Including dynamics in the equation: Tree growth rates and host specificity of vascular epiphytes

Katrin Wagner1 | Gerhard Zotz1,2

1Institute for Biology and Environmental Sciences, AG Functional Ecology, Universität Oldenburg, Oldenburg, Germany
2Smithsonian Tropical Research Institute, Balboa, Panama

Correspondence
Katrin Wagner
Email: ka.wagner@uni-oldenburg.de

Funding information
Deutsche Forschungsgemeinschaft, Grant/Award Number: WA 3936/1-1 and ZO 94/5-1

Handling Editor: Kun-Fang Cao

Abstract

1. The forest canopy is home to a rich biota. One salient feature are the dynamics of the habitat-building trees, which are growing and eventually vanishing. Tree species strongly differ in growth rates, final size and longevity. Nevertheless, these inherent dynamics have been a blind spot in studies on host specificity of vascular epiphytes (vascular plants dwelling on trees without parasitizing them)—not least because tree growth rates and longevity are usually unknown in highly diverse tropical forests. The present study aims at tackling this blind spot.

2. We compared epiphyte abundances (>23,000 individuals) found on 285 individuals of four focal tree species in a lowland moist forest in Panama. Data on repeated dbh censuses from a permanent tree plot provided the unique opportunity to estimate the age of our sampled trees. We compared the relative importance of tree longevity for host biases with that of other host tree characteristics, namely microclimatic conditions and bark acidity, rugosity and stability.

3. The studied tree species differ in host quality and epiphyte species partly differ in host preferences. The conclusions concerning relative host tree quality depend hugely on whether or not different tree growth rates are considered. Comparing these conclusions allows important insights into the role of tree longevity in shaping epiphyte communities. Relating tree trait differences to the observed distributions of epiphytes among the focal tree species shows how the simultaneous action of various tree characteristics causes host biases.

4. Synthesis. This study highlights the substantial but, up to now, hidden role of different tree growth rates for host tree specificity of vascular epiphytes. Future investigations need to consider this possibly confounding factor adequately to avoid spurious conclusions.

KEYWORDS
annual diameter increment, bark acidity, bark stability, canopy openness, host bias, host preference, tree growth rate
1 | INTRODUCTION

Why are there so many species in the tropics? This question has been posed time and again since the first systematic explorations of tropical species diversity in the 19th century. Today, it is generally accepted that a combination of mechanisms work together to cause the latitudinal diversity gradients that can be observed for most groups of organisms (Hillebrand, 2004), although their relative importance is still debated (Brown, 2014; Leigh et al., 2004; Mittelbach, 2012). Proposed mechanisms comprise geometric constraints on species ranges (Colwell & Hutt, 1994), climatic effects on population sizes (Wright, 1983), the greater age and area of tropical environments (Chown & Gaston, 2000) and higher diversification rates in the tropics (McKenna & Farrell, 2006). Higher tropical diversification rates may, for example, be caused by a greater importance of biotic as opposed to abiotic selection pressures in the tropics, resulting in an increased likelihood of co-evolution (Schemske, 2009).

In a cascading effect, the high diversity of one group may then facilitate the diversity of other groups of species (Thomsen et al., 2018). In tropical forests, a wide array of organisms depends on trees for food and habitat, while at the same time species richness of trees can be impressive (e.g. Pitman et al., 2002). It is thus conceivable that the diversity of tree-dependent organisms is, among other factors, driven by the species richness of trees. This hypothesis has been put forward for herbivorous insects (Novotny et al., 2006). Similar to insect herbivores, vascular epiphytes (vascular plants dwelling on trees without parasitizing them, simply 'epiphytes' in the following) closely depend on trees. With more than 27,000 species (i.e. almost 10% of global vascular plant diversity), this plant group is extremely species-rich—especially in the tropics (Zotz, 2013b). Consequently, epiphytes are an excellent group for a second test of the hypothesis that tree diversity begets the diversity of tree-dependent organisms.

