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

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Abstract

Question: Do vascular epiphyte species have a metapopulation structure? What are the qualitative and quantitative long-term changes of the complete vascular epiphyte vegetation in a particular host tree species?

Location: Lowland forest on Barro Colorado Island (9°10' N, 79°51' W), Republic of Panama.

Methods: In 1994 and 2002 we conducted a census of all vascular epiphytes growing on more than 1000 *Annona glabra* trees (= patches). Epiphyte species abundances were recorded at the tree level in each census.

Results: The number of epiphyte individuals increased from ca. 15 000 to ca. 23 700 individuals during the census interval while the species composition on *Annona glabra* as a whole was rather stable. There was a strong positive relationship between occurrence in patches and local abundance of the species, and between species richness and host tree stand size. The dynamics of local populations of a given species were uncorrelated to each other; small and large local populations of most species had the same probability to go extinct. The frequency distribution of species on all host trees was not bimodal, but on a subset of heavily colonized host tree stands it was. Numbers of species and individuals were correlated with tree size which was not due to a correlation of tree size and tree age.

Conclusions: As far as the most abundant epiphyte species with metapopulation structures are concerned, these species belong to diverse families, e.g. *Orchidaceae*, *Bromeliaceae* and *Polypodiaceae*. Even ca. 80 years after the initial establishment of the host tree species in the study area epiphytes are still in the stage of initial colonization and have not reached a steady state as indicated by the strong increase in individuals and the ongoing colonization of empty trees.

Keywords: Barro Colorado Island; Density dependence; Occupancy frequency distribution; Patch dynamics; Population growth rate.

Nomenclature: D'Arcy 1987) for flowering plants; Croat (1978) for ferns.

Abbreviation: BCI = Barro Colorado Island.

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 & Wilson 1967) has made a major contribution to this field and stimulated the development of the concept of the metapopulation (Levins 1969, 1970), defined as an assemblage of populations where typically migration from one local population to at least some other local populations is possible, eventually resulting in a balance between extinction and colonization of these local populations. During the last decades, metapopulation models have developed into a widely recognized theory, which is used to explain different ecological and evolutionary phenomena on larger spatial scales, e.g. the geographical distribution of species, large-scale population dynamics, and maintenance of genetic variation. Moreover, metapopulation models became an important tool to explain species persistence in fragmented landscapes with great implications for conservation biology (Nee & May 1992; Tilman et al. 1994; Zartman & Shaw 2006).

The initial form of the metapopulation concept was derived from the study of animal populations and the concept has been improved by numerous zoological studies (e.g. Addicott 1978; Nee & May 1992; Hanski & Gilpin 1997; Gonzalez et al. 1998), while relatively few data are available for plants (for a review see Eriksson 1996, Husband & Barrett 1996, Freckleton & Watkinson 2002, Ouborg & Eriksson 2004). This scarcity is arguably due to methodological difficulties imposed by their biology. Freckleton & Watkinson (2002) suggested 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 major assumptions of metapopulation models, 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 candidate species showing metapopulation structure. They inherently lack the above mentioned shortcomings of plant assemblages. First, local populations occupy individual trees that can be conveniently defined 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 & Gilpin 1997). Second, there is no evidence that bark dwelling epiphytes have seed banks and, hence, (re)colonization of patches can be unambiguously accounted for by immigration processes. Finally, the extinction of a local epiphyte population can be detected unambiguously as soon as the last individual disappears.

Recent work has focused on temperate non-vascular epiphyte communities (Snäll et al. 2003, 2005a, b; Löbel et al. 2006) and on a single vascular epiphyte species (Tremblay et al. 2006). Here, we present a long-term data set documenting the dynamics of an entire vascular epiphyte assemblage. The current report builds on an earlier census of the epiphyte vegetation of the host tree *Annona glabra* in 1994 (Zotz et al. 1999) and a repetition of this census eight years later, in 2002. We ask whether community structure and dynamics in these vascular epiphyte populations can be explained by metapopulation processes.

Material and Methods

This study was conducted on Barro Colorado Island (BCI), (9°10' N, 79°51' W), Republic of Panama. The vegetation in this biological reserve is classified as tropical moist forest (Holdridge et al. 1971). BCI receives ca. 2600 mm of rain annually with a pronounced dry season from late December to April. With the construction of the Panama Canal and the creation of Lake Gatun in 1914, the hill top Barro Colorado became an island. The focal tree species of the present study, *Annona glabra* (*Annonaceae*), is restricted to marshy areas and shore lines that were established during the rise of the water level, hence even the oldest tree is < 80 years old. *Annona glabra* is a small, evergreen species with a wide geographical distribution, it is multiple-stemmed in most cases and rarely exceeds 7 m in height (Croat & Busey 1975). Air temperature and relative humidity (RH) were measured in the upper canopy of the forest and at the lake shore by Zotz & 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. Notable exceptions are species associated with nests of ants or stingless bees such as *Codonanthe crassifolia* (*Gesneriaceae*) or *Peperomia cordulata* (*Piperaceae*). The current report is based on two censuses of the vascular epiphytes on this tree species, one conducted in 1994 (Zotz et al. 1999), the other one eight years later in 2002.

