. Freckleton and Watkinson (2002) argued that important parameters of metapopulation theory like colonization, re-colonization and extinction are difficult to measure for many plant populations, in particular for populations with long-lived seed banks. Moreover, one of the concept's assumptions, i.e. that suitable habitat occurs as discrete patches within a matrix of unsuitable habitat, causes methodological difficulties since suitable patches for plants may be hard to define *a priori*.

Among plants, epiphytes seem to be ideal candidates to apply the concept of metapopulation to plants. Due to their biology they inherently lack the above mentioned shortcomings of plant assemblages. First, bark dwelling epiphytes virtually do not have seed banks and, hence, (re)colonization of patches can be unambiguously accounted for by immigration processes. Similarly, the extinction of a local epiphyte population can be clearly noted when the last individual disappears. Finally, epiphytes occur on well-defined substrates, i.e. the trunk and the branches of trees, in an inhospitable matrix were they are unable to survive. Thus, the concept of unoccupied, yet suitable sites can be readily applied.

Recent work has focused on temperate non-vascular epiphyte communities (Snäll et al., 2003; Snäll et al., 2005a; 2005b; Löbel et al., 2006) and single species populations of vascular epiphytes (Tremblay et al., 2006). Here, we present a long-term data set on the dynamics of a vascular epiphyte assemblage and whether diversity and dynamics in these vascular epiphyte populations growing on the host tree species, *Annona glabra*, can be explained by metapopulation processes. Further, we report the changes in species composition and abundance of the vascular epiphytes over a period of eight years. The current report builds on an earlier census of the epiphyte vegetation of the host tree *Annona glabra* in 1994 (Zotz et al., 1999). Eight years later in 2002 this census was repeated to document long-term changes.

Material and Methods

Study area and epiphyte census

This study was conducted on Barro Colorado Island (BCI, 9°10'N, 79°51'W), Republic of Panama. For a detailed description of the area and the epiphyte census see Chapter 2. In concordance with the initial census, small individuals, i.e. plants <20 % of the maximum size of a given species, were not counted but recorded as present when found on a tree. Individuals that were recorded as recruits in the second census but not the first were either juveniles already present in the first census and smaller than 20 % maximum plant size, or newly established individuals that had reached 20 % maximum plant size during the census interval. If not stated otherwise we excluded juveniles found in both census events from analysis. In total 28 km of shore line were surveyed in detail corresponding to 46 % of the entire shore line. Similar to the original census, the remaining 34 km of shore line (the 60 "intersectors") were later surveyed for those additional epiphyte species on *Annona glabra* that were not found in the 60 sectors.

If not stated otherwise, results on changes in species and individual numbers and overall population growth rates are based on the findings in the sectors. Moreover, a clear distinction of the multiple stemmed tree individuals, especially when growing in dense stands, was often difficult. However, we found 1012 of the original 1210 trees. Of those, 724 could be unambiguously paired with trees of the original census or had died. This subset of *Annona glabra* trees thus allowed us to directly compare changes in epiphyte vegetation at the level of individual trees. Results on epiphyte colonization and extinction are based on the data of this subset.

Epiphytes are unevenly distributed in space, with local populations occupying an individual *Annona glabra* tree that we define as a patch, i.e. a continuous area of space with all necessary resources for the persistence of a local population and separated by unsuitable habitat from other patches (Hanski and Gilpin, 1997). Defining an individual tree *a priori* as a patch certainly has shortcomings since trees are often not sufficiently well spaced from each other, i.e. the local dispersal range of an epiphyte can involve several neighbouring trees and therefore a local population may be scattered over several trees. Trees growing in close proximity to each other, i.e. within local dispersal of epiphytes, may rather be considered as one patch while trees that grow farther apart clearly constitute two separate patches. However, the assumption of our study that each individual tree represents a patch may serve as a useful approximation until local dispersal (and pollinator) ranges of vascular epiphyte species have been thoroughly studied. The density of *Annona glabra* trees is varies substantially ranging from 1 - 96 trees per 100 m shore line (Zotz et al., 1999). Trees in close proximity with a maximum distance of 25 m between two neighbouring trees were defined as one stand of trees. Single, solitarily growing trees were also defined as a stand. Stand area was measured as the area bounded by the outer trees of a stand using the software Universal Desktop Ruler (Version 2.8.1110, AVPSoft.com) and detailed maps of the BCI shore line in which *Annona glabra* tree locations were drawn per hand. For stands consisting of a single tree the tree crown's projected area (measured as $A = 0.25 \text{ Pi} \times Cw^2$) was taken as stand area.

The studied epiphyte species occur on forest trees on BCI as well. The median distance to the adjacent forest vegetation was 5 m (range 0-50 m; Zotz et al., 1999) but the spatial distribution and the population sizes of patches in the forest are unknown, thus, the rate of long-distance migration of epiphyte seeds between forest trees and *Annona glabra* patches remains obscure. Data on long-distance migration of epiphyte seeds are scarce. Murren and Ellison (1998) found that effective long-distance seed dispersal in an orchid may be quite rare in most cases when released from heights similar to *Annona glabra* trees, as general dispersal distances amounted to few meters. Similarly, Bernal et al. (2005) reported that less than 0.6 % of released bromeliad seeds reached the crowns of neighbouring trees in a distance of 10 m. However, we suggest that large-scale movement of seeds between patches occurs due to the movement of seeds by animals or trade winds at the end of the dry season, when most wind dispersed epiphyte species release their seeds. Recruitment of epiphytes on *Annona glabra* is either sexual or vegetative from already established epiphyte species or through immigration of seeds. Seeds directly establish on the bark of trees in most cases (pers. observation) and may germinate on rarely occurring bryophyte mats. Due to the lack of humus accumulations in *Annona glabra* there is no seed bank.

Data analysis

The Chao-Sørensen estimated abundance based similarity index was used for comparing changes in the epiphyte vegetation of trees using the software EstimateS Version Win 7.5.0 (Colwell, 2005). This index differs from the classical Sørensen index in having a probability-based approach that reduces undersampling bias by estimating and compensating for the effects of unseen, shared species (Chao et al., 2005). Like the classical Sørensen index it varies between 0 and 1 with 0 for species assemblages that are completely different and 1 that are identical.

We investigated the species-area relationship by fitting linear regression models (Statistica 6.0, Statsoft Inc., Tulsa, USA) predicting species richness as a function of *Annona glabra* stand area and number of host trees in a stand. Preliminary analysis suggested an exponential relationship between species number (S) and area (A), therefore, we used the power function model in its log-transformed form ($\ln S = c + z \ln A$).

The relationship between patch occupancy and local population size of species was tested by fitting linear regression models predicting patch occupancy as a function of mean local population size of the species. Both variables were log-transformed with the natural logarithm.

We used Tokeshi's test for bimodality to determine whether species frequency distributions were significantly uni- or bimodal (Tokeshi, 1992; Barreto et al., 2003). The probability (P) of occurrence of a given absolute frequency f or higher is given by the upper-probability of a binomial distribution:

$$P(F > f) = \sum_{i=f}^{N} \frac{N!}{i!(N-1)!} h^{i} (1-h)^{N-i},$$

where F is a random variable that describes the event of a species occurring in a given size bin with the probability $h=1/n_c$ where n_c is the number of size bins, and N is the total number of sampled species. Bimodality is judged based on the probability of obtaining the observed number of species in the rarest species group, $P_{0\text{-}10\%}$, and commonest species group, $P_{90\text{-}100\%}$, under the null hypothesis of a random distribution. If $P_{0\text{-}10\%} < 0.25$ and $P_{90\text{-}100\%} < 0.25$ the frequency distribution is bimodal. $P_{0\text{-}10\%} < 0.05$ and $P_{90\text{-}100\%} < 0.05$ indicates a strong bimodal pattern. If $P_{0\text{-}10\%} < 0.05$ and $P_{90\text{-}100\%} \geq 0.5$, or vice versa, the frequency distribution is unimodal (Tokeshi, 1992). To compare the epiphyte species frequency distribution in all *Annona glabra* stands with those stands that were already abundantly occupied with epiphytes we had to define "abundantly occupied". The latter group included all stands in which (1) >90 % of all trees were occupied by epiphytes and (2), trees with epiphytes hosted at least an average of 44 individuals, which corresponds to the upper quartile boundary of the number of epiphyte individuals in all separated stands. A total of four *Annona glabra* stands fulfilled these requirements. These stands were located in sectors 4, 24, 25 and 44.

To compare the rates of temporal change among tropical tree communities Condit et al. (1992) suggested using the coefficient of determination, R^2, from the regression analysis of species abundance change through time as a quantitative measure of the degree to which the vegetation composition has changed: the lower the R^2, the greater the change in the community or assemblage.

We created a null model of species colonization assuming neutrality of colonization in epiphyte species, i.e. the probability of colonizing a tree is the same for all species, to determine the effect of abundance on colonization. We did not include distance in our model, since not only *Annona glabra* trees scattered along the shore line but also trees of the BCI forest with unknown position serve as potential dispersal sources. Considering neutrality, in our model an abundant species should colonize proportionally more trees with proportionally more individuals than a less abundant species. We later compared null model predictions with the actual colonization rates for each species to determine its colonizing ability. The null model was created by randomly choosing 721 individuals, i.e. the number of individuals that colonized empty *Annona glabra* trees during the census interval, from a complete list of epiphyte individuals occurring on occupied host trees in the 1994 census. Individuals were drawn from the list without replacement. We repeated this process 120 times calculated the sum of individuals for each species drawn from the list for each repetition and obtained 95 % confidence intervals for each species by discarding the 3 highest and the 3 lowest values. For each species, ranges expected by random chance were then compared with the actual number of individuals that colonized empty trees by 2002. Similarly, we created a second null model for the epiphyte colonization of *Annona glabra* as a random sample based on the number of trees that were colonized by a given epiphyte species. A total of 103 empty *Annona glabra* trees were colonized by epiphyte species during the census interval. Again, assuming neutrality the probability for colonizing a tree by a given epiphyte species is the same as in all other species. For this second model we randomly chose 721 individuals from the list and put them in 103 groups (=trees). The number of individuals per group was defined by the actual colonization pattern. Using presence/absence we determined the number of colonized tree per species. This process was again repeated 120 times and 95 % confidence intervals obtained as described above.

Results

Epiphyte vegetation

Despite its small size and its restriction to the shore line, *Annona glabra* hosts 80 of the c. 160 species of the BCI vascular epiphyte flora (Zotz et al. 1999). In 2002, eight additional species were found on this host species. Overall epiphyte species richness, however, including both sectors and intersectors, decreased from 80 to 68 species due to the disappearance of a number of rare species mostly in the intersectors (Appendix 5).

