RESEARCH ARTICLE

Long-term community dynamics in vascular epiphytes on Annona glabra along the shoreline of Barro Colorado Island, Panama

Helena J. R. Einzmann1 | Letizia Weichgrebe1 | Gerhard Zotz1,2

1Carl von Ossietzky Universität Oldenburg, Institut für Biologie und Umweltwissenschaften, AG Funktionelle Ökologie der Pflanzen, Oldenburg, Germany
2Smithsonian Tropical Research Institute, Panamá, República de Panamá

Correspondence
Helena J. R. Einzmann
Email: helena.einzmann@uol.de

Funding information
Smithsonian Tropical Research Institute

Handling Editor: María Umaña

Abstract

1. Despite the ecological importance of vascular epiphytes in the tropics, even basic information on the processes that form epiphyte communities is scarce. This is partially due to an almost complete lack of long-term studies.

2. Here, we present data that were collected in three consecutive censuses over 21 years in a monospecific host tree system that is about 100 years old and interpret them in an empirical and a metapopulation/metacommunity framework.

3. We documented an ongoing increase in abundance and diversity at the level of the entire system (metacommunity) and at the level of communities (all epiphytes growing on individual Annona glabra tree stands). This was also reflected at the population level; >2/3 of the species showed positive population growth rates. Similarly, colonisation of empty Annona trees was still ongoing, with the most abundant species being also the first to colonise empty trees. The community composition of colonised trees became more similar with time. In all three censuses, habitat size of epiphytes explained much of the variation in species richness among stands (groups of trees with individual trees within 25 m of each other) and overall abundant species tended to be more abundant at the stand scale. The species frequency distribution was unimodal, regardless of whether considering all stands or only stands with very large epiphyte communities, indicating that the metacommunity still has not reached an equilibrium phase. Similarly consistent in both census intervals, population growth rates decreased with increasing population size with substantial asynchrony among populations.

4. Synthesis. In contrast to a typical herbaceous plant community, this epiphyte metacommunity is still expanding after one century of development. Our study shows that previously reported short-term patterns of epiphyte community dynamics hold true in the long term. It remains to be shown, however, whether results from this monospecific host tree system are really representative for epiphyte community dynamics in more diverse tropical forests.

KEYWORDS
epiphyte census, long-term study, metacommunity, population growth, tropical lowlands
INTRODUCTION

Tropical forests host the highest terrestrial plant diversity (Gentry, 1988a, 1988b; Gentry & Dodson, 1987). A substantial part of this diversity is made up by epiphytes: they can account for up to 50% of a local vascular flora (Kelly et al., 1994). Epiphytes as a life-form are found in a wide variety of plant families and make up almost 10% of all vascular plant species globally (Zotz, 2013b). They provide a variety of ecological services to the system, for example, water and nutrient retention and habitat to other organisms (Bruijnzeel et al., 2011; Chang et al., 2002; Jarvis, 2000; Mulligan et al., 2011; Stanton et al., 2014). Despite the prominent role that epiphytes play in tropical forest systems, we still know very little about the determinants of epiphyte diversity and community composition and dynamics (Kitching, 2006).

This lack of theory on epiphyte community assembly contrasts strongly with the scientific attention given to trees. Numerous studies have focused on the patterns and processes of tropical tree communities (e.g. Baldeck et al., 2013; Condit et al., 1995; Feeley et al., 2011; Forrister et al., 2019; Volkov et al., 2003), which has led to the current thorough understanding of tropical tree ecology with a strong theoretical and empirical basis. Arguably, the establishment of long-term study sites in the ForestGEO network (formerly CTFS, first study site established in 1980 on Barro Colorado Island) has played a pivotal role in this development.

The lack of theory in epiphyte research is slowly filled. There are several recent developments regarding epiphyte theory (Blick & Burns, 2009; Burns & Zotz, 2010; Mendieta-Leiva & Zotz, 2015; Spruch et al., 2019; Taylor & Burns, 2015) but long-term data for epiphyte communities are still rare. To our knowledge, there are only four studies that directly followed the development of epiphyte communities over time spans longer than the typical project length of 3 years (Einzmann & Zotz, 2017; Laube & Zotz, 2006a, 2007; Schmit-Neuergur, 2002). These studies revealed a common pattern, that is, increasing abundance over time. In three natural systems the increases ranged from 30% over 5 years (Laube & Zotz, 2006a) to a 60% increase of epiphyte abundance over 4 and 8 years (Laube & Zotz, 2007; Schmit-Neuergur, 2002). Such remarkable increases were not restricted to these natural systems: over just 7 years, Einzmann and Zotz (2017) documented a 300% increase in abundance of epiphytes growing on pasture trees in western Panama. There are also a few manipulative studies over longer time periods (Acuña-Tarazona et al., 2015; Nadkarni, 2000; Toledo Aceves et al., 2012), but comparability with our system is limited due to differences in (a) forest type (lowland forests vs. cloud forests), (b) sample size (complete inventories on hundreds of trees vs. bark sections on only three to 10 trees), (c) duration (21 years vs. 5–10 years) and (d) research scope (complete large- and small-scale community dynamics vs. small-scale recolonisation dynamics on stripped trunk and branch portions).

Epiphytes, mostly herbaceous perennials, differ from trees in many ways and hence, the wealth of knowledge on trees is hardly applicable to these mechanically dependent plants (Mendieta-Leiva & Zotz, 2015). For example, in contrast to tree communities, there seems to be little competition for space between epiphytes in lowland forests, although this topic still lacks quantitative investigation (Zotz & Hietz, 2001), and their substrate is constantly growing (Flores-Palacios & García-Franco, 2006; Spruch et al., 2019). Similarly, the well-documented importance of herbivore and pathogen pressure on the community structure of trees (e.g. Bagchi et al., 2014; Janzen, 1970) seems to have no equivalent in epiphytes, although here again more data are needed (but see Palacios-Mosquera et al., 2019; Winkler et al., 2005; Zotz et al., 2005). Yet, some aspects of the biology of epiphytes show surprising resemblance to their long-lived hosts, more than to terrestrial herbs. Applying Silvertown et al.’s (1993) approach of comparative plant demography to analyse the relative contributions of different life-history components (fecundity, survival, growth) suggests that population growth rates are almost exclusively driven by survival, both in trees and epiphytes (Zotz, 2016).

Various authors pointed out that for an epiphyte, trees represent potentially inhabitable ‘islands’, as only trees, but not the ground, offer adequate and safe sites for germination, establishment and growth (e.g. Einzmann & Zotz, 2017; Laube & Zotz, 2007; Matelson et al., 1993; Patiño et al., 2018; Taylor & Burns, 2015). Such an island biogeographical approach has also been successfully applied to other arboreal organisms, for example, arthropods (Adams et al., 2017; Southwood & Kennedy, 1983). Epiphytes hardly build up seed banks (at least in tropical lowland forests; Benzing, 1990; Cota-Sánchez & Abreu, 2007; Mondragón et al., 2015), which makes it easy to determine if a population has gone extinct at a given location. This represents a major difference between epiphytes and most terrestrial herbs, for which the use of metapopulation theory to explain regional dynamics is more problematic (Freckleton & Watkinson, 2002). Epiphytes do not pose this problem because their habitat unit can be easily identified and delimited from unsuitable habitat, and extinction of a population can be assessed without reasonable doubt. Thus, metapopulation and metacommunity theory have been applied successfully to analyse the dynamics of epiphyte populations (e.g. Johansson et al., 2012; Laube & Zotz, 2007; Snäll et al., 2003) and communities (e.g. Burns, 2007; Einzmann & Zotz, 2017; Löbel & Rydin, 2009).