Epiphyte census

The sampling protocol was similar in 1994 and 2002 (cf. Zotz et al. 1999). Briefly, the 62 km of shoreline of BCI were divided into 120 sectors of 3° each. In every other sector the epiphytes on *Annona glabra* were surveyed quantitatively. 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 & Holbrook 1986). 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. Conspecifics growing in close proximity were occasionally not distinguishable from each other. These 'epiphyte stands' were counted as one individual (cf. Sanford 1968). Small juveniles, i.e. plants ≤ 20% of the maximum size of a given species, were not counted but recorded as 'present' on a tree. Consequently, individuals > 20% maximum size that were recorded in the second census but not the first were either juveniles in 1994, or newly established individuals that had grown to > 20% maximum plant size during the census interval. We excluded juveniles of either census from analysis. The following measurements for each tree, with or without epiphytes, 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). Crown volume (C_V) was estimated as an ellipsoid. The distance to the closest *Annona* tree was also measured and all trees were mapped.

Along the originally censused shoreline, we were able to relocate 1012 of the 1210 trees (= 84%) found in 1994. An unambiguous identification of the multiple-stemmed tree individuals, especially when growing in dense stands, was often difficult. Therefore, only 725 trees could be unequivocally paired individually with trees of the original census, or had died. This subset of *Annona glabra* trees allowed us direct comparisons of changes in epiphyte assemblages at the level of individual trees, i.e. determine colonization and extinction rates, overall population growth rates, and Chao-Sørensen similarity indices.

There is a potential problem in defining an individual tree *a priori* as a patch (Hanski & Gilpin 1997) because trees are often not sufficiently spaced, i.e. the local dispersal range of an epiphyte may cover neighbouring trees, and therefore a local population may be scattered over several trees. The density of *Annona glabra* trees varies substantially ranging from 1 - 96 trees per 100 m shore line (Zotz et al. 1999). Available evidence from genetic (Trapnell et al. 2004), community (Zotz et al. 1999) and dispersal studies (Bernal et al. 2005) unanimously indicate a prevalence of very local dispersal, even in wind-dispersed taxa. For example, only 0.6% of *Tillandsia recurvata* seeds reached a distance of more than 10 m from a dispersal source (Bernal et al. 2005). Therefore, we analysed our data not only at the level of individual trees, but also at the level of 'tree stands', defined as any group of trees with a minimum distance to any other group of trees of 25 m. This definition, which includes solitary trees as independent entities, yielded 84 stands. Stand area was estimated as the area bounded by the outer trees of a stand using the software Universal Desktop Ruler (Version 2.8.1110, define AVPSoft.com) with detailed maps of the BCI shoreline 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 $A = 0.25\, p \times C_w^2$) was taken as stand area.

Data from tree stands were used in bimodality tests of the frequency distribution of epiphyte species, and when analysing the relationship of epiphyte species richness and stand area.

Data analysis

The Chao-Sørensen Similarity Index based on estimated abundance values (Chao et al. 2005) was used to compare changes in the epiphyte assemblages 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 effect 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 analysed the species-area relationship by fitting linear regression models (Statistica 6.0, Statsoft Inc., Tulsa, OK, US) predicting species richness as a function of *Annona glabra* stand area and the number of host trees in a stand, using the power function model in its log-transformed form ($\ln S = c + z \ln A$), where S is species number, c and z are constants, and A is area or number of trees in a stand, respectively.

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.

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

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

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 $P_{90\text{-}100\%} \geq 0.25$, or vice versa, the frequency distribution is unimodal (Tokeshi 1992). After analysing the species frequency distribution of all *Annona glabra* stands we studied those *Annona glabra* stands with a particularly high abundance of epiphytes that arguably have reached a state of saturated epiphyte colonization. We included all stands in which (1) > 90% of all trees were occupied by epiphytes, and (2) trees with epiphytes hosted, on average, at least 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 located in four different sectors fulfilled these requirements.

Temporal changes in the composition of the epiphyte assemblage on *Annona glabra* were analysed following Condit et al. (1992), who suggested for tropical tree communities the use of the coefficient of determination, R^2, from the regression analysis of species abundance in different years as a quantitative measure: the lower R^2, the greater the change in the community or assemblage.

Species differences in colonization ability were analysed with a series of null models in which the probability of colonizing a tree was simply a function of initial species abundance. We did not include distance in our models, because epiphytes on *Annona glabra* trees scattered along the shoreline as well as in forest trees can serve as potential sources. The null models used two basic measures of abundance, (1) the number of individuals and (2) the number of occupied trees. The first 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 three highest and the three lowest values. For each species, ranges expected by chance were then compared with the actual number of individuals that colonized empty trees until 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). This process was again repeated 120 times and 95% confidence intervals obtained as described above.

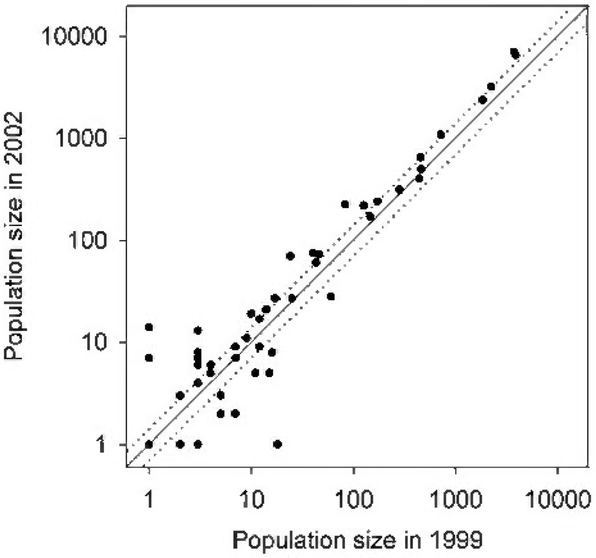

Fig. 1. Changes in total abundance of epiphyte species in *Annona glabra*. The solid line represents the line of equality of 1994 and 2002 abundances. Data points above and below this line represent species with increasing and decreasing populations, respectively. The distance to the solid line indicates proportional population change regardless of density. The two dashed lines signify an annual change of 5%.