In the census sectors, the total number of species found in 2002 was slightly higher (63 species) than in the initial 1994 census (59 species). Here, the number of holo-epiphytes and secondary hemi-epiphytes contributed to the increase in species number (49 species in 1994 vs. 56 species in 2002) while the number of woody hemi-epiphyte species decreased from ten to seven. The number of epiphyte individuals on *Annona glabra* trees increased substantially by 63 % from c. 15,000 to c. 23,700 individuals. This increase represents a yearly average change of +6 %. The increase of individuals was largely found in the three most common species which accounted for about 80 % of it. The seven most common species accounted for even 94 % of the increase in abundance (Appendix 5).

Species composition

When comparing the composition of the epiphyte vegetation of individual trees with each other in a given census we found a significant increase in the mean Chao-Sørensen index from 0.34 ± 0.34 in 1994 to 0.40 ± 0.34 in 2002 (means ± SD, unpaired t-test, $P<0.001$). After eight years, the ten most abundant species remained the same, and there was only a single change among the 20 most abundant taxa (*Epidendrum difforme*, Orchidaceae, dropped to rank 54 and *Ananthacorus angustifolius*, Vittariaceae, rose to rank 19; Appendix 5).

Population change

Annona glabra trees growing in the sectors in 1994 and 2002 had 47 epiphyte species in common which were used for calculating population growth. Seventy percent of the species had a positive population growth rate (λ) while 25.5 % were declining and 4.5 % had a constant population size. The majority of epiphyte populations changed strongly over the eight years: 29 species changed by more than 5 % annually (Fig. 5-1). Very high or negative λ could frequently be related to low individual numbers in the initial census. For example, when

17 out of 18 individuals of *Epidendrum difforme* (Orchidaceae) died, an average decline of -36.1 % per year was the consequence. On the other hand, population growth rate could be very high when few individuals occupied patches, e.g. *Epidendrum schlechterianum* (Orchidaceae) experienced a population growth of 18.3 % per year when individual numbers increased from 3 to 13 during the census interval. However, species with 20 or more individuals in one census also showed considerable variation in gross population change which ranged from -9.5 % decrease for *Catopsis sessiliflora* (Bromeliaceae) to 13.4 % increase for *Codonanthe crassifolia* (Gesneriaceae, Appendix 5). From the regression of the data in Fig. 5-1, an R^2 of 0.98 for the epiphyte vegetation on *Annona glabra* trees was calculated.

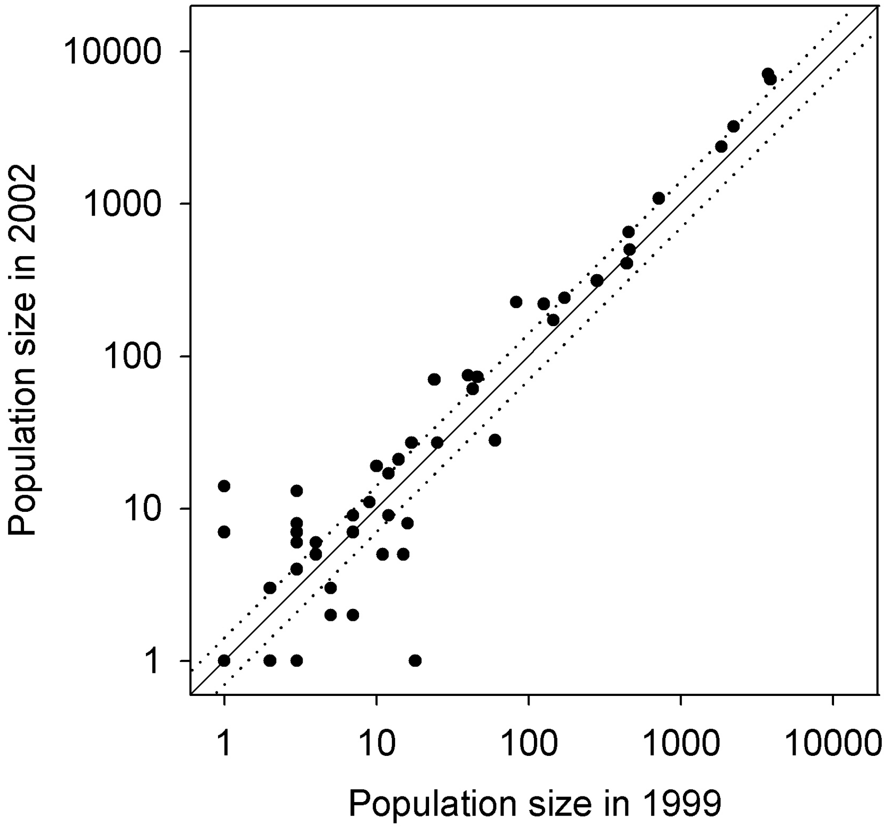

FIG. 5-1. Changes in the total abundance of epiphyte species on *Annona glabra*. The solid line represents the line of equality of 1994 and 2002 abundances. Data points below this line represent declining species and points above represent increasing species. Distance from the line indicates percent population change regardless of density. The two dashed lines show where a population that increased or decreased by 5 % per year would fall on the graph. An annual 5 % change is substantial: after eight years it yields a 47 % increase or a 33 % decline. Any point falling outside the dashed lines indicates a rapidly changing population.

Species-area relationship, distribution-abundance relationship, regional patch frequency distribution

The area of an *Annona glabra* stand explained about a third of the variation in species richness among stands (Fig. 5-2a, R^2=0.36). However, the explanatory power when relating species richness to host tree number was higher (Fig. 5-2b, R^2=0.52).

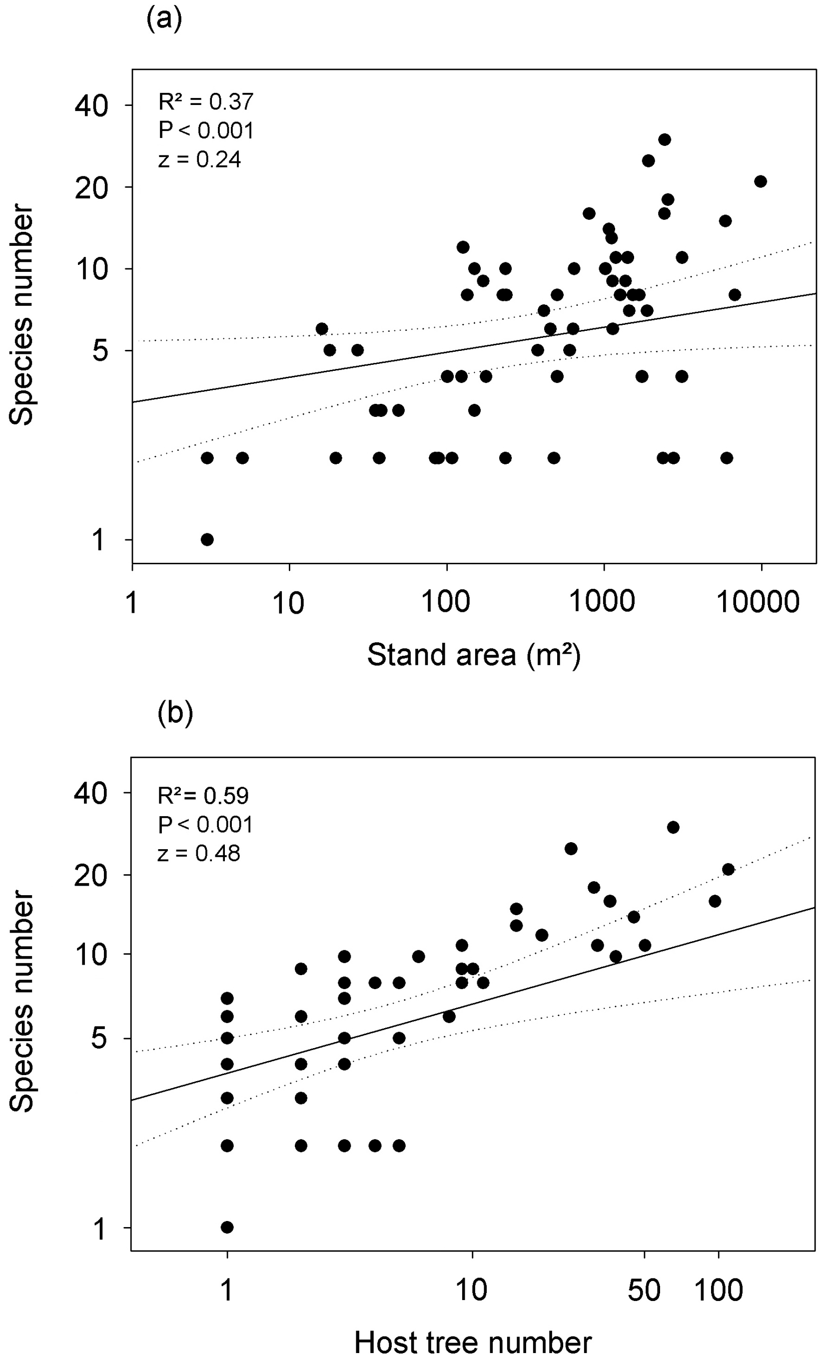

FIG. 5-2. Relationship between (a) epiphyte species richness and *Annona glabra* stand area and (b) epiphyte species richness and host tree number in *Annona glabra* stands (lnS = c + z lnA in each case). Dotted lines represent 95 % confidence intervals of the linear regression line.

We observed a strong positive relationship between a species' regional occurrence in patches and its patch population size (Fig. 5-3, linear regression, log-transformed). Separate analyses of wind and animal dispersed epiphyte species did not reveal regression lines of significant difference.