From a theoretical perspective, host tree specificity of epiphytes should be relatively weak. Strong host specificity should evolve in antagonistic or mutualistic species relationships as a result of mutual selection (Blüthgen, Menzel, Hovestadt, Fiala, & Blüthgen, 2007; Ehrlich & Raven, 1964). However, the relationship between epiphytes and their hosts is generally regarded as commensalistic: while trees constitute the habitat for (obligatory) epiphytes, their impact on their host trees seems generally negligible, even though negative (or even positive) effects have been observed in some cases (Zotz, 2016 and references therein). Even without driving forces for co-evolution, a certain degree of host specificity may still be expected, simply because tree species differ in many traits and these differences should affect their suitability as hosts for epiphytes. Candidate traits related to host specificity are tree architecture, physical bark properties and chemical properties of leaf and bark, which affect substrate stability, microclimate, mineral nutrition or toxicity of the epiphytic habitat (Wagner, Mendieta-Leiva, & Zotz, 2015 and references therein). Bark stability is one trait that has been invoked repeatedly to cause host specificity. Trees with flaking or peeling bark should be poor hosts, because epiphytes may come off together with the unstable bark (Schimper, 1888). Another frequently mentioned trait is bark ruggedness. Epiphytes may benefit from rugose bark for two reasons. First, it may offer a better foothold, preventing seeds and plants from being dislodged from the tree (e.g. Callaway, Reinhart, Moore, Moore, & Pennings, 2002). Second, epiphytes on trees with fissured bark may enjoy a more continuous water supply as water is withheld longer within bark crevices. Bark acidity may play a role for host specificity, by influencing germination or mineral nutrition (Johansson, 1974). Yet other tree traits may influence the overall microclimate in the crown of a tree. For example, two trees, both reaching the forest’s overstorey, but differing in foliage density, offer epiphytes very different light and humidity conditions in their crowns. The fact that trees constitute a growing and ageing habitat introduces additional levels of complexity. Especially old trees may offer a very diverse set of environmental conditions to epiphytes (e.g. bark of young branches may be much smoother than the bark of the tree trunk) and the environmental conditions (microclimate, bark traits, substrate diameter) at any given growing site in the tree may change substantially over time (Rasmussen & Rasmussen, 2018).

The empirical evidence for host specificity of vascular epiphytes has been reviewed by Wagner et al. (2015). In accordance with the outlined expectations, most epiphytes can grow on the entire range or at least the majority of tree species occurring within their habitat. At this level, they are thus usually complete generalists. The notion that host specificity of epiphytes is weak in comparison to mutualistic systems of species-interaction has recently received support by a study that compared network metrics among both types of systems (Naranjo, Iriondo, Riofrío, & Lara-Romero, 2019). However, shifting the focus from host range (i.e. the number of host species) to the abundance of epiphytes per tree makes differences between tree species almost ubiquitous (Wagner et al., 2015). This indicates that there are ‘host biases’, that is, colonization probability and population growth depend on host species identity. Such host biases could be consistent for all epiphyte species (i.e. all epiphyte species prefer the same tree trait attributes) or depend on the epiphyte species (i.e. tree preferences differ with epiphyte species). The latter scenario would be a prerequisite for the hypothesis that tree diversity begets epiphyte diversity. In studies that compared the pooled abundance of all epiphyte species among tree species, some tree species typically have a larger epiphyte load (all epiphyte species combined) than others (Einzmann, Beyschlag, Hofhansl, Wanek, & Zotz, 2015; Wyse & Burns, 2011), indicating that many (or at least the most abundant) epiphyte species have the same requirements with regard to tree traits. However, when host bias patterns of numerous epiphyte species at the same study site are analysed separately, differential host biases also regularly emerge (Benavides, Vasco, Duque, & Duivenvoorden, 2011; Laube & Zotz, 2006; Vergara-Torres, Pacheco-Alvarez, & Flores-Palacios, 2010).