Results

Species composition

In 1994, *Annona glabra* trees hosted a total of 59 of the ca. 160 species of the BCI vascular epiphyte flora (Zotz et al. 1999). In 2002, eight additional species were found on these trees, but others disappeared (Table 1). With a net increase of 4 species, the total species number in 2002 was 63 species. The number of holo-epiphytes and secondary hemi-epiphytes increased (56 species in 2002 vs. 49 species in 1994), that of woody hemi-epiphyte species decreased from initially 10 to 7. The number of epiphyte individuals increased considerably by > 60% from ca. 15 000 to ca. 23 700 individuals. The three most common species accounted for almost 80% of this increase (Table 1).

Between censuses the epiphyte assemblages on a given tree compared to those on all other trees became more similar. The Chao-Sørensen index increased significantly from 0.34 ± 0.34 in 1994 to 0.40 ± 0.34 in 2002 (means ± SD, unpaired *t*-test, $p < 0.001$). In contrast, temporal changes on any given tree were low. A comparison of the epiphyte assemblages in time from all trees with at least one epiphyte in 1994 and 2002 yielded a mean Chao-Sørensen index of 0.80 ± 0.27 (mean ± SD, $n = 371$).

After eight years, the rank of the ten most abundant species remained the same. There was a single change among the 20 most abundant taxa (*Epidendrum difforme*, *Orchidaceae*, dropped to rank 54 and *Ananthacorus angustifolius*, *Vittariaceae*, rose to rank 19; Table 1).

Population growth rates

The average population growth rate of the 47 epiphyte species found on *Annona glabra* trees both in 1994 and 2002 was +2.3% per year. Seventy percent of the species had a positive population growth rate (λ) while in 26%, populations were declining. Not surprisingly, very high or very low λs were mostly associated with low species abundances in the initial census (Fig. 1). For example, the death of 17 out of 18 individuals of *Epidendrum difforme* (*Orchidaceae*) resulted in an average decline of 36.1% per year. Conversely, an increase from 3 to 13 individuals in *Epidendrum schlechterianum* (*Orchidaceae*) represented an annual population growth rate of 18.3%. Overall, population sizes in 1994 and 2002 were highly correlated ($R^2 = 0.98$, Fig. 1) suggesting a very low change in the species composition of the assemblage.

Table 1. List of epiphyte species occurring in the 1994 and 2002 census on the host tree *Annona glabra* at BCI. - **I** -: previously reported from *Annona glabra* on BCI outside the sectors (Zotz et al. 1999). Ind. = individuals; *r* is in % per year