One of the four long-term studies mentioned above, on the epiphyte community on Annona glabra (for simplicity referred to by genus name in the following) at the shore of Barro Colorado Island (BCI), Panama, included data on more than 1,000 trees and covered two censuses spanning a period of 8 years (Laube & Zotz, 2007). The documented patterns in this epiphyte community could be explained by metacommunity processes. All four conditions for a viable metacommunity given by Hanski and Gilpin (1997) were met: (a) suitable habitat occurred in discrete stands (i.e. Annona trees isolated from other individuals and groups); (b) even the largest populations had a substantial risk of extinction; (c) habitat patches (i.e. stands) were not too isolated to prevent recolonisation; and (d) local populations showed partly asynchronous dynamics (Laube & Zotz, 2007). Laube and Zotz (2007) also showed a positive...
relationship between local abundance and regional distribution of species, together with a decreasing probability for a local population to go extinct with increasing distribution of a species. The influence of stand occupancy on the probability of extinction will drive a metapopulation in equilibrium towards either extinction or complete occupancy. Hanski (1982) and Gotelli (1991) stated that species that share a habitat will show a bimodal distribution of stand occupancy, that is, a species occurs either in most stands or only in very few stands. However, this bimodal pattern was not detected in the Annona system at large, only for a small subset of trees (Laube & Zotz, 2007). An important aspect of this particular system is the fact that the host trees did not establish before 1914, because their current habitat formed with the flooding of Lake Gatún during the construction of the Panama Canal. Thus, we know that colonisation went on for a maximum period of 100 years. A bimodal pattern would indicate that the metapopulation of the region has reached an equilibrium phase.

The current study followed up on the previous work by repeating the census 21 years after the initial one, thus documenting the development of this community over at least a fifth of its time of existence. This unique dataset allows us for the first time to directly document the long-term dynamics of a diverse epiphyte community in the tropical lowlands on one host tree species along the shoreline of BCI, Panama. It allows us to test how consistent changes are over time, which, none of the previous studies with just one repetition was able to achieve. We repeated many of the analyses of Laube and Zotz (2007) to test whether the patterns observed in the first census interval were found to be consistent over the longer term. This kind of information is not available for epiphytes in this or any other system, although such long-term studies are ‘invaluable’ (Herben, 1996) by creating and constraining testable hypotheses and by checking model predictions. Our expectations regarding the results were based on two concepts: modelling and empirical studies, and metapopulation theory. Based on modelling studies (Spruch et al., 2019) and the results of the four empirical studies that covered between 5 and 8 years, we formulated the following expectations. (a) The increase in abundance and diversity of epiphytes at the level of the entire system, but also at the level of small groups of Annona trees (stands), continues. (b) Due to newly recruited yet previously not colonised trees and/or extinction events, there are always a certain number of empty sites, that is, trees. (c) The community composition of colonised trees becomes more similar with time because the regional species pool of epiphytes is limited and with time, more species from that pool will be shared between the trees. (d) At the level of host tree stands, habitat size affects epiphyte species diversity, as larger habitats usually also provide a larger variety of habitat niches and have existed for longer time, increasing the chance of colonisation. (e) Abundant species are more likely to colonise empty sites. Metapopulation theory predicts species’ frequency distribution to be bimodal when colonisation and extinction rates are a function of regional occurrence (Gotelli, 1991; Hanski, 1982; Laube & Zotz, 2007).

2 | MATERIALS AND METHODS

The study was conducted on BCI (9°10’N, 79°51’W), located in Lake Gatún that was formed in 1914 with the construction of the Panama Canal in the Republic of Panama. The area is dominated by semi-deciduous lowland forest that receives, on average, 2,600 mm annual precipitation with a pronounced dry season of 4 months (Windsor, 1990). The study system encompasses the epiphyte communities growing on the marsh tree Annona glabra (Annonaceae) that grows along the shoreline of BCI. The species is of rather small stature, often multi-stemmed and usually does not exceed 6 m in height (Croat, 1978), which makes epiphytes on Annona easily accessible from the lake (Appendix S1). Despite their small stature, Annona trees offer a habitat similar to the upper canopy of the adjacent forest regarding air temperature and relative humidity (Zotz et al., 1999). The present study is based on three censuses conducted over 21 years in 1994, 2002 and 2015.

2.1 | Epiphyte censuses

All three censuses followed the same protocol. For a detailed description of the selection of the study area, see Zotz et al. (1999). In short, the shoreline of BCI was divided into sectors of 3° each and all epiphytes growing on Annona trees were counted in every other sector (Figure 1). Individuals were identified to species level, and hemiepiphytes (sensu Zotz, 2013a) were also included. Species names follow The Plant List (2013). In some cases, it was impossible to tell if an ‘epiphyte stand’ consists of one or several individuals. Such stands were counted as one individual, following Sanford (1968). Epiphytes were counted when they were >20% of the maximum size of a given species. Smaller individuals were only recorded as present but excluded from quantitative analysis. For each tree, the number of stems was recorded in each census. In 2015, GPS data were recorded for each censused tree. The censuses were conducted over several months each, spanning parts of both the dry and wet season in each respective year.

In 1994, almost 1,200 trees were included in the census (Figure 2). In 2002, the number of trees decreased to 1,041, and 982 were found in 2015. Over the last 20 years, there seems to be no recruitment of Annona trees (G. Zotz, pers. obs.). Although all trees had been mapped and tagged in previous censuses, the unambiguous identification of tree individuals was not always possible. A direct comparison of epiphytes on individual trees was done only for trees that could be matched without doubt for all three censuses. This was the case for 571 trees.

2.2 | Host trees and host tree stands

Laube and Zotz (2007) defined both individual trees and ‘tree stands’ as spatial habitat units of epiphyte populations. A host tree is a natural habitat unit in epiphyte studies (Mendieta-Leiva &
FIGURE 1 Map of Barro Colorado Island (BCI) showing the GPS locations of trees (red open circles) studied in 2015. Note that in places with substantial overlap individual circles are undistinguishable. Inset zooms into a small section, illustrating the difference between a stand of Annona trees and individual Annona trees that are >25 m away from their next conspecific. Also given are graphic definitions of the terms 'epiphyte community' and 'epiphyte population' (closed symbols = epiphytes): these can either be on an individual Annona (red circle) or in an Annona stand (black circle). All epiphytes on all included Annona trees are defined as 'epiphyte metacommunity' and all individuals of a species represent its 'metapopulation'.