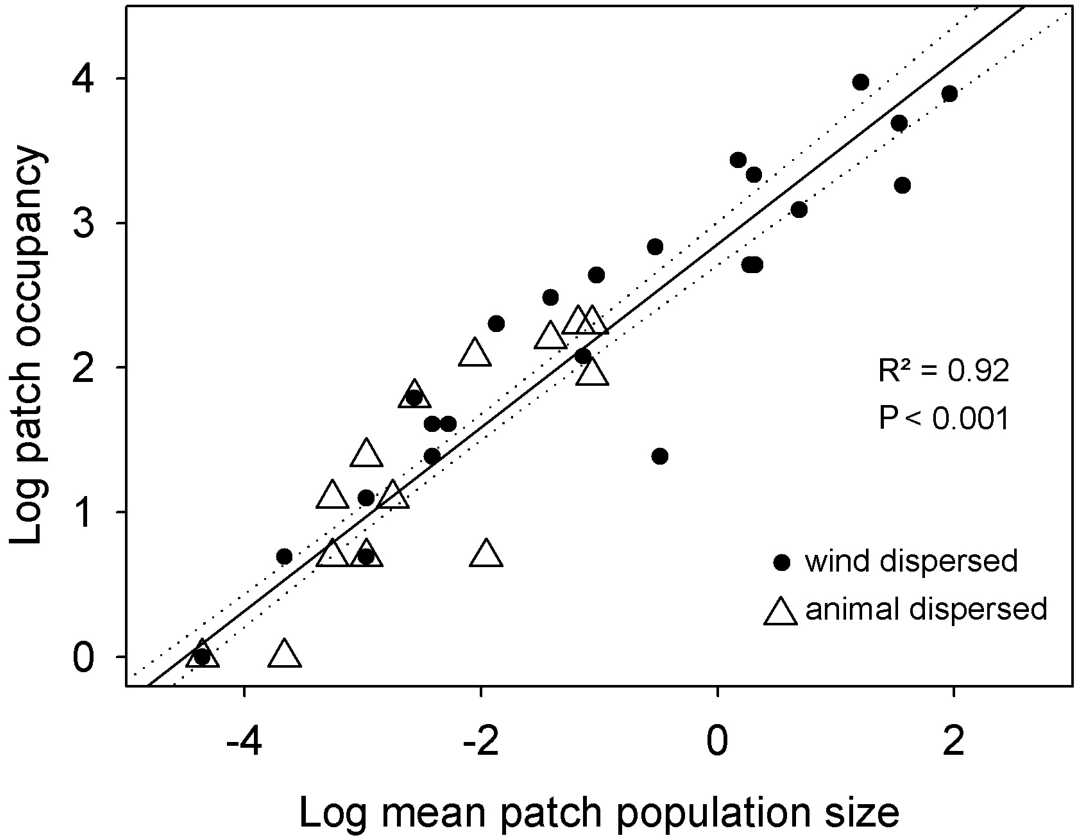

FIG. 5-3. Relationship between the regional occurrence and the local abundance of species. The natural logarithm of mean local patch population size is plotted against the natural logarithm of number of occupied *Annona glabra* patches. Dotted lines represent the 95 % confidence interval of the linear regression line.

The regional patch frequency distribution of the species in 2002 was strongly unimodal, with 53 species occurring in only up to 10 % of all occupied patches (Fig. 5-4a). However, after epiphyte colonization of patches has reached an equilibrium we expect to find a bimodal frequency distribution. This pattern can be observed in *Annona glabra* stands where epiphytes are already very abundant (mean individual number per tree ≥44, >90 % of trees are occupied, Fig. 5-4b). These stands may reflect an epiphyte occurrence at a late stage of epiphyte colonization.

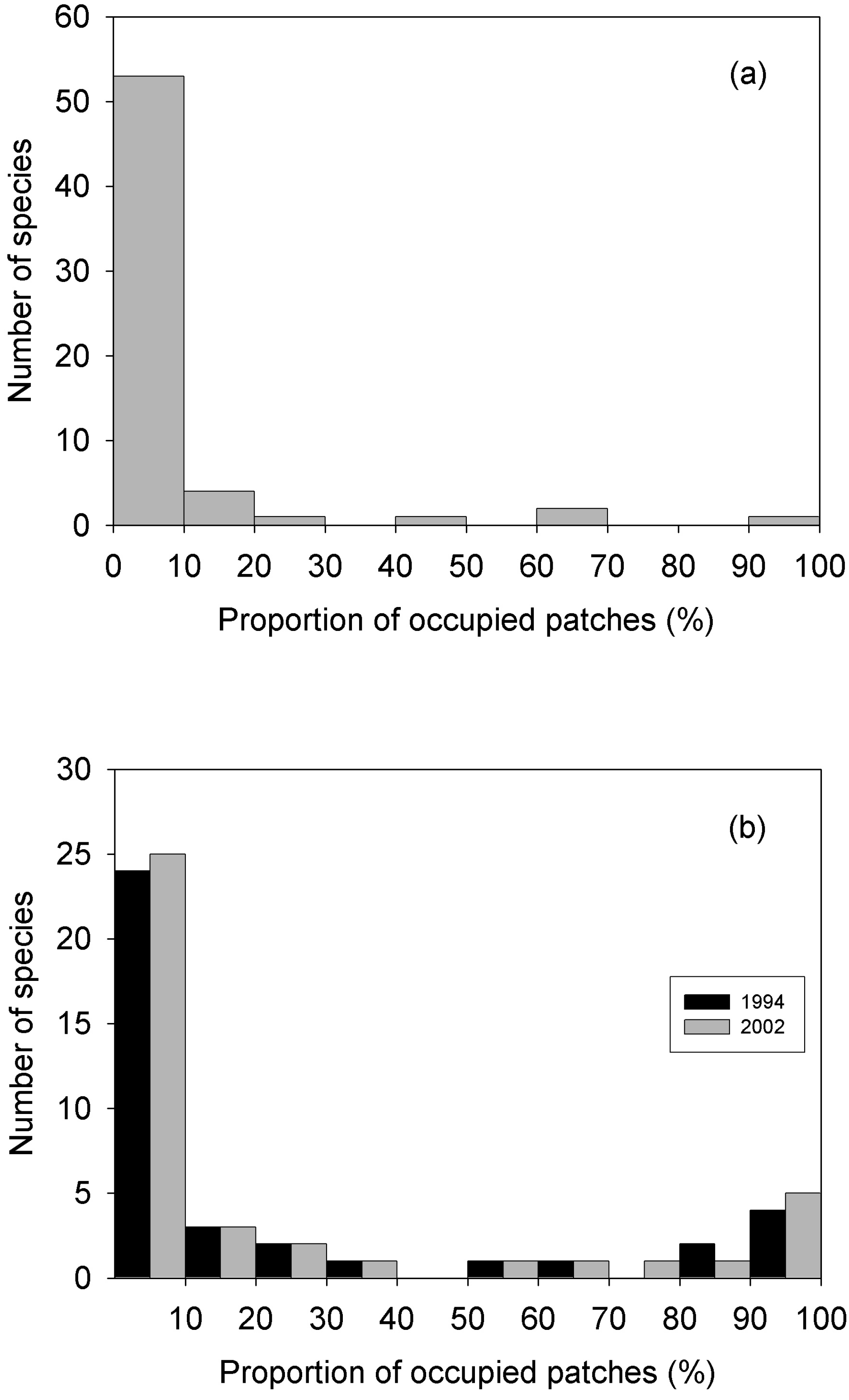

FIG. 5-4. Frequency distributions of epiphyte species' distributions in (a) all *Annona glabra* patches in 2002 where distribution is strongly unimodal ($P_{0\text{-}10\%}<0.01$; $P_{90\text{-}100\%}=0.99$), and (b) stands, in both census years, where >90 % of the trees were occupied by on average more than 44 epiphyte individuals in 2002. Here, the distribution is bimodal in the 2002 census ($P_{0\text{-}10\%}<0.01$; $P_{90\text{-}100\%}=0.21$, see Material and Methods for probability limits).

Subset of 725 Annona glabra trees

The following analyses and results are based on the subset of 725 trees as described in Material and Methods.

Patch dynamics - In the 1994 census, 400 trees (55 %) hosted epiphytes. During the census interval 25 trees (3.4 %) died, six of which had epiphytes. These trees submerged and epiphyte populations went extinct. Until 2002, the number of colonized trees increased to 476 (65.7 %). This net change was the result of a number of successful colonizations of formerly uninhabited trees and the reverse process: 103 of the 325 formerly empty trees (31.7 %) were colonized by epiphytes, whereas 25 trees (6.3 %; without fallen trees) of the initial 400 occupied trees lost all their epiphytes. In the second census, the initial set of epiphyte species remained unchanged in 77 *Annona glabra* trees (10.6%), and 219 trees (30.2%) were hosting the initial set plus newly colonized species. Epiphyte species were lost in 175 trees (24.1%), the average loss being 1.7 ± 1.1 species (mean ± SD), while 250 trees (34.5%) were colonized by additional species (1.9 ± 1.5 species). The comparison of epiphyte vegetation on a given *Annona glabra* tree in 1994 and 2002 hosting at least one epiphyte yielded a mean Chao-Sørensen index of 0.80 ± 0.27 (mean ± SD, n=369).

Colonization - In their paper Zotz et al. (1999) concluded from comparison of differently colonized trees that the four most common epiphyte species also are the first that colonize empty *Annona glabra* trees. By direct comparison of tree epiphyte vegetation in time we can now show that this conclusion was correct (Table 5-1). After eight years a total of 20 species colonized trees that were empty in the first census. The four most common epiphyte species accounted for the colonization of 88 % of all newly colonized trees. Although, as our census data show, *Annona glabra* trees can be colonized by epiphytes when reaching a height of 1 m (= crown volume of 0.25 m³) empty trees that were colonized during the census interval differed significantly in both tree height and crown volume from not colonized conspecifics ($h_{colonized}$: 5.82 ± 2.87 m,; $h_{uncolonized}$: 4.13 ± 1.79 m; $Cv_{colonized}$: 5.21 ± 3.66 m³; $Cv_{uncolonized}$: 2.5 ± 2.41 m³, unpaired t-test, $P<0.001$, $n_{colonized}=107$, $n_{uncolonized}=199$, means ± SD). In this group of newly colonized trees larger individuals, in terms of tree height, were colonized significantly more often by epiphyte species and individuals than smaller trees, although this correlation was weak (Spearman Rank correlation, $R_{species}=0.30$, $P<0.01$; $R_{individuals}=0.40$, $P<0.001$, n=107 trees). The correlation between crown volume and colonization was slightly weaker (Spearman Rank correlation, $R_{species}$=0.28, P<0.01; $R_{individuals}$=0.34, P<0.001, n=107 trees).

TABLE 5-1. Ranking of epiphyte species that colonized empty *Annona glabra* trees during the census interval. A total of 306 empty trees were available for colonization of which 103 were colonized by the listed epiphyte species by 2002.