Species	Family	Ind. 1994	Ind. 2002	Rank 1994	Rank 2002	*r*
Dimerandra emarginata (G. Meyer) Hoehne	*Orchidaceae*	3876	6562	1	2	6.6
Caularthron bilamellatum (Reichb.f.) Schult.	*Orchidaceae*	3741	7137	2	1	8.1
Tillandsia bulbosa Hook.	*Bromeliaceae*	2223	3222	3	3	4.6
Niphidium crassifolium (L.) Lellinger	*Polypodiaceae*	1847	2365	4	4	3.1
Werauhia sanguinolenta (Cogn. Marchal) J.R. Grand	*Bromeliaceae*	716	1087	5	5	5.2
Vittaria lineata (L.) J. Sm.	*Vittariaceae*	463	502	6	7	1.0
Tillandsia subulifera Mez	*Bromeliaceae*	454	645	7	6	4.4
Tillandsia fasciculata Sw. var. *fasciculata*	*Bromeliaceae*	441	399	8	8	-1.3
Guzmania monostachia (L.) Rusby ex Mez	*Bromeliaceae*	282	306	9	9	1.0
Epidendrum nocturnum Jacq.	*Orchidaceae*	172	241	10	10	4.2
Sobralia suaveolens Reichb.f.	*Orchidaceae*	145	172	11	13	2.1
Catasetum viridiflavum Hook.	*Orchidaceae*	126	220	12	12	7.0
Polystachia foliosa (Lindl.) Reichb.f.	*Orchidaceae*	83	227	13	11	12.6
Catopsis sessiliflora (R. & P.) Mez	*Bromeliaceae*	60	28	14	18	-9.5
Anthurium brownii Mast.	*Araceae*	46	73	15	15	5.8
Oncidium stipitatum Lindl. in Benth.	*Orchidaceae*	43	61	16	17	4.4
Anthurium durandii Engl.	*Araceae*	40	75	17	14	7.9
Campyloneurum phyllitidis (L.) C. Presl	*Polypodiaceae*	25	27	18	19	1.0
Codonanthe crassifolia (Focke) Mort.	*Gesneriaceae*	24	70	19	16	13.4
Epidendrum difforme Jacq.	*Orchidaceae*	18	1	20	55	-36.1
Ananthacorus angustifolius (Sw.) Und. & Max.	*Vittariaceae*	17	27	21	19	5.8
Anthurium clavigerum Poepp.	*Araceae*	16	8	22	30	-8.7
Epidendrum rigidum Jacq.	*Orchidaceae*	16	0	22	64	
Polypodium pectinatum L.	*Polypodiaceae*	15	5	24	39	-13.7
Clusia uvitana Pitt.	*Clusiaceae*	14	21	25	21	5.1
Aspasia principissa Reichb.f.	*Orchidaceae*	12	17	26	23	4.4
Philodendron tripartitum (Jacq.) Schott	*Araceae*	12	9	26	28	-3.6
Ficus citrifolia Mill.	*Moraceae*	11	5	28	39	-9.9
Nephrolepis pendula (Raddi) J. Sm.	*Polypodiaceae*	10	19	29	22	8.0
Philodendron radiatum Schott	*Araceae*	9	11	30	26	2.5
Aechmea setigera Mart. Ex Schult.	*Bromeliaceae*	7	9	31	28	3.1
Philodendron scandens K. Koch & Sello	*Araceae*	7	7	31	33	0.0
Polypodium triseriale Sw.	*Polypodiaceae*	7	2	31	51	-15.7
Ficus obtusifolia H.B.K.	*Moraceae*	5	3	34	44	-6.4
Ficus trigonata L.	*Moraceae*	5	2	34	51	-11.5
Notylia pentachne Reichb.f.	*Orchidaceae*	5	0	34	64	
Cattleya patinii Cogn.	*Orchidaceae*	4	6	37	36	5.1
Encyclia chimborazoensis (Schlechter) Dressl.	*Orchidaceae*	4	5	37	39	2.8
Monstera adansonii Schott.	*Araceae*	4	0	37	64	
Epidendrum schlechterianum Ames	*Orchidaceae*	3	13	40	25	18.3
Brassavola nodosa (L.) Lindl.	*Orchidaceae*	3	8	40	30	12.3
Encyclia chacaoensis (Reichb.f.) Dressl.	*Orchidaceae*	3	7	40	33	10.6
Aechmea tillandsioides (Mart.) Baker var kienastii	*Bromeliaceae*	3	6	40	36	8.7
Epiphyllum phyllanthus L.	*Cactaceae*	3	4	40	43	3.6
Monstera dubia (H.B.K.) Engl. & K. Krause	*Araceae*	3	1	40	55	-13.7
Coussapoa asperifolia Trecul.	*Moraceae*	2	3	46	44	5.1
Pleurothallis verecunda Schlechter	*Orchidaceae*	2	1	46	55	-8.7
Drymonia serrulata (Jacq.) Mart.	*Gesneriaceae*	2	0	46	64	
Souroubea sympetala Gilg	*Marcgraviaceae*	2	0	46	64	
Ficus perforata L.	*Moraceae*	2	0	46	64	
Philodendron inconcinnum Schott	*Araceae*	1	14	51	24	33.0
Peperomia cordulata C. DC.	*Piperaceae*	1	7	51	33	24.3
Cosmibuena skinneri Pitt.	*Rubiaceae*	1	1	51	55	0.0
Stelis crescentiicola Schlechter	*Orchidaceae*	1	0	51	64	
Trigonidium egertonianum Batem. ex. Lindl.	*Orchidaceae*	1	0	51	64	
Topobaea praecox Gleason	*Melastomataceae*	1	0	51	64	
Ficus poponoei Standl.	*Moraceae*	1	0	51	64	
Monstera dilacerata (K.Koch & Sello) K. Koch	*Araceae*	1	0	51	64	
Anthurium salviniae Hemsl.	*Araceae*	1	0	51	64	
Anthurium tetragonum Hook. ex Schott	*Araceae*	0	10	60	27	
Pleurothallis brighamii S. Wats. **- I -**	*Orchidaceae*	0	8	60	30	
Coussapoa panamensis Pitt. **- I -**	*Moraceae*	0	6	60	36	
Anthurium friedrichsthalii Schott. **- I -**	*Araceae*	0	5	60	39	
Dichaea panamensis Lindl.	*Orchidaceae*	0	3	60	44	
Scaphyglottis longicaulis S. Watson	*Orchidaceae*	0	3	60	44	
Anthurium flexile Schott	*Araceae*	0	3	60	44	
Syngonium erythrophyllum Birdsey ex G.S. Bunting	*Araceae*	0	3	60	44	
Rhipsalis cassytha Gaertn. **- I -**	*Cactaceae*	0	3	60	44	
Maxillaria alba (Hook.) Lindl.	*Orchidaceae*	0	2	60	51	
Syngonium podophyllum Schott	*Araceae*	0	2	60	51	
Maxillaria uncata Lindl. **- I -**	*Orchidaceae*	0	1	60	55	
Maxillaria variabilis Batem. Ex Lindl. **- I -**	*Orchidaceae*	0	1	60	55	
Anthurium scandens (Aubl.) Engl. **- I -**	*Araceae*	0	1	60	55	
Polypodium hygrometricum Splitg.	*Polypodiaceae*	0	1	60	55	
Polypodium lycopodioides L. **- I -**	*Polypodiaceae*	0	1	60	55	