Unfortunately, field studies typically suffer from a number of serious methodological issues, nourishing doubts about the drawn conclusions (Wagner et al., 2015). These issues result from the enormous species richness and structural complexity of tropical forests. Many
studies test host specificity by comparing epiphyte abundances on different tree species. However, deducing host specificity from distributional data strongly depends on the accurate formulation of the null expectation. For example, epiphyte occupancy and abundance per tree generally increases with tree size (Flores-Palacios & García-Franco, 2006; Zotz & Vollrath, 2003) because a larger surface area intercepts more diaspores (size effect) but also because of an age effect: larger trees are generally older and cumulative colonization probability is higher for older trees. Moreover, epiphyte accumulation accelerates on older trees once they host reproductive epiphytes, which strongly augments the seed rain on the tree’s surface. As trees vary considerably in their growth rates and thus in their age at comparable sizes, it is crucial that both tree size and age are considered as covariates in statistical analyses when testing for host specificity. However, tree age is generally unknown in tropical systems and has thus almost never been considered as a covariate, the only exception being a study on per tree bromeliad biomass in experimental monocultures of known age (Merwin, Rentmeester, & Nadkarni, 2003). Moreover, in typical plot-based sampling designs, most of the observed epiphyte and tree species are rare (e.g. Laube & Zotz, 2006). For species with small sample sizes, the outcomes of statistical tests are inevitably unreliable. The problem of low replication seems even more worrying if one considers that other effects, unrelated to tree species identity, strongly influence per tree epiphyte abundance and can easily override the effects of host tree traits. For example, the location of a tree within the forest matrix (on a ridge or in a valley, close or far from a water body, next to a treefall gap or in a closed forest stand) strongly influences the light climate and humidity in a tree crown. In addition, other tree-dependent flora, that is, lianas and hemiepiphytes (i.e. plants germinating in the tree crown but producing feeder roots that reach the ground, Zotz, 2013a) may modify the microclimate experienced by epiphytes.

The present study addresses many of these methodological issues. In particular, taking advantage of permanent tree plot data from the study site, there was the unique opportunity to estimate tree age and include tree species-specific growth rates in our analyses. Moreover, instead of choosing a plot-based sampling design, we focused on a small number of host tree species. This allowed us to sample an unusually large number of trees per species with a good representation of large, overstorey individuals. The aim was to investigate host specificity in an assemblage of vascular epiphytes in a tropical lowland forest by documenting distributional patterns of epiphytes among different host tree species at different levels. We focused on four tree species, identifying and counting all epiphytes on a total of 285 trees, including the entire range of tree sizes, and quantified a number of tree traits (bark stability, rugosity and acidity) as well as light climate, temperature and humidity. Using these data, we asked four questions: (a) Are some of the tree species better overall epiphyte hosts than others (‘parallel host specificity’)? (b) Do epiphyte species differ regarding their preferences for tree species (‘differential host specificity’)? (c) How strongly do conclusions change if tree age instead of tree size is used as a predictor for epiphyte abundance? (d) Can differences in trait attributes among tree species be related to differences with regard to epiphyte abundance? This last question was treated in Appendix S2 to keep the main text focused on the most important question (i.e. the effect of different tree growth rates).

2 | MATERIALS AND METHODS

2.1 | Field site and focal tree species

The study site is located at 130 m a.s.l. within a 12,000-ha reserve on the Caribbean slope of Panama (San Lorenzo forest reserve, 9°17’N, 79°58’W). Mean annual air temperature and precipitation in this lowland rainforest are 25.2°C and 3,360 mm respectively (Paton, 2017). During the dry season, which lasts from mid-December to the end of April, precipitation averages <650 mm. It has been suggested that the forest has been free of severe human disturbance for at least 200 years (Condit et al., 2004). Emergent trees reach a height of about 45 m. The study site comprises a 6-ha permanent sample plot for trees run by the Center for Tropical Forest Science (CTFS-ForestGeo; Condit, 1998; Condit, Perez, Aguilar, & Lao, 2009). Within this plot, all trees with a diameter at breast height (dbh) of >1 cm have been identified and tagged. Dbh measurements of all trees are repeated regularly. Our study was not only conducted within the permanent tree plot but also in its immediate vicinity to increase the number of large trees (Figure S1-1). The terrain of the study site gradually descends towards the north. A small brook and its temporarily aquiferous confluent flow through the site and the slopes towards the brooks are up to 35° steep.

We focused on four tree species, all of them being tall growing trees (reaching c. 35–40 m) and among the most abundant species at the study site, which allowed for a large number of replicates: Aspidosperma spruceanum Benth. ex Müll.Arg. (Apocynaceae), Brosimum utile (Kunth) Oken (Moraceae), Calophyllum longifolium Willd. (Clusiaceae) and Manilkara bidentata (A.DC.) A.Chev. (Sapotaceae). In the text, we only use genus names.