FIGURE 2 Net losses and gains of epiphyte individuals and species from the original set of trees over the two census intervals. White arrows indicate net gain resulting from additions and losses, black arrows indicate documented losses, patterned arrows indicate additions from outside the monitored trees and the grey arrow indicates the species that were found in all three censuses. In the second census interval, three of the 11 new species had been found in 1994 but not in 2002. Round-edged boxes indicate the number of trees censused (in the grey area) and lost (in the white area) up to the respective years.
Zotz, 2015). Although most epiphytes are anemochorous and release their diaspores from high above the ground, which makes long-distance dispersal much more likely than in small terrestrial herbs (Tackenberg, 2003), most seedlings establish close to their mother plant (Mondragón & Calvo-Irabien, 2006; Paggi et al., 2010; Trapnell & Hamrick, 2004). Since epiphytes may as easily disperse into a tree in close proximity as to the other side of the crown of the same tree, a group of neighbouring trees is also a meaningful spatial unit. With GPS data of the Annona trees taken in 2015, we defined a group of trees as a stand, when individual trees were within 25 m of each other. Excluding rare long-distance dispersal events, this distance approximately doubles the documented maximum distance epiphyte seeds are commonly dispersed to (Bernal et al., 2005; Mondragón & Calvo-Irabien, 2006; Paggi et al., 2010; Trapnell & Hamrick, 2004), which makes sure that habitat units are largely independent of each other. This distance was also chosen to create groups as similar as possible to the analysis conducted by Laube and Zotz (2007). Solitary trees, with no neighbouring Annona tree within 25 m, were included as independent entities (Figure 1, cp. to Laube & Zotz, 2007). This yielded 112 tree stands for the 2015 data and 93 and 97 tree stands for the 2002 and 1994 data respectively. The divergence in number of tree stands from the previous study is due to the definition of stands using GPS data instead of hand-drawn maps. More than 40% of these stands consisted of single trees (49 in 2015, 37 in 2002 and 43 in 1994). Stand area was estimated as the sum of the number of stems in a stand (and as projected crown cover and number of hosts, Appendix S2). Stands were used as spatial units of epiphyte populations for the analyses of species–area- and distribution–abundance relationship and frequency distributions.

### 2.3 | Synopsis of terminology

For reasons of clarity, we define the following terms used in this paper (see also Figure 1): the ‘epiphyte metacommunity’ is the sum of all epiphytes found in the entire study system around BCI, the term ‘community’ refers to all epiphytes on an individual tree (or several trees growing in close vicinity, i.e. a ‘stand’). Analogously, we define the sum of all individuals of a species in the entire study system as a ‘metapopulation’, while a ‘population’ represents all conspecifics on an individual tree (or in a ‘stand’). ‘Local abundance’ refers to the abundance of individuals on an individual tree, whereas ‘regional abundance’ refers to the abundance of individuals on all studied trees.

### 2.4 | Data analysis

Analyses were conducted with R 4.0.0 (R Core Team, 2020) and the package tidyverse version 1.2.1 (Wickham, 2017). Means ± SD are given throughout the paper. Confidence intervals (CI) plotted with linear regressions are at the 95% interval throughout the paper.

#### 2.4.1 | Species composition

Changes in the metacommunity were analysed by allocation of ranks, as well as, a regression analysis of species abundances of consecutive censuses (cp. Condit et al., 1992). Without change in abundance in any of the overlapping species, the numbers will form a line with slope 1 in a logarithmic regression. Species with increased abundance will plot above and species with decreased abundance below this line. In the analysis of these data, a low coefficient of determination, $R^2$, indicates a larger change in the community assemblage. This analysis was conducted with the 571 unambiguously matched trees. We determined if the relationships were allometric by extracting the slope estimate from the regression analyses with the ordinary least squares (OLS) method (r package lmodel2 version 1.7-3, Legendre, 2018).

To test if the epiphyte species composition on individual trees became more similar over time, we calculated the Chao-Sørensen dissimilarity index, which is based on estimated abundance values (cp. Chao et al., 2005). This was done with trees that hosted at least one epiphyte and could be matched in all three censuses (292 trees). We used the implemented function ‘dis.chao’ in the r package ComMEcol (Melo, 2017) with emphasis on rare species. Calculated as dissimilarity index it varies between 0 and 1, with 0 for species communities without change and 1 for completely different communities.

#### 2.4.2 | Species–area- and distribution–abundance relationship

To study the effect of habitat size on species richness, we used linear regression models, using the number of stems in an Annona stand to predict species richness. We used the log-transformed form of the power function model:

$$ \log(S) = \log(c) + z \log(A), $$

where $S$ is species number, $c$ and $z$ are constants and $A$ is the number of stems contributing to the stand. The number of stems was chosen because we did not have data on the projected crown cover of the individual trees for each census. To test if the correlation coefficient increased from census to census, we used a Fisher’s r-to-z comparison (r package psych version 1.9.12, Revelle, 2019), and to test if slopes differed between censuses, we used version 2.30-0 of the r package lme4 (Lenth, 2016).

We tested if local abundance can be predicted from regional abundance by plotting the local population size (the number of individuals of a species in a stand) against the regional occurrence (the number of occupied stands per species).

#### 2.4.3 | Colonisation

To analyse the colonisation ability of epiphyte species in the Annona system, we created null models and compared the results
to the documented colonisations. Null models assumed that the probability to colonise a tree was simply a function of a species’ initial abundance (cp. Laube & Zotz, 2007). We conducted these analyses for the subset of 571 host trees for both census intervals. To create the null models, (a) the number of epiphyte individuals that colonised formerly empty hosts between time points \((t) 1\) and 2 \((E_{\text{col}})\), and (b) the number of newly colonised hosts at \(t = 2 (H_{\text{col}})\) were calculated. For the first null model, one randomly chooses \(E_{\text{col}}\) from the list of species in the metacommunity at \(t1\), without replacement. This was repeated 5,000 times and the sum of individuals drawn from the list calculated for each species. Discarding the 2.5% highest and lowest values for each species yielded 95% confidence intervals. The expected ranges were then compared to the actual number of individuals that had colonised empty trees at \(t2\). For the second null model, one, again, chooses \(E_{\text{col}}\) from the list of individuals at \(t1\) and groups them in \(H_{\text{col}}\) repeats the process 5,000 times and obtains confidence intervals as described.

2.4.4 | Frequency distributions

Laube and Zotz (2007) found the epiphyte community in the Annona system at large to be in a non-equilibrium state, that is, new colonisations of empty trees exceeded extinctions. In contrast, epiphyte communities of stands in which most trees hosted epiphytes and the average number of epiphyte individuals was within the upper quartile of the number of individuals hosted in all stands did show a bimodal pattern, hinting at an equilibrium phase. They tested the frequency distributions at stand level for bimodality with Tokeshi’s test (Tokeshi, 1992). We applied this test to all three censuses. For the test, all species are grouped into frequency intervals according to their abundance from rare to abundant into 10 groups. The null hypothesis underlying the test is a random distribution of species among the frequency intervals. Consequently, bimodality is judged based on the probability of obtaining the observed number of species at the two extremes of the distribution, where \(p_{\text{10}}\) represents the group of rarest species and \(p_{\text{90–100}}\) the group with the most common species. If the probability to obtain the observed number of species in both extreme groups is \(<0.25\), the frequency distribution is seen as bimodal. If both extreme groups are \(<0.05\), the pattern is strongly bimodal. If either of the extreme groups is \(<0.05\) and the other \(>0.25\), the frequency distribution is unimodal. In a first step, we analysed the frequency distribution of the epiphyte species in all Annona stands for each of the three censuses. This first step would illustrate the current state of the metacommunity. A bimodal frequency distribution is expected in a saturated system. Assuming that communities with high abundances are close to saturation, we then selected only those stands in the 2002 and 2015 dataset in which (a) \(>90\)% of all trees were occupied by epiphytes, and (b) the trees hosted at least as many epiphyte individuals as corresponding to the upper quartile of the number of individuals hosted in all stands. This yielded 10 and 18 stands for 2002 and 2015 respectively. We then compared the frequency distributions of these stands with those of the respective stands of the preceding census.