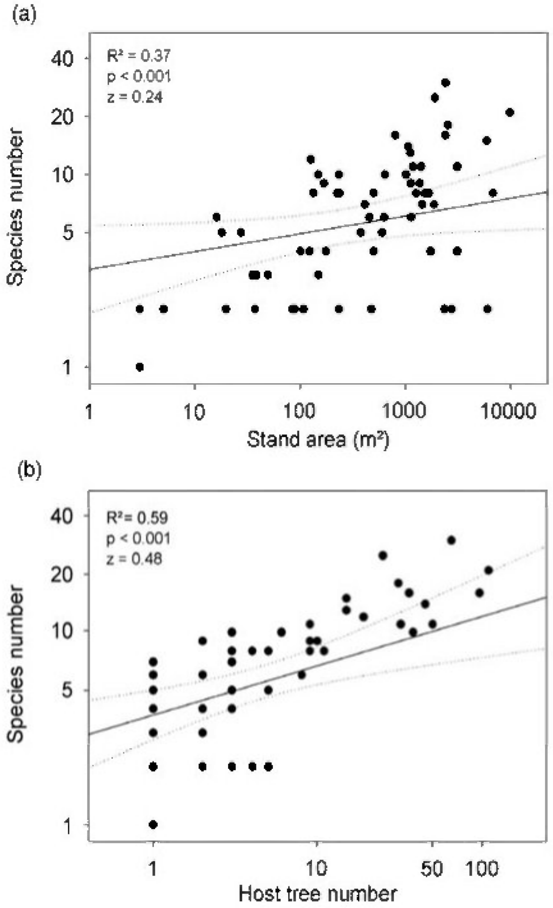

Fig. 2. Relationship between (**a**) epiphyte species richness (S) and *Annona glabra* stand area (A) and (**b**) epiphyte species richness and host tree number in *Annona glabra* stands. Dotted lines represent 95% confidence intervals of the linear regression, the solid lines are: $\ln S = C + z \ln A$.

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

The size of the area of an *Annona glabra* stand explained about one third of the variation in species richness among stands (Fig. 2a, $R^2 = 0.37$). However, the explanatory power when relating species richness to host tree number was slightly higher (Fig. 2b, $R^2 = 0.59$). We observed a strong positive relationship between a species' regional occurrence in patches, i.e. number of trees occupied by a species, and its average local abundance in a patch, i.e. number of individuals in a tree (Fig. 3, linear regression). Separate analyses of wind- and animal-dispersed species yielded no significant differences in slope or y-intercept, but the correlation was significantly tighter in wind-dispersed taxa ($R^2 = 0.97$) compared to animal-dispersed species ($R^2 = 0.89$; $p = 0.02$).

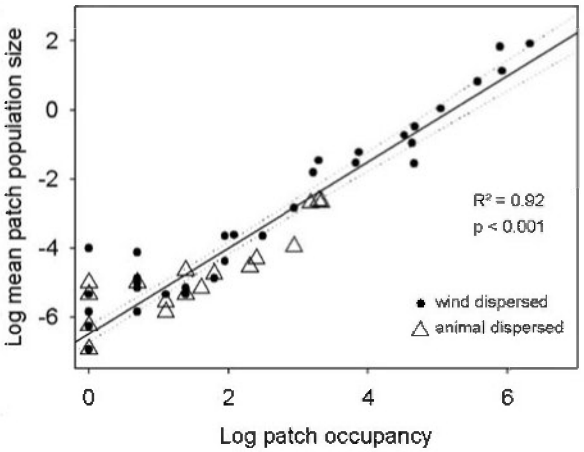

Fig. 3. Relationship between the regional occurrence and the local abundance of species. The natural logarithm of mean local patch population size is plotted against the natural logarithm of number of occupied *Annona glabra* patches. Dotted lines represent the 95% confidence interval of the linear regression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

The frequency distribution of the species in all tree stands in 2002 was unimodal, with 53 species occurring in 10% or fewer of all occupied *Annona* trees (= patches; Fig. 4a). However, after epiphyte colonization of patches reaches an equilibrium a bimodal frequency distribution is expected. This pattern could indeed be observed in those stands in which epiphytes showed the highest occurrence in terms of patch occupation and abundance (> 90% of patches in a stand occupied and mean individual number per tree ≥ 44, Fig. 4b). These stands likely represent a late stage of epiphyte colonization.

Evidence for a metapopulation structure

The following analyses are based on the subset of 725 paired trees (see Material and Methods section).

Patch dynamics

In the 1994 census, 400 trees (55%) hosted epiphytes. Until 2002, 25 trees (3.4%) died, six of which had epiphytes. These trees submerged in the lake and epiphyte populations invariably went extinct. During the 8-year census interval, 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 the six fallen trees) of the initial 400 occupied trees lost all their epiphytes.

The initial species composition remained unchanged in 77 *Annona glabra* trees (10.6%), while 219 trees

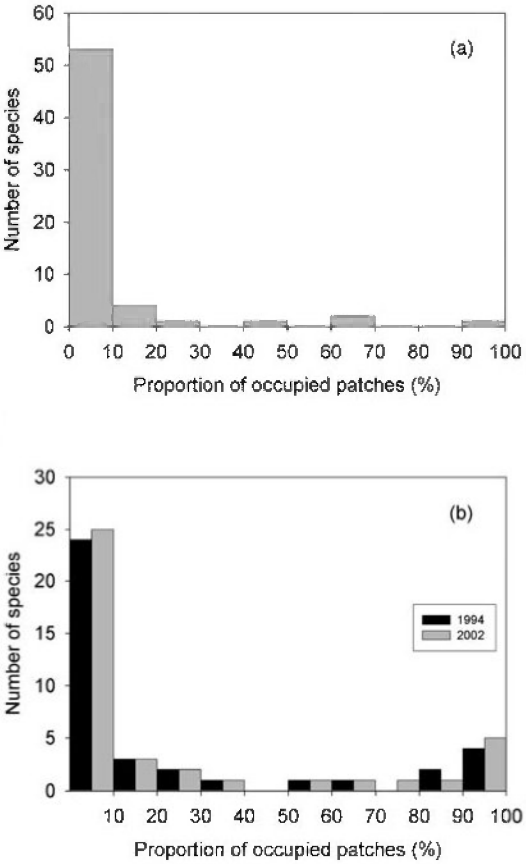

Fig. 4. Frequency distributions of epiphyte species' distributions in (**a**) all *Annona glabra* patches in 2002 where distribution is strongly unimodal ($P_{0\text{-}10\%}$ <0.01; $P_{90\text{-}100\%}$ = 0.99), and (**b**) stands, in both census years, where >90% of the trees were abundantly occupied by epiphytes in 2002. Here, the distribution is bimodal in the 2002 census ($P_{0\text{-}10\%}$ < 0.01; $P_{90\text{-}100\%}$=0.21). We used Tokeshi's (1992) test for bimodality where $P_{0\text{-}10\%}$ < 0.25 and $P_{90\text{-}100\%}$ < 0.25 suggests a bimodal distribution (see Material and Methods section for detailed information).