Species	Family	Colonized trees	Individuals per tree
Caularthron bilamellatum	Orchidaceae	55 (18.2%)	5.0
Tillandsia bulbosa	Bromeliaceae	42 (13.9%)	3.8
Niphidium crassifolium	Polypodiaceae	24 (7.9%)	2.5
Dimerandra emarginata	Orchidaceae	17 (5.6%)	8.5
Catasetum viridiflavum	Orchidaceae	8 (2.6%)	1.3
Tillandsia fasciculata	Bromeliaceae	6 (2.0%)	2.0
Tillandsia subulifera	Bromeliaceae	6 (2.0%)	3.5
Polystachia foliosa	Orchidaceae	4 (1.3%)	1.8
Philodendron radiatum	Araceae	3 (1.0%)	1.0
Oncidium stipitatum	Orchidaceae	2 (0.7%)	2.0
Catopsis sessiliflora	Bromeliaceae	2 (0.7%)	1.5
Werauhia sanguinolenta	Bromeliaceae	2 (0.7%)	1.5
Campyloneurum phyllitidis	Polypodiaceae	2 (0.7%)	1.5
Codonanthe crassifolia	Gesneriaceae	2 (0.7%)	1.0
Brassavola nodosa	Orchidaceae	1 (0.3%)	1.0
Epidendrum nocturnum	Orchidaceae	1 (0.3%)	4.0
Anthurium flexile	Araceae	1 (0.3%)	1.0
Anthurium fragrantissimum	Araceae	1 (0.3%)	5.0
Vittaria lineata	Vittariaceae	1 (0.3%)	1.0
Epiphyllum phyllanthus	Cactaceae	1 (0.3%)	1.0

Epiphyte species, like other plants, differ in their ability to colonize new habitat patches. We created a null model that helped us to determine which species in the epiphyte community of *Annona glabra* are good colonizers and which perform less efficiently independent of their abundance. Therefore, we created a null-model of the number of patches colonized and the number of individuals colonizing empty patches assuming the same colonization probability in all epiphyte species as described in Material and Methods. We then compared the data ranges derived from the null-model with the observed species colonization data (Table 5-2). Species colonizing more empty patches than expected by their abundance were not only abundant species like *Caularthron bilamellatum* and *Niphidium crassifolium* but also less abundant species like *Polystachia foliosa* and *Catasetum viridiflavum*. Surprisingly, lower than expected colonization success was found in two currently abundant species, i.e. *Dimerandra emarginata* and *Werauhia sanguinolenta* (cf. Appendix 5).

TABLE 5-2. Number of formerly empty *Annona glabra* trees a given epiphyte species colonized (Trees) and number of individuals colonizing these trees (Individuals). Numbers in brackets are generated numbers of a random colonization based on the total abundance of a given species. They indicate lower and upper boundary of random generated tree numbers and numbers of colonizing individuals, respectively. Bold numbers indicate species colonizing a higher number of trees, and colonizing trees with a larger amount of individuals than expected by random colonization. Underlined numbers indicate species that colonized fewer trees, and species that colonized trees with a lower amount of individuals than expected. Species are sorted by their abundance in 1994. Only the 20 most common species are shown.

Species	Family	Trees	Individuals
Dimerandra emarginata	Orchidaceae	17 (61;78)	145 (168;211)
Caularthron bilamellatum	Orchidaceae	55 (60;74)	**274** (156;199)
Tillandsia bulbosa	Bromeliaceae	42 (46;59)	**161** (93;125)
Niphidium crassifolium	Polypodiaceae	24 (38;55)	59 (72;103)
Werauhia sanguinolenta	Bromeliaceae	2 (18;32)	3 (26;44)
Tillandsia subulifera	Bromeliaceae	6 (11;25)	21 (13;31)
Vittaria lineata	Vittariaceae	1 (11;23)	1 (12;30)
Tillandsia fasciculata	Bromeliaceae	6 (11;24)	12 (13;31)
Guzmania monostachia	Bromeliaceae	0 (6;19)	0 (7;21)
Epidendrum nocturnum	Orchidaceae	1 (4;12)	4 (4;13)
Sobralia suaveolens	Orchidaceae	0 (2;11)	0 (2;12)
Catasetum viridiflavum	Orchidaceae	8 (2;10)	10 (2;11)
Polystachia foliosa	Orchidaceae	4 (1;7)	7 (2;8)
Anthurium brownii	Araceae	0 (0;5)	0 (0;5)
Catopsis sessiliflora	Bromeliaceae	2 (0;6)	3 (0;6)
Oncidium stipitatum	Orchidaceae	2 (0;5)	4 (0;6)
Anthurium durandii	Araceae	0 (0;5)	0 (0;5)
Codonanthe crassifolia	Gesneriaceae	2 (0;3)	2 (0;3)
Campyloneurum phyllitidis	Polypodiaceae	2 (0;3)	3 (0;3)
Ananthacorus angustifolius	Vittariaceae	0 (0;3)	0 (0;3)

A replacement of early colonizing vascular epiphytes by other species was not observed. Rather than exhibiting true succession with characteristic pioneer species and replacing species (Crawley, 1997), the epiphyte species on *Annona glabra* can be divided into three groups differing in their colonizing abilities on the basis of tree colonization intensity (how many individuals colonize a tree on average) and time of colonization (when does a species colonize). First, there is the group of permanent colonizers: Species like *Caularthron bilamellatum* (Orchidaceae), *Niphidium crassifolium* (Polypodiaceae) or *Tillandsia bulbosa* (Bromeliaceae) colonize suitable trees at any given time, and their colonization rates are more or less stable with increasing species richness on a host tree (Table 5-3). The second group are the late colonizers, i.e. species that colonize a tree mainly after other species have established (e.g. *Tillandsia fasciculata*, Bromeliaceae, and *Polystachia foliosa*, Orchidaceae). Sporadic colonizing species belong to the third group. Here, species like *Brassavola nodosa*, *Scaphyglottis sessiliflora* (both Orchidaceae) or *Anthurium clavigerum* (Araceae) colonize trees infrequently and with low individual numbers.

TABLE 5-3. Colonization of differently occupied host trees by epiphyte species. Species are grouped into three categories according to their colonizing ability, i.e. the percentage of trees colonized and average number of individuals that colonized a tree, dependent on the occurrence of already established epiphyte species. Note that in the "sporadic colonizers" group only five species are listed as examples. Remaining species not listed (cf. Appendix 5) belong to the "sporadic colonizers" group.

	percentage of trees colonized by a species																	
number of epiphyte species already occupying a tree	Permanent colonizers						Late colonizers							Sporadic colonizers				
	Cb	De	Tb	Nc	Ws	Cv	Tf	Pf	Cc	Ts	En	Vl	Gm	Ac	Se	Bn	Os	Sl
0 (n=306)	18	5.6	15	7.8	0.7	2.6	2.6	1.3	0.7	2	0.3	0.3	0	0	0	0.3	0.7	0
1 (n=115)	28	25	13	12	7	4.3	1.7	2.6	0.9	2.6	3.5	3.5	0	1.7	1.7	0.9	0.9	0.9
2 (n=89)	13	22	10	11	5	9	2	2	1	1	3	3	0	0	0	0	0	0
3 (n=68)	15	10	13	13	7.4	7.4	8.8	1.5	1.5	2.9	4.4	5.9	0	1.5	0	0	0	0
4 (n=46)	6.5	20	11	22	8.7	4.3	13	4.3	6.5	11	6.5	6.5	4	0	0	0	2.2	0
5 (n=18)	11	17	5.6	5.6	5.6	0	5.6	5.6	5.6	17	0	17	17	0	0	0	5.6	0
6 (n=16)	6.3	25	6.3	25	0	6.3	13	6.3	0	19	0	38	6	0	0	0	0	0
7 (n=12)	8.3	17	8.3	0	8.3	8.3	17	25	8.3	8.3	0	17	17	0	0	8.3	0	0
8 (n=12)	17	0	17	8.3	0	8.3	0	0	8.3	17	8.3	42	0	0	0	0	0	0
	average number of individuals colonizing a tree																	
0	5	8.5	4	2.5	1.5	1.3	2	1.8	1	3.5	4	1	0	0	0	1	2	0
1	8.3	6.5	4.7	5.6	2	1.2	2	2	1	2	3.5	2.8	0	2	1	1	4	1
2	15	25	11	12	5.6	10	2.2	2.2	1.1	1.1	3.4	3.4	0	0	0	0	0	0
3	7.3	16	6.9	4.9	2.6	1.4	2.5	2	2	1.5	8.7	3	0	2	0	0	0	0
4	18	10	3.4	3.6	2	2	1	5	1.7	6.8	3.3	4	6	0	0	0	1	0
5	5	4.3	8	5	2	0	2	1	1	10	0	3	6	0	0	0	3	0
6	1	6.8	4	4.3	0	9	3	2	0	5	0	3.7	2	0	0	0	0	0
7	4	4.5	1	0	4	1	6	2	2	4	0	5	4	0	0	1	0	0
8	3	0	6	2	0	1	0	0	2	4	3	3.6	0	0	0	0	0	0

Species abbreviations refer to: *Caularthron bilamellatum* (Cb), *Dimerandra emarginata* (De), *Tillandsia bulbosa* (Tb), *Niphidium crassifolium* (Nc), *Werauhia sanguinolenta* (Ws), *Catasetum viridiflavum* (Cv), *Tillandsia fasciculata* (Tf), *Polystachia foliosa* (Pf), *Codonanthe crassifolia* (Cc), *Tillandsia subulifera* (Ts), *Epidendrum nocturnum* (En), V*ittaria lineata* (Vl), *Guzmania monostachia* (Gm), *Anthurium clavigerum* (Ac), *Syngonium erythrophyllum* (Se), *Brassavola nodosa* (Bn), *Oncidium stipitatum* (Os), *Scaphyglottis longicaulis* (Sl).

Local population growth, extinction, and colonization - We examined the local population growth rates of epiphyte species with at least 20 local populations surviving the census interval, resulting in a number of nine species. All species showed the same density dependent pattern with population growth rates declining with increasing population size (Fig. 5-5). Further, the broadly scattered values in equally sized populations expressed by the rather low R² that varied between species from 0.07 to 0.38 show that in all examined species population growth rates were asynchronous between patches.