2.4.5 | Population growth and extinction

We expected an increase in abundance in the majority of species, leading to an expanding metacommunity with relatively few new species immigrating from the regional species pool. Therefore, we calculated metapopulation growth rates for the species registered on all host trees that were found in each census:

\[
\lambda = \frac{\ln(N_{t2}) - \ln(N_{t1})}{\Delta t} \times 100, \tag{2}
\]

where \(N\) is the epiphyte abundance in the first \((t1)\) and second \((t2)\) census and \(\Delta t\) is the number of years between censuses.

For populations growing on individual Annona trees, we determined the effect of initial population size on population growth (population growth rate calculated with Equation 2, where \(N\) is the epiphyte abundance on a single tree). We used a linear regression with population growth rate as dependent variable and the logarithm of the initial population size as independent variable. Only epiphyte species with at least 30 populations were considered. With the same dataset, we tested for each species if there was a significant difference in initial population size between the group of populations that were lost and those that survived between censuses.

3 | RESULTS

3.1 | Community dynamics

The percentage of inhabited trees increased over time. Among the 571 trees followed over three censuses, 59% (336) hosted at least one epiphyte in 1994. In the second census, the proportion of occupied trees had increased to 71% (404), and in the third census almost four fifths (79%, 450) of the trees hosted at least one epiphyte. Quite remarkable, this increase is compatible with the notion of a linear colonisation pattern (% colonised trees = 0.920 year - 1774, \(R^2 = 0.94\)) that would have started in the year 1928 and would approach 100% in 2037.

The initial species composition remained unchanged in 11% of the trees after the first interval (65 trees), while only 6% remained unchanged in the second interval (33 trees). While about 21% of the trees (119 trees) hosted their initial species composition plus additional species in the first interval, this percentage increased to almost a third in the second (29%/166 trees). In the first interval, 92 (16%) formerly empty trees were colonised by epiphytes and 24...
(4%) formerly inhabited trees lost all epiphytes. A similar degree of change was observed in the second interval, when 79 (14%) formerly empty trees were colonised, and 33 (6%) formerly inhabited trees lost all epiphytes. Half of the trees (12) that lost all their epiphytes during the first census interval were subsequently recolonised during the second. From 1994 to 2002, a quarter of the trees (152 trees) lost epiphyte species, which changed to more than a third of all trees (205 trees) in the second interval. The percentage of trees in which new arrivals overcompensated species losses was identical in both intervals (13%).

3.2 | Species composition

Of the original 1,188 trees, only 1,041 were found again in the second and 982 in the third census. Despite a reduced number of host trees, the epiphyte abundance in the metacommunity increased substantially (Figure 2). A similar increase was observed in the number of epiphyte species, which increased from 58 in 1994 to 69 and 72 in the second and third census respectively. This net increase reflected both immigration from the regional species pool and local extinctions. A total of 45 species was found in all three censuses.

Without labelling individual plants, it is unclear how many individual epiphytes were lost and how many colonised the studied trees. The net increase in abundance was larger in the first census interval, with almost 9,000 individuals in 8 years, compared to 7,000 individuals in 13 years during the second interval. The number of epiphytes per tree (including empty trees) increased from 12.6 in 1994 to 22.7 in 2002 and 31.3 in 2015 (for SDs and numbers for the 571 unambiguously matched trees see Appendix S3). The four species with more than 1,000 individuals in the first census contributed >85% to the increase in individuals from 1994 to 2002 but only c. 31% to the increase from 2002 to 2015. This drop was mainly caused by Dimerandra emarginata and Tillandsia bulbosa. The average population size of Dimerandra emarginata strongly decreased in the second interval, while population sizes of Tillandsia bulbosa increased, albeit very little.

We used two approaches to analyse changes in the overall species composition. First, we assigned ranks to all species according to their abundance. The ranks of the 10 most abundant species changed in only two positions from the first to the second census (Appendix S4). In the second interval, more positional changes among the first 10 ranks occurred, but only one of the species formerly ranked among the first 10 was replaced.

In the second approach, we correlated species abundances of consecutive censuses against each other for the epiphytes growing on the 571 unambiguously matched trees. The coefficients of determination were high ($R^2 = 0.84$ and $R^2 = 0.88$, $p < 0.001$, Figure 3), which is expected given the relatively similar species composition over time (Appendix S4). We tested if population growth was higher in more abundant species, that is, if the slope of the regression model was >1. The slope was not significantly different from 1 in either case (OLS method: first census interval slope = 0.96 with 95% CI [0.84, 1.09], second census interval slope = 0.97 with 95% CI [0.87, 1.08]).

Over time, the epiphyte communities on a given tree became more similar compared to those on other trees. The Chao-Sørensen dissimilarity index decreased from 0.63 ± 0.34 in 1994 to 0.54 ± 0.33 in 2002 and 0.46 ± 0.32 in 2015 (means ± SD, Kruskal–Wallis rank-sum test: $\chi^2 = 5,747.4$, $df = 2$, $p < 0.001$, post hoc Nemenyi: all $p < 0.001$). As expected, dissimilarity between years on any given tree was low (0.20 ± 0.25 in the first interval and 0.19 ± 0.25 in the second interval).
3.3 | Species–area- and distribution–abundance relationships

The relationship between habitat size and species numbers became tighter over time (Figure 4). The number of stems in a stand explained from 30% to 50% of the variation in species richness. Fisher’s r-to-z comparison did not indicate any significant differences between the correlations (all \( p \geq 0.15 \)). The slopes of the regression did not differ significantly between censuses (ANCOVA interaction term: \( p = 0.06 \)). Following Laube and Zotz (2007), we also tested the species–area relationship using host tree number or stand area as proxies for habitat size (Appendix S2). Invariably, the relationship became more pronounced with time.

A strong positive relationship between regional occurrence (=number of occupied Annona stands) and the average local abundance of a species in a stand (=mean number of individuals in a stand) was consistently found in all three censuses (Figure 5, \( R^2 > 0.7 \)).

![Figure 4](image1)

**Figure 4** Relationship between epiphyte species richness \( (S) \) and number of Annona stems \( (A) \). Shaded areas represent 95% confidence intervals of the linear regression, the straight lines represent linear regressions \( \log(S) = \log(I) + z \log(A) \)

![Figure 5](image2)

**Figure 5** Relationship between the regional occurrence (stand occupancy, i.e. number of stands occupied by a species) and the mean population size of species. The logarithm of mean population size is plotted against the logarithm of the number of occupied Annona stands. Shaded areas represent the 95% confidence interval of the linear regression. The number of patches \( (n) \) included in this analysis is given for each census.
3.4 | Colonisation

The most common species in the Annona system were the first to colonise empty trees. Five species colonised more than 10 trees each during both census intervals, with only one change in species identity (Tillandsia fasciculata vs. T. subulifera; Appendix S5). The four species that remained among the five most successful colonisers accounted for 86% and 84% of the colonisation events in the first and second interval respectively. Note that this only represents colonisation events of trees that were empty in the preceding census. Colonisation success was assessed by a null model, assuming the probability of colonisation being a function of initial species abundance. With one exception, fewer trees than expected were colonised by the five most successful species (Appendix S5). In contrast, the number of individuals that colonised formerly empty trees was more often within the expected range or even higher. Surprisingly poor colonisers in both intervals were the otherwise abundant species Dimerandra emarginata and Vriesea sanguinolenta.