(30.2%) were hosting the initial set plus newly colonized species. Epiphyte species were lost in 425 trees (58.6%). Of these, less than half (175 trees) experienced a net loss of species (1.7 ± 1.1 species, mean ± SD), while 250 trees more than compensated losses by new colonizations. The average number of additional species was 1.9 ± 1.5 species.

Colonization

Zotz et al. (1999) concluded from comparison of differently colonized trees that the four most common epiphyte species were also the first to colonize empty *Annona glabra* trees. By direct observation we can now confirm their conclusion (Table 2). After eight years a total of 20 species had 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. Our null models which assumed colonization success to be merely a function of initial abundance identified both good and poor colonizers (Table 3). Species colonizing empty patches with more individuals than expected were abundant taxa like *Caularthron bilamellatum* and *Niphidium crassifolium* but also less abundant *Polystachia foliosa* or *Catasetum viridiflavum*. Surprisingly, lower than expected colonization success was found in two abundant species, i.e. *Dimerandra emarginata* and *Werauhia sanguinolenta*.

Table 2. Colonizing epiphyte species between 1994 an 2002. A total of 103 trees out of 306 originally empty *Annona* trees were colonized.

Species	Family	Colonized trees	Individuals / 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

Although quite small *Annona glabra* trees are occasionally colonized by epiphytes when reaching a height of 1 m (= crown volume of 0.25 m^2), trees empty in 1994 that were colonized during the census interval differed significantly both in tree height (*h*) and crown volume (*Cv*) from uncolonized conspecifics (h_{col}: 5.8 ± 2.9 m; h_{uncol}: 4.1 ± 1.8 m; Cv_{col}: 5.2 ± 3.7 m^2; Cv_{uncol}: 2.5 ± 2.4 m^2, unpaired *t*-test, p < 0.001, n_{col} = 107, n_{uncol} = 199, means ± SD). Moreover, among newly colonized trees we detected a significant correlation between tree height and the number of colonizing epiphyte species and individuals (Spearman rank correlation, $R_{species}$ = 0.30, p < 0.01; $R_{individuals}$ = 0.40, p < 0.001, n = 107 trees). Crown volume was a similarly good proxy of colonization success (Spearman Rank correlation, $R_{species}$ = 0.28, p < 0.01; $R_{individuals}$ = 0.34, p < 0.001, n = 107 trees).

Table 3. Number of former 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 abundance of a given species on all *Annona glabra* trees. They indicate the lower and upper boundary of random generated tree numbers and number of colonizing individuals, respectively. Bold numbers in the individual column indicate species that colonized trees with a higher number of individuals than expected by random colonization. Underlined numbers indicate species colonizing fewer trees than expected by random colonization and species with a lower number of individuals colonizing these trees than expected by random colonization, respectively. 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 Mast.	*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)

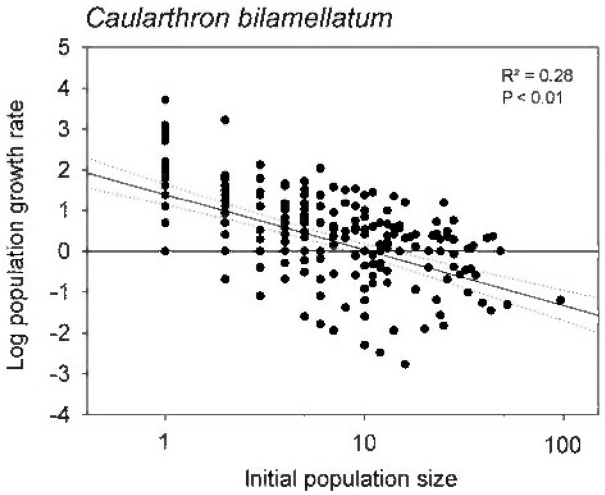

Fig. 5. Population growth rate (calculated as ln N_t/N_{t-1}) of the epiphytic orchid *Caularthron bilamellatum* in discrete patches (*Annona glabra* trees) along the shoreline of Barro Colorado Island. Values above and below zero represent populations with positive and negative growth, respectively. Dotted lines represent the 95% confidence interval.

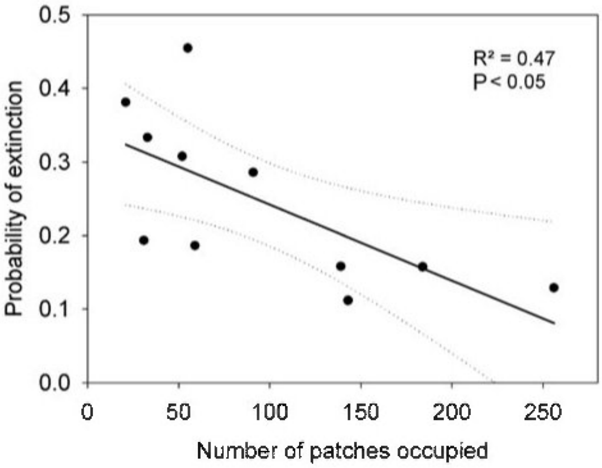

Fig. 6. Relationship between the probability of extinction and distribution of patches of epiphyte species in the host tree *Annona glabra*. Only the 11 species that occurred in more than 20 patches were considered. Data are net extinction rates over the course of eight years. The solid line represents the regression line, the dotted lines represents 95 % confidence intervals.