We took advantage of already existing epiphyte data (‘census data’) and complemented these by systematically sampling the focal tree species in a larger area (‘2017 data’). The census data cover 10–46 individuals per focal tree species and were collected in 2009–2011 in the 0.9-ha accessible by a canopy crane operated by the Smithsonian Tropical Research Institute (G. Mendoza-Leiva et al. unpubl. data, see Zotz & Schultz, 2008 for methodology). To increase sample sizes and especially the number of large trees, we sampled 22 trees with a dbh <40 cm (‘small trees’) and 20 trees with a dbh ≥40 cm (‘large trees’) of each species in 2017. We obtained dbh data for all trees and GPS coordinates (recorded with eTrex® 30, Garmin) for all trees not pertaining to the census data. In all species except Calophyllum (maximum dbh: 104 cm) the largest sampled tree had a dbh of c. 120 cm. For all trees sampled in 2017, we collected the following additional data: (a) extent of the crown in the direction of its greatest extension and in the direction perpendicular to the first axis, (b) height above the forest floor of the highest branches of the tree, (c) percentage of projected crown area covered by lianas
and woody hemiepiphytes, respectively and (d) number of shoots of woody and herbaceous climbing plants around the base of the trunk. We used the two estimates of crown extension to calculate projected crown area assuming the shape of an ellipse.

### 2.2 Epiphyte sampling

On each sampled tree we counted all epiphytes except small seedlings (<c. 5% of the maximum size of a given species). In the case of smaller trees, we counted the epiphytes from the ground with the aid of binoculars. However, epiphytes in the crown of larger trees (>c. 15 m height) cannot be observed from the ground without missing a large proportion of individuals. Therefore, we used the canopy crane to access such trees for the census data, while in 2017, we used a combination of single and double rope climbing techniques. In addition to epiphytes, we also recorded abundances of hemiepiphytes sensu Zotz (2013a), that is, mostly woody plants that germinate in tree crowns but send roots to the forest floor and, thus establish soil contact at some point during their life. We also recorded epiphytes that were not directly growing on the host tree but rather on lianas or hemiepiphytes—but noted these separately. As it is sometimes difficult to delimit individual epiphytes growing very close together, we considered a group of rhizomes and leaves forming a clearly delimited stand as one individual (Sanford, 1968). In the case of epiphytes with a creeping growth form, parts of rhizomes were considered separate individuals if they were growing on different branches and we could not observe a connecting rhizome. In the case of the tiny epiphytic filmy ferns (Hymenophyllaceae) counting individuals is not feasible. To obtain estimates of their abundance, we laid out 25 cm × 25 cm plots and noted presence/absence in each of the 5 cm × 5 cm subplots. These plots were positioned at the base of the trunk (1.3 m above the forest floor) of the 80 ‘large trees’, in each cardinal direction. Due to their small size, we refrained from identifying Hymenophyllaceae to species level and treated them as a single group. In the case of all other epiphyte species, we were able to identify the majority of individuals in situ—owing to our prior knowledge of most epiphytes at the site (exceptions are described in Section 2.5). In doubtful cases, we took photos for later identification or collected specimens to be kept until flowering to confirm putative identifications. Herbarium vouchers were deposited at the herbarium of the University of Panama.

### 2.3 Estimation of tree age

The most accurate method to determine tree age is to count tree rings either from dead trees or via increment bore coring of living trees. Although even in tropical trees annual tree rings exist—at least in climates with seasonal precipitation patterns or in seasonally flooded areas (Fichtler, Clark, & Worbes, 2003), reliable dendrochronology is far less developed for tropical as compared to temperate trees (Worbes, 2002). Moreover, tree coring always incurs a risk of damage (Tsen, Sitzia, & Webber, 2016) which would not have been justifiable for our purpose. We thus chose an indirect method to estimate tree age. Using tree census data from 1999, 2009 and 2016 supplied by CTFS-ForestGeo (Condit, 1998; Condit et al., 2009), we were able to estimate average diameter growth rates of the focal species. We calculated annual dbh increments for the periods 1999–2009 and 2009–2016 representing, respectively, 595, 579, 159 and 533 observations for Aspidosperma, Brosimum, Calophyllum and Manilkara. Annual diameter increment varies strongly with tree size: it is typically small for small trees, tends to peak in the early- to midlife of a tree and gradually decreases thereafter (Bowman, Brienen, Gloor, Phillips, & Prior, 2013). We estimated tree age from dbh data as follows. First, we fitted a double exponential model to the increment-diameter data for each species (Figure S1-2a). Then we used the model equations to calculate dbh iteratively as a function of age (Figure S1-2b).