3.5 | Frequency distribution

The frequency distribution of the species in all tree stands was consistently unimodal over the 21 years covered by this study (Figure 6a). Laube and Zotz (2007) expected a bimodal frequency distribution after the epiphyte colonisation of stands reaches an equilibrium and analysed stands with very high abundance to test this notion. However, the frequency distribution of stands with large epiphyte communities in 2002 and 2015 (Figure 6b,c) yielded no bimodal pattern in either year.

3.6 | Population growth and extinction

The average population growth rate of the epiphyte species on Annona trees between the first and second census was 3.5 ± 12.7% per year and did not change significantly in the second census interval (5.3 ± 8.5% per year, Wilcoxon rank-sum test: p = 0.35). The large majority of species showed positive population growth rates in both intervals (70 and 79%, respectively, in the first and second interval). The proportion of species with mean negative population growth rates was higher in the first interval than in the second (27% vs. 16%). Excluding species with <30 individuals in 1994 or 2002, respectively, from the calculation of the average population growth rate of species did not lead to a different result (Wilcoxon rank-sum test: p = 0.21).

Population growth was analysed as a function of initial population size for epiphyte species with at least 30 populations (all individuals of one species growing on a single tree, Figure 1) in the initial and the consecutive census. In the first census interval, these were Caularthron bilamellatum, Dimerandra emarginata, Niphidium cassinifolium, Tillandsia bulbosa, Tillandsia fasciculata, Vittaria lineata and Vriesea sanguinolenta. In the second census interval, Guzmania monostachia and Tillandsia subulifera were also found on at least 30 trees. Density dependence was universally found, that is, population growth rates decreased with increasing population size (shown for Caularthron bilamellatum in Figure 7, all others in Appendix S6). In the first census interval, 7%–34% of the variation was explained by initial population size (n = 7; all p < 0.05), compared to 22%–53% (n = 9; all p < 0.001) in the second interval. In both intervals, scatter was considerable in all species, indicating substantial asynchrony among populations.

Local extinction was also examined for species with at least 30 populations in the initial census. Testing a possible link between population size and future extinction probability, we compared the...
mean population size of populations that went extinct with those that were still present in the following census. In the first census interval, extinct populations had been significantly smaller in only three of nine species (Wilcoxon rank-sum test: all \( p < 0.05 \)). This proportion slightly increased during the second census interval, when initial population size of extinct populations was significantly smaller in six of eleven species.

4 | DISCUSSION

We followed the development of the epiphyte communities growing on Annona trees along the shoreline of BCI over 21 years with three censuses and compared the patterns of community development between two census intervals. The metacommunity appeared to be still growing (a 60% increase in abundance during the first and a 30% increase during the second census interval along with increasing species numbers, Figure 2). Similar patterns could be observed in both census intervals, for example, a relatively conserved set of common species, a comparable frequency distribution of epiphyte species, and a dependence of population growth rate on initial population size. Mean population growth rates were mostly positive, and the percentage of inhabited trees increased in both intervals. The consistent large-scale changes partly mask considerable dynamics at a smaller scale in the system. These were beyond the scope of the current study because the dynamics at a smaller temporal and spatial scales can only be detected with marked individuals and with shorter census intervals (e.g. annual, Zotz et al., 2005).

We based our expectations of the results on modelling and empirical studies, and on metapopulation theory. From modelling and empirical studies (Einzmann & Zotz, 2017; Flores-Palacios & García-Franco, 2006; Spruch et al., 2019), we expected increasing epiphyte abundance and diversity at the scale of the entire metacommunity and at the level of Annona tree stands, and at the same time we expected some Annona trees to be still empty. Annona trees without epiphytes were significantly smaller in DBH, projected crown cover and crown volume (data not shown), which can be explained by smaller target size or slow colonisation of new trees. We observed no recruitment of new host trees in the two decades, and growth of established Annona trees is quite slow (G. Zotz, unpubl. obs.). Despite the slow development of the host tree system and slow growth of individual trees, colonisation of empty trees is apparently still too slow to fill all available empty trees. This is in line with the findings of observational studies in other vegetation types (Einzmann & Zotz, 2017) and expectations based on modelling studies (Spruch et al., 2019). The continuous increase in abundance is remarkable in comparison to other (terrestrial) systems, but consistent with the results of other studies of epiphyte metacommunities with repeated censuses over much shorter periods (Einzmann & Zotz, 2017; Laube & Zotz, 2006a; Schmit-Neuerburg, 2002). Considering that the Annona trees around BCI are at most as old as the Gatún Lake, the still growing epiphyte metacommunity indicates that the system is not saturated after c. 100 years. Unsaturated epiphyte communities were also reported for a fragmented lower montane cloud forest and isolated pasture trees in Mexico (Flores-Palacios & García-Franco, 2006). Modelling the community assembly of ‘growing habitat islands’, Spruch et al. (2019) found that there is a constant number of empty sites as habitat size and the number of colonising individuals continuously increase. Our observations fully support this theoretical expectation in the real world over a long period. Apart from slow growth, strong dispersal limitation must be invoked to explain the pattern of expansion in this system. The studied Annona trees grow in a narrow zone around BCI. Thus, although we assume that the epiphytes in the neighbouring Annona trees are the primary source of diaspores, it is likely that the adjacent forest also plays a role. Irrespective of idiosyncrasies of our study system, substantial dispersal limitation among epiphytes has been demonstrated repeatedly (e.g. Cascante-Marín et al., 2009; Trapnell et al., 2004, 2013).
The available evidence from population studies suggests that, in general, growth in epiphytes is very slow (Mondragón et al., 2015; Schmidt & Zotz, 2002). Juvenile epiphytes are particularly vulnerable to abiotic stress, which is reflected in their high mortality rate (Benzing, 1990; Winkler et al., 2005). A prominent cause may be their unfavourable surface/volume ratio that leads to rapid desiccation (Zotz, 1998; Zotz & Andrade, 1998). After the juvenile stage, the most likely cause of death seems to be substrate failure in general (Zotz. 1998; Zotz et al., 2005) and branch fall in particular (Cabrál et al., 2015; Hietz, 1997; Zuleta et al., 2016). Thus, one would expect little change in the established composition over time spans of a few years. The first census interval covered 8 years with little change in the rank order of the most abundant species. In the second interval, which was >50% longer (13 years), there were more changes. Nevertheless, the population sizes of the first and consecutive census correlated very well in both census intervals (Figure 3) and a core of 45 species was found in all three censuses. This suggests that the general species composition of the epiphyte metacommunity on Annona is relatively stable. A similar observation was made for the epiphyte metacommunity growing on the palm Socratea exorrhiza in the San Lorenzo Forest in Panama (Laube & Zotz, 2006a).