Local population growth, extinction, and colonization

We examined the local population growth rates of epiphyte species with at least 30 local populations surviving the census interval. All eight species included in this analysis (*Caularthron bilamellatum*, *Dimerandra emarginata*, *Niphidium crassifolium*, *Tillandsia bulbosa*, *Tillandsia fasciculata*, *Tillandsia subulifera*, *Vittaria lineata*, and *Werauhia sanguinolenta*) showed the same density dependent pattern: population growth rates declining with increasing population size as shown in Fig. 5 for *Caularthron bilamellatum*. Initial population size explained 7 - 38% of the variation. The strong scatter in all species (data not shown) suggests asynchrony among patches.

A total of 302 patch populations went extinct during the census interval and 16 (ca. 5%) of these extinctions were caused by stem breakage or tree fall. Excluding the latter populations we tested if there was an effect of initial population size on future extinction probability. We performed a Mann-Whitney *U*-test for differences in mean population size in the 1994 census between populations on patches that went extinct until 2002 vs. those that did not. Again, the test was limited to those species occupying more than 30 patches in 1994. In four of the nine tested epiphyte species (*Caularthron bilamellatum, Tillandsia bulbosa, Niphidium crassifolium,* and *Werauhia sanguinolenta*) the persisting populations were initially significantly larger compared to the extinct populations, while persisting and extinct populations of the remaining species were indistinguishable statistically

Table 4. Patch population colonization and extinction events. Given are the number of populations that either colonized new patches (Col) or went extinct on a patch (Ext) during the census interval, and size (number of individuals) of populations that went extinct or persisted (Per) on a patch and respective P-values of a Mann-Whitney U-test for all populations, and separately for small and large populations of a given species. Large and small refer to populations with an individual number of ≤ and > than the median population size in 1994, respectively. Only species occurring in more than 30 patches in 1994 are included. Species are sorted by the total number of patches they inhabited in 1994. Significant results are indicated by asterisks.

		No. of populations		All populations			Small populations			Large populations		
Species	Family	Col	Ext	Ext	Per	P	Ext	Per	P	Ext	Per	P
Caularthron bilamellatum	*Orchidaceae*	120	33	5.8	10.1	0.03*	2.5	3.0	0.26	11.7	17.9	0.03*
Tillandsia bulbosa	*Bromeliaceae*	90	29	7.9	19.9	0.09	2.4	3.7	0.04*	14.9	33.6	0.28
Dimerandra emarginata	*Orchidaceae*	94	16	5.2	9.8	0.02*	2.3	2.7	0.23	10.6	16.7	0.05*
Niphidium crassifolium	*Polypodiaceae*	75	22	6.9	11.4	0.03*	1.5	2.1	0.03*	14.7	18.9	0.27
Werauhia sanguinolenta	*Bromeliaceae*	27	26	4.1	9.4	0.25	2.4	1.9	0.30	6.8	15.4	0.12
Tillandsia fasciculata	*Bromeliaceae*	26	11	13.3	5.5	0.37	1.8	1.6	0.60	27.0	10.3	0.02*
Catasetum viridiflavum	*Orchidaceae*	34	25	2.2	4.9	0.29	1.4	1.1	0.64	4.3	8.7	0.28
Vittaria lineata	*Vittariaceae*	32	16	1.3	7.7	0.01**	1.2	1.7	0.02*	4.0	11.5	-
Tillandsia subulifera	*Bromeliaceae*	30	11	1.2	2	0.12	1.0	1.0	1.00	2.0	3.6	0.04*

(Table 4). We conducted additional tests after dividing populations into two categories: (1) small ($n \leq$ median population size) and (2) large ($n >$ median population size). Invariably, both small and large populations had a measurable probability of extinction (Table 4). Consistent with the results of the first analysis, persistent populations tended to be larger in the majority of all species, although the inverse case was also detected (*Tillandsia fasciculata*, large populations). As expected from the correlation of the size of local populations and patch occupancy (Fig. 3), the probability of local extinction decreased with increasing regional distribution (Fig. 6, $R^2 = 0.47$). No species showed an equilibrium between colonization and extinction events: the former exceeded the latter up to fivefold (Table 4).

Discussion

Increasing individual numbers in most species and continuous colonization of empty trees suggest that the epiphyte vegetation on *Annona glabra* around BCI has not reached a steady state during the ca. 80 years since the first establishment of the host trees. On the other hand, the minor changes in species ranking and the close correlation between population sizes in 1994 and 2002 (Fig. 1) suggest that the composition of the epiphyte community is quite stable in time, despite a substantial increase in individual numbers. Comparisons of the epiphyte vegetation on individual host trees, as well as in the entirety of host trees show that the temporal changes of the epiphyte vegetation on a single tree were low, and the epiphyte vegetation on *Annona glabra* as a whole became more homogeneous. A different pattern was found by Laube & Zotz (2006) in another lowland forest for the epiphyte vegetation on the palm *Socratea exorrhiza*. They showed that the similarity of an epiphyte vegetation on a single tree decreased considerably in time while the vegetation on all studied host trees in the area became more similar.

The species-area relationship for epiphytes on *Annona glabra* stands was better explained by host tree number than stand area. In contrast, at 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-value (Fig. 2) is within the range of values reported by many studies of habitat islands (Begon et al. 1999).