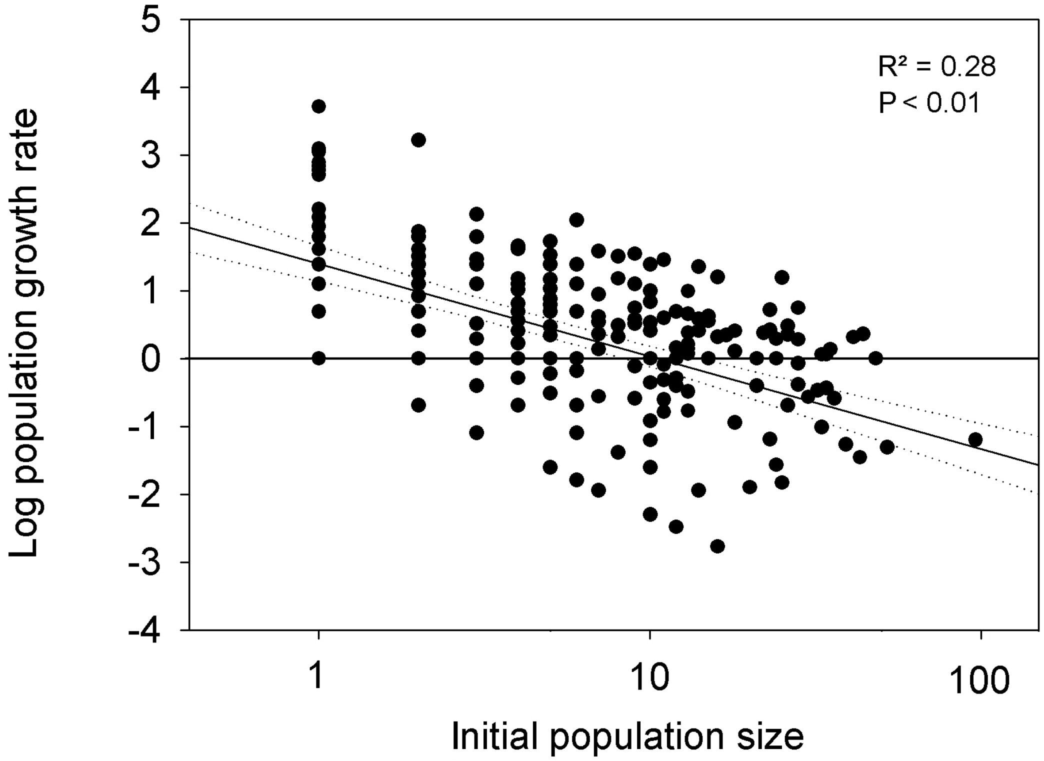

FIG. 5-5. Population growth rate λ (calculated as $\ln(N_t/N_{t-1})$) of the epiphytic orchid *Caularthron bilamellatum* in discrete patches along the shore line of Barro Colorado Island. Values above and below zero represent populations with positive growth and negative growth, respectively. All other analyzed epiphyte species occurred in fewer patches but show similarly scattered λ with significant R^2 ranging from 0.07 to 0.38 (except *Guzmania monostachia*, here R^2 was marginally significant with P=0.056). Dotted lines represent the 95 % confidence interval. Other analyzed species were: Tb, Nc, De, Ws, Vl, Ts, Tf, Gm (see legend of Table 5-3 for species names).

A net number of 302 patch populations went extinct in the census interval of which only 16 extinctions were caused by stem breakage or tree fall. After excluding these 16 populations we tested if there was an effect of previous population size on future extinction probability. First, epiphyte populations on occupied *Annona glabra* patches were divided into two size categories: (1) small (n ≤ median population size) and (2) large (n > median population size). Then a Mann-Whitney U-test was performed for differences in mean population size at the 1994 census between populations on patches that went extinct by the 2002 census versus those that did not. The test was confined to those species occupying more than 20 patches in 1994 to account for sufficient statistical power. Results were very heterogeneous. Patch population size n was negatively correlated with the likelihood of extinction only in six of the analyzed 11 species (Table 5-4). Only populations of *Dimerandra emarginata*, *Niphidium crassifolium* and *Werauhia sanguinolenta* in the first category (small population size) that went extinct were significantly smaller than persisting populations. In *Caularthron* *bilamellatum*, *Tillandsia bulbosa* and *Catasetum viridiflavum* only populations in the second category (large population size) that went extinct were significantly smaller than persisting populations. Four species (*Guzmania monostachia*, *Vittaria lineata*, *Tillandsia fasciculata* and *Polystachia foliosa*) showed no correlation and *Tillandsia subulifera* showed even a positive correlation: here significantly larger populations in the second category were more likely to go extinct.

Table 5-4. Mean population size of extinct and persisting local patch populations of epiphyte species for small and large patch populations. Bold P values of a Mann-Whitney U-test denote significant differences in size between extinct and persisting populations. "Small" and "Large" refer to populations with an abundance ≤ and > than the median population size in 1994, respectively. Only species occurring in more than 20 patches in 1994 are included. Species are sorted by the total number of patches they occupied in 1994. Large populations in *Werauhia sanguinolenta* were not tested due to low number of extinct populations.

Species	Small population		P	Large population		P
	Extinct	Persistent		Extinct	Persistent	
Caularthron bilamellatum	2.5	3.0	0.26	11.7	17.9	**0.03**
Tillandsia bulbosa	2.3	2.7	0.23	10.6	16.7	**0.05**
Dimerandra emarginata	2.4	3.7	**0.04**	14.9	33.6	0.28
Niphidium crassifolium	1.5	2.1	**0.03**	14.7	18.9	0.27
Werauhia sanguinolenta	1.2	1.7	**0.02**	4.0	11.5	-
Tillandsia fasciculata	1.4	1.1	0.64	4.3	8.7	0.28
Catasetum viridiflavum	1.0	1.0	1.00	2.0	3.6	**0.04**
Vittaria lineata	2.4	1.9	0.30	6.8	15.4	0.12
Tillandsia subulifera	1.8	1.6	0.60	27.0	10.3	**0.02**
Guzmania monostachia	2.0	1.9	0.81	-	10.9	-
Polystachia foliosa	1.4	1.4	0.92	4.6	8.1	0.06

Only in large populations of *Guzmania monostachia* extinction could not be detected while in all other analyzed species large populations had a measurable probability of extinction (Table 5-5). Further, the probability of local extinction decreased with increasing regional distribution (Fig. 5-6, $R^2=0.47$). In all 11 analyzed species colonization of new patches by epiphyte populations was higher than population extinction (Table 5-5).

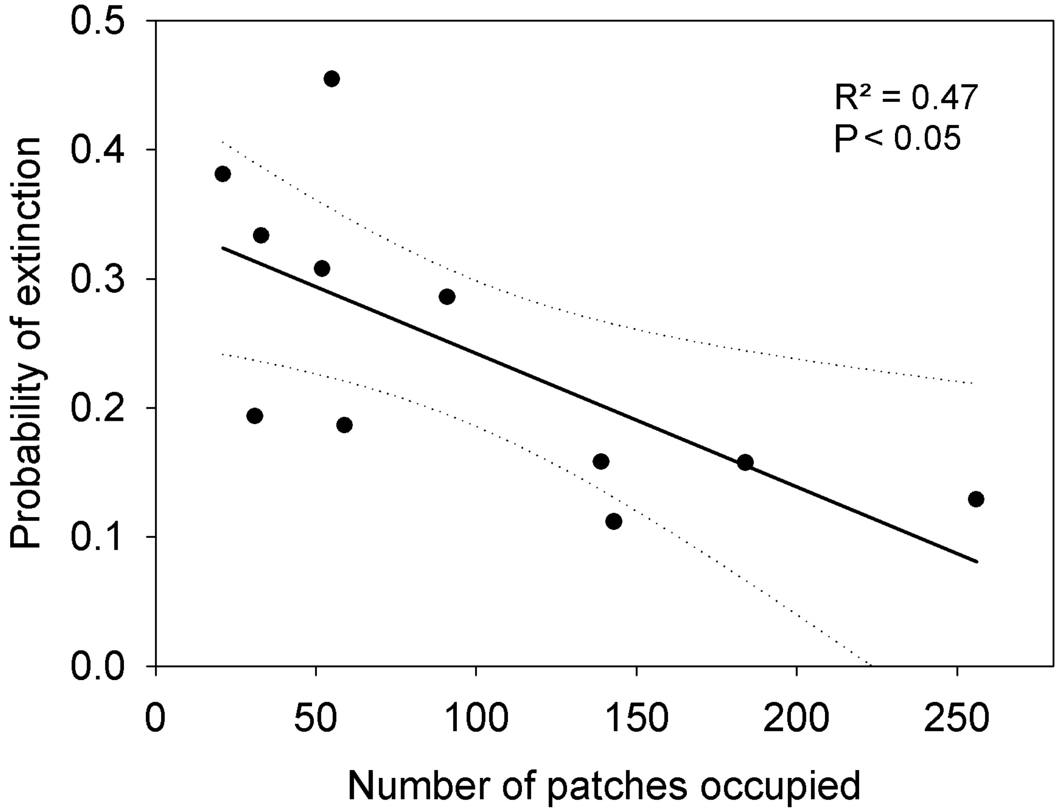

FIG. 5-6. Relationship between the probability of extinction and distribution of patches of epiphyte species on the host tree *Annona glabra*. Only species occurring in more than 20 patches were considered. Data are net extinction rates over the course of eight years. Dotted lines represent the 95 % confidence interval.

Local dispersal - We compared the net colonization rates of individuals of all epiphyte species during the census interval on originally empty trees and the rates of establishment of individuals on trees that were already occupied by a given epiphyte species. In this analysis we also considered if a tree had juvenile epiphytes (<20 % of maximum plant size) in 1994 that we normally omitted due to their high turnover. In a tree that already hosted a given epiphyte species significantly more conspecifics established after eight years (7.0 ± 4.9 individuals, mean ± SD) than on trees lacking this species (3.3 ± 1.7 individuals, pairwise t-test, $P<0.001$, $n=20$ species). To exclude an effect of tree size on colonization we considered only trees with a crown volume of more than 5 m³, since trees of this size in both groups showed no significant difference in crown volume (unpaired t-test, $P=0.29$, $n_{\text{tree hosting species}} = 180$, $n_{\text{tree lacking species}} = 201$).

TABLE 5-5. Local patch population colonization and extinction events. Given are the number of populations that either colonized new patches (Colonized) or went extinct on a patch (Extinct) during the census interval and number of patches (percentage from all occupied patches) with different sized epiphyte populations that went extinct. Large N and small N refer to populations with total abundance less than and greater than the median population size in 1994, respectively. Only species occurring in more than 20 patches in 1994 are included. Species are sorted by the total number of patches they occupied in 1994.

Species	Family	Number of populations		Extinct patches	
		Colonized	Extinct	Large N	Small N
Caularthron bilamellatum	Orchidaceae	120	33	10 (9.6%)	23 (15.1%)
Tillandsia bulbosa	Bromeliaceae	90	29	10 (11.2%)	19 (19.8%)
Dimerandra emarginata	Orchidaceae	94	16	7 (9.2%)	9 (13.4%)
Niphidium crassifolium	Polypodiaceae	75	22	13 (20%)	9 (12%)
Werauhia sanguinolenta	Bromeliaceae	27	26	1 (2.4%)	25 (50%)
Tillandsia fasciculata	Bromeliaceae	26	11	8 (25%)	3 (11.1%)
Catasetum viridiflavum	Orchidaceae	34	25	5 (29.4%)	20 (52.6%)
Vittaria lineata	Vittariaceae	32	16	10 (38.5%)	6 (23.1%)
Tillandsia subulifera	Bromeliaceae	30	11	6 (33.3%)	5 (33.3%)
Guzmania monostachia	Bromeliaceae	9	6	0 (0%)	6 (28.6%)
Polystachia foliosa	Orchidaceae	19	8	3 (33.3%)	5 (41.7%)

Discussion

Increasing individual numbers in most species and colonization of empty trees suggest that the epiphyte vegetation on *Annona glabra* around BCI has not reached a steady state during the maximal 80 years since the establishment of the host trees. The minor changes in the species ranking and the high coefficient of determination of the regression line in Fig. 5-1 show that, despite the massive increase in epiphyte abundance, the composition of epiphyte assemblages on the host tree species is very stable. Comparisons of the epiphyte vegetation in individual host trees, as well as in the entirety of host trees show that the epiphyte vegetation on a single tree decreased in similarity with time, while the epiphyte vegetation on *Annona glabra* as a whole became more homogeneous.