### 2.4 Tree traits

To assess trait differences among the focal tree species, we carried out microclimate measurements, determined canopy openness via hemispherical photographs and assessed bark acidity, stability and rugosity. To keep the present text concise and focused on its main topic, the respective methods, results and discussion are presented in Appendix S2.

### 2.5 Data analyses

In total, 92% of all epiphyte individuals were identified to species level. In the remaining cases, species identification was not possible for various reasons. Some rare species were never seen in flower (Table S1-1) — here, we used our own morphospecies names in the statistical analyses. In about 0.5% of the cases, individuals could not be assigned to one of several possible species, because they were too small or not readily visible from the point of observation. We excluded these individuals from analyses on species composition. More importantly, there were some species that were indistinguishable from each other in the immature stage for which we thus have no species-specific abundance and occupancy data. This was the case for the ‘Sobralia group’ (Sobralia fenziiana and Sobralia macrophylla, n = 96), for three small, caespitose Pleurothallidinae species (‘Stelis group’, n = 1,521: Stelis cf. crescentiocola, Stelis sp1, and Specklinia acrisepala), and for three hemiepiphytic Clusia species (‘Clusia group’, n = 276, Clusia peninsulae, Clusia valerioi and Clusia cf. uvitana). Running analyses of species composition with and without these individuals left results qualitatively unaffected. The results presented in this paper are based on the dataset in which the respective species were treated as morphospecies.

All statistical analyses were carried out with R version 3.3.2 (R Core Team, 2016). Graphs were produced using the r package ggplot2 (Wickham, 2009). Other r packages are cited below. The significance level was set to $\alpha = .05$ in all cases. In case of more than one explaining variable, minimal adequate models were chosen by deleting terms
stepwise, starting from the full model and comparing model fit via the F-test. Whenever appropriate (numeric dependent vs. factorial explaining variable(s)) we either performed an ANOVA followed by Tukey’s test, or, if visual inspection of the residuals indicated violation of the ANOVA assumptions, the Kruskal–Wallis rank sum test followed by Dunn’s test of multiple comparisons with Bonferroni adjustment.

In order to estimate tree age, we first modelled annual diameter increment as a function of diameter at breast height (dbh, see above). Based on the typical shape of the tree diameter increment–dbh relationship (Bowman et al., 2013), we chose to fit a double exponential model with the form annual dbh increment = \( a (e^{b \text{dbh}} - e^{c \text{dbh}}) \) to the permanent sample plot data, using the nlsLM function from the minpack.lm package (version 1.2-1).

To model epiphyte abundance per tree as a function of tree species and tree diameter or tree age, respectively, we used Quasi-Poisson GLMs as they account for the detected overdispersion. A pseudo \( R^2 \) was calculated using the formula 1 − (residual deviance/ null deviance) as a measure for goodness-of-fit (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). To assess whether focal tree species differ in their suitability for epiphytes in general, we used the abundance of all encountered epiphyte individuals as a response variable. To assess whether single epiphyte species differed from each other in their host preferences, we conducted equivalent analyses for single epiphyte species. To ensure sufficient statistical power, these tests were only conducted on epiphyte species with >500 individuals in the whole dataset (10 species). Due to the identification problems described above the ‘Stelis group’ was not considered in this analysis, although its pooled abundance was >1,000 individuals. To test whether the abundance of lianas and hemiepiphytes influenced the per tree epiphyte abundance we reran the above described analyses adding the percentage of the tree’s crown that was influenced by either lianas or woody hemiepiphytes (see Section 2) as a covariate in the model. We only have estimates for liana and hemiepiphyte abundance for the 2017 data. Moreover, lianas or woody hemiepiphytes are expected to modulate the microclimate on a tree most strongly if the tree reaches the overstorey of the forest. The models were thus fitted on the subset of ‘large trees’ (>40 cm dbh) sampled in 2017.