Comparing the four conditions outlined by Hanski & Gilpin (1997) with the observed properties of the epiphyte vegetation in *Annona glabra* suggest that species dynamics are indeed 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 shoreline 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 many species. In all other cases we invariably found measurable probabilities of extinction even in large populations (Table 3). 3. Habitat patches must not be too isolated to prevent recolonization. Although two censuses do not allow the direct documentation of recolonization events, it seems highly plausible that at least a certain proportion of the 103 trees that were empty in 1994 and colonized in 2004 hosted epiphytes at some time before the initial census. A similar argument applies for the additional epiphyte species found on epiphyte-bearing trees in 2002 but not in 1994. 4. Local populations do not have completely synchronous dynamics. Our data on the population growth in all analysed epiphyte species (Fig. 5) suggest that patch dynamics were indeed asynchronous. During the census interval we found patch population extinction, increases and decreases in local populations and the establishment of new ones.

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 flaking) constitutes the major cause of death in epiphytes on *Annona glabra*. Support for this notion comes from detailed demographic studies (Zotz et al. 2005). For example, a study on *Werauhia sanguinolenta* conducted on *Annona glabra* trees close to the study area over the course of eight years revealed that most losses occurred due to substrate instability (Zotz et al. 2005). This finding is at odds with the results of studies with epiphytic mosses, which showed that extinction of a local population was exclusively driven by patch dynamics (Snäll et al. 2003, 2005a).

A positive relationship between local abundance and regional distribution (Fig. 3) lends additional support to a metapopulation structure in the studied epiphyte system, and has been found in many other metapopulation studies (Addicott 1978; Hanski 1982; Gotelli 1991). However, the observation that locally abundant species are also widespread, whereas the opposite is true for locally scarce ones is not sufficient to demonstrate the presence of a metapopulation.

Hanski et al. (1993) discuss two alternative explanations. First, differences in ecological specialization: species able to exploit a wide range of resources will be both widespread and locally abundant, more specialized species will find a smaller range of resources and become less widespread and locally less abundant. Second, the positive relationship between distribution and abundance may simply be a sampling artefact. Locally rare species are more difficult to detect than are locally abundant species and therefore the number of sites a rare species occupies will be underestimated. While we cannot completely discard these alternative explanations, it seems unlikely that ecological specialisation or sampling effect cause the given pattern in the present case. The species occurring on *Annona* are a non-random sample of ecologically equivalent species out of the regional species pool, e.g. species depending on shaded conditions like filmy ferns are not present at all (Zotz et al. 1999). Second, given the accessibility of the host tree and the intensity of the census, few if any rarer epiphytes will have been overlooked. Consequently, we interpret the observed occupancy frequency distributions as an indicator of the occurrence of metapopulation structure.

As a consequence of the positive occupancy frequency relationship, the probability of a local population to go extinct decreases with increasing distribution (MacArthur & 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. 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 rightmost frequency class occur either in all or most sites suitable for the species and are designated as 'core species' while species in the leftmost 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. 4a) with species mainly occurring in the leftmost frequency class. Such a unimodal pattern may be explained by a non-equilibrium metapopulation status of the epiphyte species on *Annona glabra*: new colonizations of available empty patches exceed extinction events (Table 4) which is caused by the ongoing colonization of habitat patches by epiphytes due to their, in epiphyte terms, quite recent establishment of less than 80 years. Another study by Laube & Zotz (2006) already showed that a time span of this magnitude does not allow epiphytes to colonize a patch completely. In that study the average available time for epiphytes to colonize a palm tree before it died was 60 years, which turned out to be too short to colonize a patch completely given the slow growth of epiphytes (Schmidt & Zotz 2002).

We hypothesize that after the colonization of patches has reached an equilibrium epiphyte species identified as good colonizers, e.g. *Caularthron bilamellatum* and *Tillandsia bulbosa* (Table 2), may eventually occupy a large proportion (> 90%) of all suitable patches, while poor colonizers will have established in very few patches (< 10%) and the characteristic bimodal frequency distribution can be detected. The validity of this assumption is suggested by the occupancy frequency pattern in heavily occupied stands (Fig. 4b), where almost all *Annona glabra* trees are already occupied by high numbers of epiphyte individuals. Here, a bimodal distribution of epiphyte species was detected in 2002.

Our results suggest that the metapopulation concept can be applied to vascular epiphyte populations of diverse taxonomic affiliation, such as *Orchidaceae*, *Bromeliaceae* and *Polypodiaceae*. Together with previous findings that suggest the presence of metapopulations in non-vascular epiphytes (Löbel et al. 2006) and a single epiphytic orchid (Tremblay et al. 2006) one may conclude that epiphytes in general have a metapopulation structure. However, this assumption needs more rigorous scrutiny 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 local populations.

Species richness and abundance are often found to be positively related to the size of trees (Yeaton & Gladstone 1982; Zotz & Vollrath 2003; Flores-Palacios & García-Franco 2006), and this is, although weakly, also the case in our host tree species (Zotz et al. 1999). This pattern is usually explained by two factors: (1) larger trees are usually older and were therefore available for colonization for a longer period of time, and (2) larger trees provide more surface area and a greater variety of microhabitats to be colonized by epiphytes. One-census studies cannot distinguish between both factors. Our study now directly documents a size effect. After eight years newly colonized trees differed significantly in respect to height and crown volume from unoccupied conspecifics. Moreover, among colonized trees larger individuals were colonized more often by epiphytes. Thus, tree size as such can explain variation in epiphyte species richness and abundance to some extent. However, larger trees are certainly also different qualitatively, since tree growth is accompanied by changes in, e.g. bark structure, greater structural complexity of the tree crown, creation of dead wood.

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

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