El Niño-Southern Oscillation (ENSO) anomalies occurred (cp. NOAA/National Weather Service) in both census intervals, with an exceptionally dry year in 1997 (1,700 mm/year) and 3 years of below average precipitation from 2013 to 2015, with annual precipitation ranging from 1,800 to 2,200 mm/year (Paton, 2018). A long-term population study on Annona found very little impact of such severe drought on the population growth rate of Vriesea sanguinolenta (Zotz et al., 2005). However, that study focussed on only one species and covers only one drought event. We cannot rule out that 3 dry years in a row in the second census interval affected the epiphyte community and may thus explain the lower increase in abundance and more compositional changes. If drought favoured species with the water-saving Crassulacean acid metabolism (CAM), one would expect such species to increase more than C3 species. This expectation was indeed met in the second census interval in which there was a relative increase in the abundance of individuals with CAM ($\chi^2 = 29.6, p < 0.001$, data not shown). However, in the first census interval, there was a significant decrease in CAM individuals ($\chi^2 = 46.8, p < 0.001$, data not shown).

A positive correlation between species richness and habitat size (=tree size in the case of epiphytes) is a fundamental pattern in ecology (MacArthur & Wilson, 1967). For epiphytes, this translates into a positive relationship of epiphyte species richness and number of tree stems in the present study. The $z$-value of the species-area relationship for epiphytes growing in Annona stands ranged from 0.3 to 0.5, which suggests a certain degree of isolation (Preston, 1962). Interestingly, this is quite similar to that found for the entire orchid flora of the West Indies (Ackerman et al., 2007).

There was no noticeable temporal change in the positive relationship between local abundance and regional distribution. Regionally abundant species were usually also more abundant at a smaller scale. Laube and Zotz (2007) discussed two possible explanations, that is, ecological specialisation, or a sampling artefact, and concluded that the former is more likely. The species that were most common were also those to colonise empty host trees first. However, they usually colonised fewer trees than expected from a null model, whereas the number of individuals that colonised formerly empty trees was mostly as high as or higher than expected (Appendix S5). This emphasises the problem of successful (long-distance) dispersal. Colonisation of a new habitat patch (i.e. a tree) does not only require successful dispersal of propagules to an area that may be difficult to land on, compared to simply following gravity to the uninhabitable ground, but the subsequent establishment of seedlings is similarly critical (e.g. Ackerman et al., 1996; Winkler et al., 2005). Mortality is reportedly very high in the seedling stage of epiphytic orchids (e.g. Ackerman et al., 1996) and bromeliads (e.g. Benzing, 1978; Winkler et al., 2005) and very likely related to drought stress that smaller individuals cannot withstand as well as larger ones due to their high surface/volume ratio (Zotz, 1998). Thus, seeds may arrive at a suitable spot and germinate only to die in the next drought spell. Once established on a tree, local dispersal has a much higher probability of success. What distinguishes the good coloniser among orchids, bromeliads or ferns (e.g. Cauarthron bilamellatum, Tillandsia bulbosa, Niphidium crassifolium, Appendix S5) from less successful species (e.g. Sobralia bietiae, Vittaria lineata, Catopsis sessiliflora, Appendix S5), apart from a mass effect (Shmida & Wilson, 1985), is an open question. The less successful colonisers (<10 colonised trees) often colonised as many empty trees as the model predicted or even more (11 of 16 species in the first census interval, 10 of 14 species in the second census interval, Appendix S5), whereas the numerically most successful colonisers all underperformed in that respect. All these species are wind-dispersed with dust-like seeds or structures that are conducive for airborne travel, and we are not aware that there is any height advantage for the more successful species when they release their seeds.

Not surprisingly, temporal variation in abundance was much higher among rarer species than among common ones (Figure 3; Appendix S4). Some initially rare species nevertheless show interesting trends within the metacommunity and we directly document several range expansions. Zotz et al. (1999) reported three species for BCI that had not been reported previously (Croat, 1978): Brassavola nudosa, Rodriguezia lanceolata and Tillandsia elongata. In 1988, Brassavola nodosa had already been reported to grow on Annona trees along the shoreline of one of the peninsulas opposite of BCI (Fisher & Zimmerman, 1988). In the first epiphyte census on Annona trees, this species was already found along the shore of BCI (Zotz et al., 1999) and its abundance has subsequently increased considerably (Appendix S4). Tillandsia elongata grew on numerous Annona trees in the south of BCI, but none of them was found in any of the censused sectors in 1994, nor in 2002 (G. Zotz, unpubl. obs.). However, by 2015, over 80 individuals had successfully established on 20 trees within the census area and the species is among the 20 most abundant ones in that census (Appendix S4). Rodriguezia lanceolata, so far, has only been observed with a few individuals in sectors that are not included. Yet another species, Tillandsia subulifera, that...
was described as 'rare' by Croat (1978) was already quite abundant with almost 450 individuals on >50 trees in 1994 (Zotz et al., 1999). The following years saw a steady increase in the number of individuals and hosts with more than two times the number of individuals and three times the number of hosts in 2015. The observed speed of range extension may also be important information in the context of restoration efforts (Endres Júnior et al., 2018; Fernandez Barrancos et al., 2017), and shows that the epiphyte species pool growing on the studied Annona trees is still increasing.

The strongly unimodal frequency distribution was interpreted as indication of a non-equilibrium metapopulation pattern by Laube and Zotz (2007). This pattern was also observed (Figure 6a) more than a decade later, underlining the unsaturated state of the system through ecological time (cp. Loreau, 2000). In contrast to Laube and Zotz (2007), we did not find a bimodal frequency distribution in heavily occupied stands (Figure 6b,c). This discrepancy may be due to the slightly different approach of defining tree stands. Laube and Zotz (2007) defined 84 stands and only four stands fulfilled the requirements they set to define a stand of saturated epiphyte colonisation, that is, (a) ≥90% of all trees of that stand were occupied by epiphytes; and (b) these trees hosted, on average, at least as many individuals as corresponding to the upper quartile boundary of the number of epiphyte individuals in all individual stands. In contrast, we defined 93 Annona stands for 2002 and the application of the same requirements for saturated epiphyte colonisation resulted in 10 Annona stands entering the analysis. The result of Laube and Zotz (2007) may be rather specific to the four stands that met the criteria for a saturated stand and therefore be related to the small sample size included in their analysis (McGeoch & Gaston, 2002).

Our findings fully support the conclusion drawn by Laube and Zotz (2007) over much longer time periods: species dynamics of epiphytes growing on Annona are driven by metapopulation processes. (a) The habitat occurs in discrete units, that is, Annona stands along the shoreline of BCI are clearly divided by empty space that is not habitable for epiphytes (Appendix S3). (b) The risk of extinction was unrelated to population size in half of the tested species. (c) Recolonisation of trees that had lost their entire epiphyte vegetation was observed. (d) Local populations showed asynchrony in their dynamics, reflected by the large scatter of the relationship of population size and growth rate (Figure 7). Another theory on epiphyte community assembly was put forward by Taylor and Burns (2015).

In a study of epiphyte communities in a temperate forest of New Zealand, they applied Darwin's geological theory of island ontogeny and found it to be useful for the study of epiphyte community development. Passing a threshold value epiphyte species richness scaled positively with host tree diameter. This is in line with two of our findings. First, the significantly smaller DBH of Annona trees that did not host any epiphytes (data not shown) and second, the robust relationship of habitat size (either approximated as number of stems or host trees in an Annona stand, or as stand area) and species number (Figure 4; Appendix S4).