The species-area relationship for epiphytes in *Annona glabra* stands was better explained by host tree number than stand area. In contrast, on the scale of single trees, only a weak relationship between host tree size (as crown volume) and species richness of epiphytes (Zotz et al., 1999) was observed. These findings support metapopulation dynamics as a likely explanation for the observed strong species-area relationship. The observed z-values are within the range of values reported by many studies of habitat islands (Begon et al., 1999).
Comparing the four conditions outlined by Hanski and Gilpin (1997) with the observed properties of the epiphyte vegetation on *Annona glabra* suggests that species are driven by metapopulation processes: (1) The suitable habitat occurs in discrete patches: The habitat suitable for a large amount of epiphyte species in the study area are *Annona glabra* trees, which occur as discrete patches along the shore line and small tributaries. (2) Even the largest local populations have a substantial risk of extinction: The probability of population extinction was unrelated to population size in most of the analyzed epiphyte species. Hence, populations were equally likely to become extinct. Species whose probability of extinction was related to population size also showed measurable probabilities of extinction in large populations. (3) Habitat patches must not be too isolated to prevent recolonization: Although recolonization of formerly occupied patches could not be evaluated since the census was conducted only twice, the colonization of about one third of the empty and suitable patches during the census interval suggests that patches are within dispersal ranges of epiphytes. (4) Local populations do not have completely synchronous dynamics: Patch dynamics, measured as the population growth in all analyzed epiphyte species were asynchronous (Fig. 5-5). Patch population extinction occurred during the census interval, whilst other local populations increased or decreased and new ones established.

Extinction of a patch population could be related to stem or tree fall only in a few cases but we expect that substrate failure (tree fall, branch breakage, bark defoliation) to be the major cause of death in epiphytes on *Annona glabra*. A demographic study on *Werauhia sanguinolenta* conducted on *Annona glabra* trees close to the study area over the course of eight years revealed that most epiphyte extinction events occurred due to substrate instability (Zotz et al., 2005). Further the finding that large and small populations in most analyzed species were equally likely to go extinct suggests that population extinction is regulated by patch dynamics. Thus, the local populations of epiphyte species on *Annona glabra* can be characterized as patch-tracking metapopulations (sensu Snäll et al., 2003). This finding is in accordance with other studies on epiphyte populations that also exhibit a patch-tracking metapopulation structure (Snäll et al., 2003; Snäll et al., 2005a; but see Tremblay et al., 2006).

Additional analyses support the occurrence of a metapopulation structure in the epiphyte vegetation of *Annona glabra*. Epiphyte species showed a positive relationship between local abundance and regional distribution (Fig. 5-3) as has been found in many metapopulation studies (Addicott, 1978; Hanski, 1982; Gotelli, 1991). This means that species that are locally abundant are also widespread, whereas ones that are locally scarce tend to be found in only a few sites. As a consequence, the probability of a local population to go extinct decreases with increasing distribution (MacArthur and Wilson, 1967) which has been empirically shown by several studies (Simberloff, 1976; Hanski, 1982). We found that this relationship is also true for the epiphyte species of *Annona glabra* (Fig. 5-6). When extinction is a function of patch occupancy, the metapopulation at equilibrium tends to be driven towards either extinction or complete occupancy, suggesting that species that share a particular habitat should exhibit a bimodal distribution of patch occupancy (Hanski, 1982; Gotelli, 1991). In a bimodal distribution species in the right-most frequency class occur either in all or most sites suitable for the species and are designated as core species while species in the left-most frequency class occur only in a few sites and are called satellite species (Hanski, 1982). Epiphyte species on *Annona glabra* showed a strong unimodal pattern of patch occupancy frequency distribution (Fig. 5-4a) with species mainly occurring in the left-most frequency class. The lack of a bimodal pattern, i.e. more species occurring in the right-most frequency class, can be explained with the non-equilibrium metapopulation status of epiphyte species on *Annona glabra*. In our non-equilibrium metapopulations, the colonization of available empty patches exceeds the extinction of local populations (Table 5-4) which is caused by the ongoing colonization of habitat patches by epiphytes due to their, in epiphyte terms, very recent creation. We hypothesize that after the colonization of patches has reached an equilibrium, epiphyte species identified as permanent colonizers (Table 5-3) may then have occupied a large amount (>90 %) of all suitable patches, while sporadic colonizers will have established in very few patches (<10 %) and the characteristic bimodal frequency distribution could be detected. An indication for this assumption gives the change of pattern in the species distribution in the abundantly occupied stands (Fig. 5-4b) where almost all *Annona glabra* trees are already occupied by high numbers of epiphyte individuals. Here, we found a bimodal distribution of epiphyte species in 2002 ($P_{90\text{-}100\%}$=0.21; see Material and Methods for probability limits). Furthermore, a shift of 1994 species in intermediate frequency classes towards higher classes can be seen (Fig. 5-4b).

From the results of the colonization null model (Table 5-2) together with the colonization patterns (Table 5-3) we can infer predictions on the species composition when colonization of *Annona glabra* trees has reached a steady state. Although belonging to the most abundant epiphytes *Dimerandra emarginata* and *Werauhia sanguinolenta* showed colonizing abilities lower than expected by their abundance (Table 5-2), indicating that an early colonization of trees has lead to their high position in the species ranking list. Contrasting, the relative low abundance of species like *Polystachia foliosa* or *Catasetum viridiflavum* along with their high population growth rate and good colonizing ability indicate that these species have only recently arrived on *Annona glabra*. We predict that these species will further increase in their dominance and together with the already locally abundant and regionally common species form the group of core species (sensu Hanski, 1982) once patch population colonization/extinction events have reached an equilibrium. Species in the sporadic colonizer group (Table 5-3) will still be regionally rare and of low local abundance and therefore form the group of satellite species.

Knowledge of the population structure in species is important for applying the correct conservation methods (Hanski and Gilpin, 1997). In species with metapopulation dynamics a non-metapopulation view would not lead to the recognition of the importance of currently unoccupied habitat. Our results show that the concept of metapopulation can be applied to vascular epiphyte populations comprising different plant families such as Orchidaceae, Bromeliaceae and Polypodiaceae. Together with previous findings that confirm the concept in non-vascular epiphytes (Löbel et al., 2006) and an epiphytic orchid (Tremblay et al., 2006) one may conclude that epiphytes in general have a metapopulation structure. However, this assumption needs more rigorous evidence from the study of epiphyte species with different pollination and dispersal modes than the species already studied. Animal-dispersed species in this study were of such low abundance that analysis of patch population extinction probability and population growth rates were not possible. Thus, species like these have to be studied on a larger scale that includes more patch populations.

Species richness and abundance are often found to be positively related to size of trees (Yeaton and Gladstone, 1982; Zotz and Vollrath, 2003; Flores-Palacios and García-Franco, 2006) as it is, although weakly, also the case in our host tree species (Zotz et al., 1999). This pattern can be explained by at least two factors: (1) larger trees provide more surface area and a higher number of different microhabitats that can be colonized by epiphytes. (2) Larger trees are often older and therefore longer available for colonization (Benzing, 1990). In the past, studies examining this pattern could not disentangle both factors due to their one-time performance. In our study we can now separately evaluate the effect of tree size on epiphyte colonization, as all empty *Annona glabra* trees were available for colonization for the same period. After eight years newly colonized trees differed significantly in respect to height and crown volume from unoccupied conspecifics. And within the colonized group larger trees were colonized more often by epiphytes, although this correlation was weak. Thus, differences in tree size per se can explain variation in epiphyte species richness and abundance to some extent while other factors like time and connectivity to dispersal sources may explain a larger part of epiphyte colonization.

The role of local dispersal in the establishment of epiphytes in host trees is an important one as suggested by genetic and ecological studies (Trapnell et al., 2004; Bernal et al., 2005). We indirectly show that in *Annona glabra* most recruitment of epiphytes occurs in close proximity to their mother plant. Similar to the findings in Chapter 3 host trees that were occupied by a given epiphyte species experienced a significantly higher rate of establishment by conspecifics in the following eight years than trees lacking the focal species.

In summary, we found that the epiphyte assemblage on the population of *Annona glabra* trees that established at BCI during the last 80 years ago has not reached a steady state. While the epiphyte species composition on the host tree species as a whole was rather stable, most species increased in individual numbers and continue to colonize empty patches. Although low abundance of many epiphyte species did not allow us to conclude that metapopulation criteria account for all epiphyte species on *Annona glabra*, we could show that the abundant epiphyte species exhibit metapopulation traits with asynchronous dynamics and high turnover of local populations.

Chapter 6

Conclusion

There are still many important questions that remain unanswered, but substantial progress has been made towards understanding the structure and dynamics of epiphyte vegetation in tropical lowland forest, as represented by the BCI and San Lorenzo forest.

The study in the San Lorenzo Forest gave insights into the dynamics of epiphyte vegetation in an undisturbed forest and can serve 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 and Muller-Landau, 2006). The high turnover at the level of both well-established epiphyte individuals and patch populations is mainly a result of substrate dynamics. As a consequence, the persistence of epiphyte species is dependent on the availability of suitable and empty habitat patches since local populations, regardless of their demographic characteristics, go extinct when their host tree, the host branch, or even hosting parts of it die and fall. For epiphytes living in networks of host individuals, extinction-colonization dynamics are self-evident, owing to the high turnover of the substrate and the limited lifespan of host individuals. In the studied host tree, *Socratea exorrhiza,* the available time for an epiphyte to colonize a tree and produce propagules before the host dies in the most favourable case is about 60 years. Given the low growth rate in many epiphyte species and a period of several years to more than a decade to reach maturity (Schmidt and Zotz, 2002), 60 years appear quite a short time for epiphytes to establish and complete their life cycle. Although, this is a rather extreme case compared to the much longer lived forest trees the time frame is in the magnitude of individual branches of long lived trees. This, and the finding of metapopulation processes in vascular epiphyte species, including such different groups as bromeliads, orchids and ferns, occurring on the host tree *Annona glabra* highlight the essential need of epiphytes to colonize empty and suitable habitat patches to survive in the long term.