Analysing the epiphyte metacommunity on a single host tree species, we expected to find only a subset of the regional species pool (Laube & Zotz, 2006b; Wagner et al., 2015; Zotz et al., 1999). Because Annona did not grow at the study site before Lake Gatún was established, the epiphyte metacommunity growing on those trees needed time to build up first. With time, the subset of species growing on those trees should increase, as more epiphyte species colonised the newly established trees. Apparently, this process is still ongoing after one century, as we documented an increasing number of species in each census (Figure 2). Epiphyte metacommunities in forests often show a very patchy/clumped distribution (Nieder et al., 2000; Zotz & Schultz, 2008), with large trees harbouring a disproportionate part of the local epiphyte flora (Catchpole & Kirkpatrick, 2010; Díaz et al., 2010; Zotz & Bader, 2009). In such a system the loss of one or a few large trees will have a disproportionate effect on the epiphyte metacommunity of the area (Kartzinel et al., 2013). As of now, no study has documented such a crisis let alone the recovery from it in any epiphyte metacommunity. This disproportionate importance of large trees is also relevant from a forest management point of view: the selective harvest of large canopy trees for timber most likely affects epiphyte species richness considerably (Köster et al., 2011; Wolf, 2005). The expected dynamics in the epiphyte metacommunity on Annona clearly differs in that regard from that of a forest. The Annona system shows a more homogenous distribution of epiphytes, that is, no tree hosts more than 28% of all species and 3% of all individuals of the entire community. In contrast, in a lowland forest, relatively close to our study system, a single, large host tree hosted almost 50% of all epiphyte species and the 10 largest trees >80% of all species with corresponding numbers for epiphyte individuals of 15% and almost 50% respectively (Zotz & Schultz, 2008). Another difference to a ‘typical’ forest is the lack of recruitment of Annona trees over the 21 years of the study. For the forest of BCI recruitment of tree seedlings ranges from a total of 68 to 4,143 individuals over 9 years in six hundred 1-m² plots (Wright et al., 2005). Although only a fraction of these seedlings survives, this is in stark contrast to the apparent lack of recruitment of Annona trees around the island.

Given such idiosyncrasies, how representative are our findings for epiphyte communities in other vegetation types? There are clear parallels with the few studies of repeated censuses in natural systems in tropical lowlands, for example, in Venezuela (Schmit-Neuerburg, 2002), on one palm tree species in a Panamanian lowland forest (Laube & Zotz, 2006a) or on pasture trees in Panama (Einzmann & Zotz, 2017). Testing the relationship of tree size and epiphyte species richness in a fragmented lower montane cloud forest, Flores-Palacios and García-Franco (2006) also reported comparable results: in their study area, epiphyte communities were typically not saturated. However, epiphytes are generally much more abundant and species-rich at higher elevations (e.g. Cardelús et al., 2006; Krömer et al., 2005). In such montane communities, competition for space may become much more relevant for community development than in lowland forests with low epiphyte densities. Densities are rarely quantified, but the estimated value of c. 1 epiphyte/m² substrate surface on Socratea exorrhiza (Zotz & Vollrath, 2003) should be valid for many lowland forests. Epiphyte communities in higher elevations...
probably follow different patterns. Experimental studies (Acuña-Tarazona et al., 2015; Nadkarni, 2000; Toledo Aceves et al., 2012) with stripped branches provide important insights into the initial processes of establishment in such montane vegetation, but they do not provide data for most other community processes that are captured by our study. Our study system is obviously not a typical lowland forest and may be more comparable to secondary tropical forest regarding its reduced epiphyte diversity (e.g. Einzmann & Zotz, 2016; Guzmán-Jacob et al., 2019). However, comparison with data of long-term studies in lowland forests (Laube & Zotz, 2006a; Schmit-Neuerburg, 2002) suggests that we did identify fundamental patterns of community development over a previously unmatched period.

To conclude, this long-term study of the epiphyte metacommunity growing on Annona around BCI shows that the major patterns of community and population dynamics identified after 8 years did not change over two decades. In contrast to most other terrestrial plant communities, this system is not saturated even after a century of initial establishment. This pattern of community dynamics fully agrees with theoretical predictions (Spruch et al., 2019). Empirical studies in other systems (Einzmann & Zotz, 2017; Flores-Palacios & García-Franco, 2006; Laube & Zotz, 2006a; Schmit-Neuerburg, 2002) covering much shorter time periods reported a similar pattern, that is, epiphyte metacommunities continue to expand over very long periods. Taken together, a consistent picture emerges, and we cautiously argue that our results are representative for the long-term dynamics of many other epiphyte communities.

ACKNOWLEDGEMENTS

The help of Anaïs Bonnefond, Montpellier, France, during the 2015 census is acknowledged, as are funds from the Smithsonian Tropical Research Institute to finance the 2015 fieldwork. The authors thank Calixto E. Rodríguez Quiel for editing the Spanish abstract.

AUTHORS’ CONTRIBUTIONS

G.Z. conceived the idea and provided the data of the first two censuses; L.W. conducted the third census; H.J.R.E. analysed the data and wrote the manuscript; G.Z. and L.W. contributed to the manuscript and gave final approval for publication.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/1365-2745.13618.

DATA AVAILABILITY STATEMENT

Data are archived with the figshare data repository and after a 1-year embargo available from: https://doi.org/10.25573/data.13655714 (Einzmann et al., 2021).

REFERENCES

Ackerman, J. D., Sabat, A., & Zimmerman, J. K. (1996). Seedling establishment in an epiphytic orchid: An experimental study of seed limitation. Oecologia, 106, 192–198. https://doi.org/10.1007/BF00328598

Ackerman, J. D., Trejo-Torres, J. C., & Crespo-Chuy, Y. (2007). Orchids of the West Indies: Predictability of diversity and endemism. Journal of Biogeography, 34, 779–786. https://doi.org/10.1111/j.1365-2699.2006.01676.x

Acuña-Tarazona, M., Toledo-Aceves, T., Flores-Palacios, A., Sosa, V. J., & Martínez, M. L. (2015). Post-stripping recolonization of vascular epiphytes in cloud-forest fragments in Mexico. Journal of Tropical Ecology, 31, 499–508. https://doi.org/10.1017/S0266467415000395

Adams, B. J., Schnitzer, S. A., & Yanovjak, S. P. (2017). Trees as islands: Canopy ant species richness increases with the size of liana-free trees in a Neotropical forest. Ecography, 40, 1067–1075. https://doi.org/10.1111/ecog.02608

Bagchi, R., Gallery, R. E., Gripenberg, S., Gurr, S. J., Narayan, L., Addis, C. E., Freckleton, R. P., & Lewis, O. T. (2014). Pathogens and herbivores drive rainforest plant diversity and composition. Nature, 506, 85–88. https://doi.org/10.1038/nature12911

Baldeck, C. A., Harms, K. E., Yavitt, J. B., John, R., Turner, B. L., Valencia, R., Navarrete, H., Bunyavejchewin, S., Kiratiprayoon, S., Yaacob, A., Supardi, M. N. N., Davies, S. J., Hubbell, S. P., Chuyong, G. B., Kenfack, D., Thomas, D. W., & Dalling, J. W. (2013). Habitat filtering across tree life stages in tropical forest communities. Proceedings of the Royal Society B: Biological Sciences, 280, 1–8. https://doi.org/10.1098/rspb.2013.0548

Benzing, D. H. (1978). Germination and early establishment of Tillandsia cincinnata Schlecht. (Bromeliaceae) on some of its hosts and other supports in Southern Florida. Selbyana, 5, 95–106.