The current situation for epiphytes in the *Annona glabra* host tree population is that of a primary colonization phase. After the creation of Lake Gatun in 1914 these new habitat patches came into being and since then epiphytes continue to colonize them. The studied system represents a unique opportunity to study epiphyte community processes after human disturbance lead to the creation of easy accessible new patches that are suitable for epiphyte colonization. Although an ‘equilibrium’ is not reached yet, the study gives an idea on the duration of epiphyte colonization until a steady state is reached and serves as a comparison for similar cases (e.g. epiphyte colonization after reforestation).

Epiphyte colonization is determined by different factors that can be related to the individual properties of the host tree. Of these, tree size was identified to be positively correlated with colonization in both studied host trees. Moreover, in *Annona glabra* tree size could be evaluated separately from time available for epiphytes to colonize a tree, with the finding, that tree size *per se* explained colonization only to a minor extent. In both studied host tree-systems local dispersal of epiphytes plays an important role in driving epiphyte colonization. This is indicated by a high recruitment rate in the close vicinity of already established epiphyte individuals. This pattern was found in the epiphyte assemblage of *Annona glabra* as well as *Socratea exorrhiza*.

A new quantitative approach examined the possible role of host tree identity in the structuring of a vascular epiphyte community. For the three locally common host tree species *Socratea exorrhiza*, *Marila laxiflora*, and *Perebea xanthochyma* we found that the abundances of the majority of epiphyte species (69 - 81 %) were indistinguishable from random distribution. However, almost 43 % of the epiphyte species in the local epiphyte pool showed a higher or lower abundance, respectively, on at least one of the focal tree species than expected by chance. Thus, the host tree species identity imposed a positive or negative bias on a large proportion of the epiphytes in the local species pool. Host specificity was not detected in the study area, thus Went's (1940) concept of species-specificity in the strict sense can be rejected. The extreme alternative can be rejected 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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Appendices

APPENDIX 1. Vascular epiphytes and hemi-epiphytes occurring on *Socratea exorrhiza* in three census years. Species are ranked by decreasing abundance in the first census. Species names of flowering plants follow the Flora of Panama Checklist and Index (D'Arcy 1987), and Lellinger (1989). Hemiepiphytes are marked with an asterisk. Wind-dispersed seeds are typical for 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
Guzmania subcorymbosa	Bromeliaceae	95	1	110	2	109	2
Ananthacorus angustifolius	Vittariaceae	76	2	73	4	105	3
Elaphoglossum sporadolepis	Lomariopsidaceae	71	3	128	1	151	1
Dicranoglossum panamense	Polypodiaceae	56	4	60	5	27	10
Philodendron fragrantissimum *	Araceae	54	5	42	8	82	4
Scaphyglottis longicaulis	Orchidaceae	51	6	76	3	57	7
Scaphyglottis graminifolia	Orchidaceae	35	7	44	7	37	8
Sobralia fragrans	Orchidaceae	30	8	25	11	11	16
Tillandsia anceps	Bromeliaceae	25	9	22	12	28	9
Niphidium crassifolium	Polypodiaceae	25	9	30	9	65	6
Anthurium clavigerum *	Araceae	22	11	12	19	15	14
Asplenium serratum	Aspleniaceae	17	12	18	13	23	12
Dichaea panamensis	Orchidaceae	16	13	5	24	9	18
Vriesea gladioliflora	Bromeliaceae	15	14	16	15	25	11
Epidendrum nocturnum	Orchidaceae	13	15	15	16	13	15
Polybotrya villosula *	Dryopteridaceae	12	16	15	16	18	13
Epidendrum difforme	Orchidaceae	11	17	3	32	3	31
Anthurium friedrichsthallii	Araceae	10	18	10	20	9	18
Trichomanes angustifrons	Hymenophyllaceae	8	19	0		3	31
Columnea billbergiana	Gesneriaceae	8	19	0		0	
Codonanthe macradenia	Gesneriaceae	7	21	3	32	4	26
Campyloneurum phylliditis	Polypodiaceae	7	21	13	18	10	17
Syngonium podophyllum *	Araceae	6	23	7	22	5	24
Trichomanes ovale	Hymenophyllaceae	5	24	0		1	41
Trichomanes ekmannii	Hymenophyllaceae	5	24	2	37	4	26
Peperomia rotundifolia	Piperaceae	5	24	17	14	4	26
Anthurium acutangulum	Araceae	5	24	5	24	6	22
unidentified juveniles	Polypodiaceae	4	28	49	6	0	
Topobea praecox *	Melastomataceae	4	28	3	32	2	35
Tillandsia bulbosa	Bromeliaceae	4	28	0		1	41
Scaphyglottis prolifera	Orchidaceae	4	28	3	32	3	31
Polypodium percussum	Polypodiaceae	4	28	4	28	3	31
Peperomia ebingeri	Piperaceae	4	28	5	24	5	24
Clusia cf uvitana *	Clusiaceae	4	28	2	37	2	35
Anthurium tetragonum	Araceae	4	28	2	37	2	35
Vittaria lineata	Vittariaceae	3	36	6	23	0	
unidentified juveniles	Araceae	3	36	4	28	9	18
Philodendron sagittifolium *	Araceae	3	36	0		2	35
Microgramma lycopodioides	Polypodiaceae	3	36	10	20	8	21
Encyclia fragrans	Orchidaceae	3	36	4	28	4	26

Species	Family	1999		2002		2004	
		Individuals	Rank	Individuals	Rank	Individuals	Rank
Sobralia panamensis	Orchidaceae	2	41	5	24	0	
Polystachya foliosa	Orchidaceae	2	41	3	32	4	26
Polypodium triseriale	Polypodiaceae	2	41	2	37	0	
Pleopeltis panamensis	Polypodiaceae	2	41	0		0	
Philodendron radiatum *	Araceae	2	41	1	42	1	41
Guzmania musaica	Bromeliaceae	2	41	0		0	
Campyloneurum occultum	Polypodiaceae	2	41	30	9	72	5
unidentified juveniles	Orchidaceae	1	48	0		0	
Trichomanes punctatum	Hymenophyllaceae	1	48	0		0	
Stenospermation angustifolium	Araceae	1	48	0		1	41
Pleurothallis verecunda	Orchidaceae	1	48	0		0	
Peperomia macrostachya	Piperaceae	1	48	1	42	2	35
Ornithocephalus bicornis	Orchidaceae	1	48	1	42	0	
Monstera dilacerata	Araceae	1	48	0		0	
Elleanthus longibracteatus	Orchidaceae	1	48	1	42	0	
Drymonia serrulata	Gesneriaceae	1	48	0		0	
Dimerandra emarginata	Orchidaceae	1	48	0		0	
Anetium citrifolium	Vittariaceae	1	48	1	42	6	22
Aechmea tillandsioides	Bromeliaceae	1	48	0		0	
Trichosalpinx orbicularis	Orchidaceae	0		4	28	0	
Trichomanes sp.	Hymenophyllaceae	0		0		1	41
Pleurothallis brighamii	Orchidaceae	0		0		1	41
Philodendron tripartitum	Araceae	0		1	42	1	41
Hylocereus monacanthus	Cactaceae	0		1	42	1	41
Hecistopteris pumila	Vittariaceae	0		2	37	2	35
Anthurium hacumense	Araceae	0		1	42	0	
Anthurium brownii	Araceae	0		1	42	0	
Anthrophyum lanceolatum	Vittariaceae	0		1	42	0	

APPENDIX 2. 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 observed individual numbers of a given epiphyte species 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 are species less common than expected. Species names of flowering plants follow the Flora of Panama Checklist and Index (D'Arcy 1987), and Lellinger (1989).

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	

Species	Family	Individuals on *Socratea*	Individuals of null assemblage		Rank	
			Lower boundary	Upper boundary	Null assemblage	*Socratea*
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	
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	

Species	Family	Individuals on *Socratea*	Individuals of null assemblage Lower boundary	Upper boundary	Rank Null assemblage	*Socratea*
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 3. 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*. Shown are observed individual numbers of a given epiphyte species 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 are species less common than expected. Species names of flowering plants follow the Flora of Panama Checklist and Index (D'Arcy 1987), and Lellinger (1989).

Species	Family	Individuals	Individuals of null assemblage		Rank	
		on *Marila*	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
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	

Species	Family	Individuals	Individuals of null assemblage		Rank	
		on *Marila*	Lower boundary	Upper boundary	Null assemblage	*Marila*
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	
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	

Species	Family	Individuals	Individuals of null assemblage		Rank	
		on *Marila*	Lower boundary	Upper boundary	Null assemblage	*Marila*
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 4. 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 observed individual numbers of a given epiphyte species 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 are species less common than expected. Species names of flowering plants follow the Flora of Panama Checklist and Index (D'Arcy 1987), and Lellinger (1989).

Species	Family	Individuals	Individuals of null assemblage		Rank	
		on *Perebea*	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	
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	

Species	Family	Individuals	Individuals of null assemblage		Rank	
		on *Perebea*	Lower boundary	Upper boundary	Null assemblage	*Perebea*
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	

Species	Family	Individuals on *Perebea*	Individuals of null assemblage Lower boundary	Individuals of null assemblage Upper boundary	Rank Null assemblage	Rank *Perebea*
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	

APPENDIX 5. List of epiphyte species occurring in the 1994 and 2002 census on the host tree *Annona glabra* at BCI. Location indicates occurrence of a species in sampled sectors (s), intersectors (i), or not found in a respective census (-). Species are sorted by their abundance in 1994.

Species	Family	Location		Individuals		Rank		λ in % per year
		1994	2002	1994	2002	1994	2002	
Dimerandra emarginata (G. Meyer) Hoehne	Orchidaceae	s	s	3876	6562	1	2	6.6
Caularthron bilamellatum (Reichb.f.) Schult.	Orchidaceae	s	s	3741	7137	2	1	8.1
Tillandsia bulbosa Hook.	Bromeliaceae	s	s	2223	3222	3	3	4.6
Niphidium crassifolium (L.) Lellinger	Polypodiaceae	s	s	1847	2365	4	4	3.1
Werauhia sanguinolenta (Cogn. Marchal) J.R. Grand	Bromeliaceae	s	s	716	1087	5	5	5.2
Vittaria lineata (L.) J. Sm.	Polypodiaceae	s	s	463	502	6	7	1.0
Tillandsia subulifera Mez	Bromeliaceae	s	s	454	645	7	6	4.4
Tillandsia fasciculata Sw. var fasciculata	Bromeliaceae	s	s	441	399	8	8	-1.3
Guzmania monostachia (L.) Rusby ex Mez	Bromeliaceae	s	s	282	306	9	9	1.0
Epidendrum nocturnum Jacq.	Orchidaceae	s	s	172	241	10	10	4.2
Sobralia suaveolens Reichb.f.	Orchidaceae	s	s	145	172	11	13	2.1
Catasetum viridiflavum Hook.	Orchidaceae	s	s	126	220	12	12	7.0
Polystachia foliosa (Lindl.) Reichb.f.	Orchidaceae	s	s	83	227	13	11	12.6
Catopsis sessiliflora (R. & P.) Mez	Bromeliaceae	s	s	60	28	14	18	-9.5
Anthurium brownii Mast.	Araceae	s	s	46	73	15	15	5.8
Oncidium stipitatum Lindl. in Benth.	Orchidaceae	s	s	43	61	16	17	4.4
Anthurium durandii Engl.	Araceae	s	s	40	75	17	14	7.9
Campyloneurum phyllitidis (L.) C. Presl	Polypodiaceae	s	s	25	27	18	19	1.0
Codonanthe crassifolia (Focke) Mort.	Gesneriaceae	s	s	24	70	19	16	13.4
Epidendrum difforme Jacq.	Orchidaceae	s	s	18	1	20	55	-36.1
Ananthacorus angustifolius (Sw.) Und. & Max.	Polypodiaceae	s	s	17	27	21	19	5.8
Anthurium clavigerum Poepp.	Araceae	s	s	16	8	22	30	-8.7
Epidendrum rigidum Jacq.	Orchidaceae	s	i	16		22	64	
Polypodium pectinatum L.	Polypodiaceae	s	s	15	5	24	39	-13.7
Clusia uvitana Pitt.	Clusiaceae	s	s	14	21	25	21	5.1
Aspasia principissa Reichb.f.	Orchidaceae	s	s	12	17	26	23	4.4
Philodendron tripartitum (Jacq.) Schott	Araceae	s	s	12	9	26	28	-3.6
Ficus citrifolia Mill.	Moraceae	s	s	11	5	28	39	-9.9
Nephrolepis pendula (Raddi) J. Sm.	Polypodiaceae	s	s	10	19	29	22	8.0
Philodendron radiatum Schott	Araceae	s	s	9	11	30	26	2.5
Aechmea setigera Mart. Ex Schult.	Bromeliaceae	s	s	7	9	31	28	3.1
Philodendron scandens K. Koch & Sello	Araceae	s	s	7	7	31	33	0.0
Polypodium triseriale Sw.	Polypodiaceae	s	s	7	2	31	51	-15.7
Ficus obtusifolia H.B.K.	Moraceae	s	s	5	3	34	44	-6.4
Ficus trigonata L.	Moraceae	s	s	5	2	34	51	-11.5
Notylia pentachne Reichb.f.	Orchidaceae	s	-	5		34	64	
Cattleya patinii Cogn.	Orchidaceae	s	s	4	6	37	36	5.1
Encyclia chimborazoensis (Schlechter) Dressl.	Orchidaceae	s	s	4	5	37	39	2.8
Monstera adansonii Schott.	Araceae	s	-	4		37	64	
Epidendrum schlechterianum Ames	Orchidaceae	s	s	3	13	40	25	18.3
Brassavola nodosa (L.) Lindl.	Orchidaceae	s	s	3	8	40	30	12.3
Encyclia chacaoensis (Reichb.f.) Dressl.	Orchidaceae	s	s	3	7	40	33	10.6
Aechmea tillandsioides (Mart.) Baker var kienastii	Bromeliaceae	s	s	3	6	40	36	8.7
Epiphyllum phyllanthus L.	Orchidaceae	s	s	3	4	40	43	3.6
Monstera dubia (H.B.K.) Engl. & K. Krause	Araceae	s	s	3	1	40	55	-13.7
Coussapoa asperifolia Trecul.	Moraceae	s	s	2	3	46	44	5.1
Pleurothallis verecunda Schlechter	Orchidaceae	s	s	2	1	46	55	-8.7

Species	Family	Location		Individuals		Rank		λ in % per year
		1994	2002	1994	2002	1994	2002	
Drymonia serrulata (Jacq.) Mart.	Gesneriaceae	s	i	2		46	64	
Souroubea sympetala Gilg	Marcgraviaceae	s	-	2		46	64	
Ficus perforata L.	Moraceae	s	-	2		46	64	
Philodendron inconcinnum Schott	Araceae	s	s	1	14	51	24	33.0
Peperomia cordulata C. DC.	Piperaceae	s	s	1	7	51	33	24.3
Cosmibuena skinneri Pitt.	Rubiaceae	s	s	1	1	51	55	0.0
Stelis crescentiicola Schlechter	Orchidaceae	s	-	1		51	64	
Trigonidium egertonianum Batem. ex. Lindl.	Orchidaceae	s	-	1		51	64	
Topobaea praecox Gleason	Melastomataceae	s	-	1		51	64	
Ficus poponoei Standl.	Moraceae	s	-	1		51	64	
Monstera dilacerata (K.Koch & Sello) K. Koch	Araceae	s	-	1		51	64	
Anthurium salviniae Hemsl.	Araceae	s	-	1		51	64	
Anthurium tetragonum Hook. ex Schott	Araceae	-	s		10	60	27	
Pleurothallis brighamii S. Wats.	Orchidaceae	i	s		8	60	30	
Coussapoa panamensis Pitt.	Moraceae	i	s		6	60	36	
Anthurium friedrichsthalii Schott.	Araceae	i	s		5	60	39	
Dichaea panamensis Lindl.	Orchidaceae	-	s		3	60	44	
Scaphyglottis longicaulis S. Watson	Orchidaceae	-	s		3	60	44	
Anthurium flexile Schott	Araceae	-	s		3	60	44	
Syngonium erythrophyllum Birdsey ex G.S. Bunting	Araceae	-	s		3	60	44	
Rhipsalis cassytha Gaertn.	Cactaceae	i	s		3	60	44	
Maxillaria alba (Hook.) Lindl.	Orchidaceae	-	s		2	60	51	
Syngonium podophyllum Schott	Araceae	-	s		2	60	51	
Maxillaria uncata Lindl.	Orchidaceae	i	s		1	60	55	
Maxillaria variabilis Batem. Ex Lindl.	Orchidaceae	i	s		1	60	55	
Anthurium scandens (Aubl.) Engl.	Araceae	i	s		1	60	55	
Polypodium hygrometricum Splitg.	Polypodiaceae	-	s		1	60	55	
Polypodium lycopodioides L.	Polypodiaceae	i	s		1	60	55	
Polypodium percussum Cav.	Polypodiaceae	i	i					
Sobralia panamensis Schlechter	Orchidaceae	i	i					
Philodendron sagittifolium Liebm.	Araceae	i	i					
Ficus nyphaeaefolia Mill.	Moraceae	i	-					
Polypodium costaricense H. Christ	Polypodiaceae	i	-					
Polypodium ciliatum Willd.	Polypodiaceae	i	-					
Trichopilia maculata Reichb.f.	Orchidaceae	i	-					
Maxillaria camaridii Reichb.f.	Orchidaceae	i	-					
Lockhartia acuta (Lindl.) Reichb.f.	Orchidaceae	i	-					
Epidendrum sculptum Reichb.f.	Orchidaceae	i	-					
Tillandsia elongata H.B.K. var. *subimbricata* (Bak.) L.B.Sm.	Bromeliaceae	i	-					
Aechmea pubescens Baker	Bromeliaceae	i	-					
Rodriguezia lanceolata R. & P.	Orchidaceae	i	-					

Curriculum vitae

Personal Information

Name	Stefan Laube
Date of birth	19th July 1976
Place of birth	Crivitz, Germany
Nationality	German

Education

9/1983-8/1992	High school: Polytechnische Oberschule "Sigmund Jähn", Schwerin, Germany
9/1992-6/1995	Secundary school: Schliemann-Gymnasium, Schwerin, Germany Graduation: Abitur
7/1995-9/1996	Military service
10/1996-9/1998	Biology study at the University of Greifswald, Germany
10/1998-2/2002	Biology study at the University of Bonn, Germany Graduation: Diploma („sehr gut“) Diploma thesis: “What limits vegetative growth in an epiphytic bromeliad?”
10/2002-12/2004	Field work at the Smithsonian Tropical Research Institute, Panama
10/2002-	Doctoral work at the University of Kaiserslautern, Germany Doctoral thesis: “Long-term changes of vascular epiphyte assemblages in the tropical lowlands of Panama.”

Stipends

2002	Short term fellowship by the Smithsonian Tropical Research Institute, Panama
4/2003 – 3/2005	pre-doctoral stipend by the University of Kaiserslautern, Germany

Publications

Laube, S. and Zotz, G. (2006). Neither host specific nor random: vascular epiphytes on three tree species in a Panamanian rainforest. Annals of Botany 97: 1103-1114

Laube, S. and Zotz, G. (2006). Long-term changes of the vascular epiphyte assemblage on the palm *Socratea exorrhiza* in a lowland forest in Panama. Journal of Vegetation Science 17: 307-314

Zotz, G., Laube, S. and Schmidt, G. (2005) Long-term population dynamics of the epiphytic bromeliad, Werauhia sanguinolenta. - Ecography 28: 806-814

Zotz, G. and Laube, S. (2005) Tank function in the epiphytic bromeliad, Catopsis sessiliflora. Ecotropica 11: 63-68

Laube, S. and G. Zotz (2003) Which abiotic factors limit vegetative growth in a vascular epiphyte? Functional Ecology 17: 598-604.

Contributions to Meetings

Laube S, Zotz G. Neither host specific nor random: vascular epiphytes on three tree species in a Panamanian rainforest. 19th Annual Meeting of the Society for Tropical Ecology (GTÖ) 2006, Kaiserslautern (Poster)

Laube S, Zotz G. Long-term changes in epiphyte assemblages – dynamics and underlying mechanisms, 4th International Canopy Conference 2005, Leipzig (Oral presentation)

Laube S. Long-term changes of the epiphyte communities. 17th Annual Meeting of the Society for Tropical Ecology (GTÖ) 2004**,** Bayreuth. (Poster)

Laube S, Schultz S, Zotz G. Long-term changes of the epiphyte community in *Annona glabra* trees of Barro Colorado Island, Panama. 16th Annual Meeting of the Society for Tropical Ecology (GTÖ) 2003**,** Rostock. (Poster)

Laube S, Zotz G. Which factors limit vegetative growth in vascular epiphytes? 15th Annual meeting of the Society for Tropical Ecology (GTÖ) 2002**,** Göttingen. (Poster)

Work as referee

Journals (referee)

Selbyana

Erklärung

Hiermit versichere ich, dass ich die vorliegende Dissertation in allen Teilen selbständig angefertigt und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe.

Darüber hinaus erkläre ich, dass die vorliegende Dissertationsschrift weder vollständig noch teilweise einer anderen Fakultät mit dem Ziel vorgelegt worden ist, einen akademischen Grad zu erwerben.

Kaiserslautern, den 17. Juli 2006