Benzing, D. (1990). Vascular epiphytes. General biology and related biota. Cambridge University Press.

Bernal, R., Valverde, T., & Hernandez-Rosas, L. (2005). Habitat preference of the epiphyte Tillandsia recurvata (Bromeliaceae) in a semi-desert environment in Central Mexico. Canadian Journal of Botany, 83, 1238–1247. https://doi.org/10.1139/b05-076

Blick, R., & Burns, K. C. (2009). Network properties of arboreal plants: Are epiphytes, mistletoes and lianas structured similarly? Perspectives in Plant Ecology, Evolution and Systematics, 11, 41–52. https://doi.org/10.1016/j.ppees.2008.10.002

Bruijnzeel, L. A., Mulligan, M., & Scatena, F. N. (2011). Hydrometeorology of tropical montane cloud forests: Emerging patterns. Hydrological Processes, 25, 465–498. https://doi.org/10.1002/hyp.7974

Burns, K. C. (2007). Network properties of an epiphyte metacommunity. Journal of Ecology, 95, 1142–1151. doi:https://doi.org/10.1111/j.1365-2745.2007.01267.x

Burns, K. C., & Zotz, G. (2010). A hierarchical framework for investigating epiphyte assemblages: Networks, metacommunities and scale. Ecology, 91, 377–385. https://doi.org/10.1890/08-2004.1

Cabral, J. S., Petter, G., Mendienta-Leiva, G., Wagner, K., Zotz, G., & Kreft, H. (2015). Branchfall as a demographic filter for epiphyte communities: Lessons from forest floor-based sampling. PLoS One, 10, https://doi.org/10.1371/journal.pone.0128019

Cardelús, C. L., Colwell, R. K., & Watkins, J. E. (2006). Vascular epiphyte distribution patterns: Explaining the mid-elevation richness peak. Journal of Ecology, 94, 144–156. https://doi.org/10.1111/j.1365-2745.2005.01052.x

Cascante-Marin, A., von Meijenfeldt, N., de Leeuw, H. M. H., Wolf, J. H. D., Oostermeijer, J. G. B., & den Nijs, J. C. M. (2009). Dispersal limitation in epiphytic bromeliad communities in a Costa Rican fragmented montane landscape. Journal of Tropical Ecology, 25, 63–73. https://doi.org/10.1017/s0266467408005622

Catchpole, D. J., & Kirkpatrick, J. B. (2010). The outstandingly species epiphytic flora of a single stranger fig (Ficus crustissula) in a Peruvian montane cloud forest. In L. A. Bruijnzeel, F. N. Scatena, &
Wagner, K., Mendieta-Leiva, G., & Zotz, G. (2015). Host specificity in vascular epiphytes: A review of methodology, empirical evidence and potential mechanisms. AoB PLANTS, 7. https://doi.org/10.1093/aobpla/plu092

Wickham, H. (2017). tidyverse: Easily Install and Load the ‘Tidyverse’. R package version 1.2.1. Retrieved from https://CRAN.R-project.org/package=tidyverse

Windsor, D. M. (1990). Climate and moisture variability in a tropical forest: Long-term records from Barro Colorado Island, Panamá. Smithsonian Institution Press.

Winkler, M., Hülber, K., & Hietz, P. (2005). Effect of canopy position on germination and seedling survival of epiphytic bromeliads in a Mexican humid montane forest. Annals of Botany, 95, 1039–1047. https://doi.org/10.1093/aob/mci115

Winkler, M., Hübner, K., Mehltreter, K., García-Franco, J. G., & Hietz, P. (2005). Herbivory of epiphytic bromeliads, orchids and ferns, in a Mexican montane forest. Journal of Tropical Ecology, 21, 147–154.

Wolf, J. H. D. (2005). The response of epiphytes to anthropogenic disturbance of pine-oak forests in the highlands of Chiapas, Mexico. Forest Ecology and Management, 212, 367–393. https://doi.org/10.1016/j.foreco.2005.03.027

Wright, S. J., Muller-Landau, H. C., Calderón, O., & Hernández, A. (2005). Annual and spatial variation in seedfall and seedling recruitment in a neotropical forest. Ecology, 86, 848–860. https://doi.org/10.1890/03-0750

Zotz, G. (1998). Demography of the epiphytic orchid, Dimerandra emarginata. Journal of Tropical Ecology, 14, 725–741. https://doi.org/10.1017/S026647498000534

Zotz, G. (2013a). Hemiepiphyte: A confusing term and its history. Annals of Botany, 111, 1015–1020. https://doi.org/10.1093/aob/mct085

Zotz, G. (2013b). The systematic distribution of vascular epiphytes – A critical update. Botanical Journal of the Linnean Society, 171, 453–481. https://doi.org/10.1111/boj.12010

Zotz, G. (2016). Plants on plants - The biology of vascular epiphytes. Springer International Publishing.

Zotz, G., & Andrade, J. L. (1998). Water relations of two co-occurring epiphytic bromeliads. Journal of Plant Physiology, 152, 545–554. https://doi.org/10.1016/S0176-1617(98)80276-9

Zotz, G., & Bader, M. Y. (2009). Epiphytic plants in a changing world – Global change effects on vascular and non-vascular epiphytes. Progress in Botany, 70, 147–170. https://doi.org/10.1007/978-3-540-68421-3

Zotz, G., Bermejo, P., & Dietz, H. (1999). The epiphyte vegetation of Annona glabra on Barro Colorado Island, Panama. Journal of Biogeography, 26, 761–776. https://doi.org/10.1046/j.1365-2699.1999.00304.x

Zotz, G., & Hietz, P. (2001). The physiological ecology of vascular epiphytes: Current knowledge, open questions. Journal of Experimental Botany, 52, 2067–2078. https://doi.org/10.1093/jexbot/52.364.2067

Zotz, G., Laube, S., & Schmidt, G. (2005). Long-term population dynamics of the epiphytic bromeliad, Werauhia sanguinolenta. Ecography, 28, 806–814. https://doi.org/10.1111/j.2005.0906-7590.04292.x

Zotz, G., & Schultz, S. (2008). The vascular epiphytes of a lowland forest in Panama – Species composition and spatial structure. Plant Ecology, 195, 131-141. https://doi.org/10.1007/s11258-007-9310-0

Zotz, G., & Vollrath, B. (2003). The epiphyte vegetation of the palm Socratea exorrhiza - correlations with tree size, tree age and bryophyte cover. Journal of Tropical Ecology, 19, 81–90. https://doi.org/10.1017/s026647403003092

Zuleta, D., Benavides, A. M., López-Ríos, V., & Duque, A. (2016). Local and regional determinants of vascular epiphyte mortality in the Andean mountains of Colombia. Journal of Ecology, 104, 841–849. https://doi.org/10.1111/1365-2745.12563

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Einzmann HJR, Weichgrebe L, Zotz G. Long-term community dynamics in vascular epiphytes on Annona glabra along the shoreline of Barro Colorado Island, Panama. J Ecol. 2021;109:1931–1946. https://doi.org/10.1111/1365-2745.13618