Since most small trees carry no or very few epiphytes, only trees with a dbh ≥40 cm were considered for the comparison of epiphyte assemblages between tree species (multivariate analyses). Moreover, we excluded rare epiphyte species (<30 individuals in the dataset) and all ‘empty’ tree individuals. This subsetting resulted in a dataset with 99 tree individuals (Aspidosperma: 22, Brosimum: 30, Calophyllum: 22, Manilkara: 25) and 44 epiphyte species. The number of epiphytes per tree varied between 2 and 1,672 and the number of epiphyte species per tree varied between 32 and 4,632. For the ordination of the epiphyte assemblage, we used nonmetric multidimensional scaling (NMDS), using the metaMDS function in the vegan package (Oksanen et al., 2017). Epiphyte abundances were square root transformed and standardized with the Wisconsin double standardization. The Bray–Curtis index was used as dissimilarity index. The NMDS was performed with three dimensions. To find a stable solution, 1,000 random starts were run. To test whether differences between tree species with regard to species composition are significant, the multi response permutation procedure (mrpp function, vegan package) was used. To identify epiphyte species that are good indicators for one or several focal tree species, we used indicator species analysis (Dufrêne & Legendre, 1997). To this end, we used the multipatt function in the indicspecies package (version 1.7.6) which is an extension of the original indicator species analysis and considers combinations of groups of sites (De Cáceres, Legendre, & Moretti, 2010).

To test whether the composition of epiphyte assemblages was influenced by spatial distance between tree individuals, we used a mantel test (mantel function, vegan package). GPS coordinates were only available for 80 large trees sampled in 2017 (20 trees per species). Two of the Calophyllum trees contained no epiphytes and were thus removed from the dataset for this analysis. We again used the Bray–Curtis index to calculate the distance matrix of the epiphyte assemblages.

## RESULTS

### 3.1 General description of the epiphyte assemblage

Of the 285 sampled trees, only 55% hosted at least one epiphyte. Although most empty trees were quite small (median dbh: 2.7 cm), there were also three large trees (dbh ≥ 40 cm) that were completely empty and very small trees (dbh = 1 cm) that already hosted epiphytes. The trees hosted a total of 23,207 epiphytes (99 species) and 511 hemiepiphytes (six species, Table S1-1). The most abundant species was the orchid Christensonella uncata, which accounted for c. 20% of all individuals, while the fern Niphidium crassifolium occupied the largest number of trees (Table S1-1). These figures do not include the filmy ferns (eight additional species), for which we have not counted individuals. The species abundance distribution shows the typical, extreme bias: while there were 28 species represented by <10 individuals, nine species contributed >1,000 individuals each to the dataset (Tables S1-2 and S1-3). Not surprisingly for a lowland rainforest, the most important plant family, in terms of both individuals and species numbers, were the Orchidaceae with 47% of all species and 68% of all individuals (Table S1-2).

About 5% of the epiphytes in the dataset were not directly growing on the bark of the host tree, but on climbing plants or hemiepiphytes, which in turn used the sampled tree as support. This interaction is not surprising since herbaceous climbers, lianas and hemiepiphytes occupied almost all larger trees. Vines climbing addressed to the tree trunk, for example, Philodendron inaequilaterum Liebm., are very common. Only 3% of the 80 ‘large trees’ in 2017 were completely void of them and sometimes they were so dense as not to leave any space for epiphytes on the tree trunk. In one case, we counted >200 stems of an herbaceous climber around the trunk of a sampled tree. Moreover, lianas and larger hemiepiphytic individuals (at least ‘shrub size’) occurred in the crowns of 55% and 31% of the ‘large trees’ sampled in 2017 respectively. However, the focal
3.2 | Size–abundance relationships

As expected, there was a nonlinear relationship between tree size, that is, diameter at breast height (dbh), and the number of hosted epiphytes for all focal tree species (Figure 1). The accumulation of epiphytes with increasing dbh shows no signs of saturation. However, tree diameter is not an exact predictor of epiphyte abundance, as at a given dbh the variation of epiphyte abundance per tree is enormous. For example, the three tree individuals in our dataset that hosted the largest number of epiphyte individuals each (maximum number of counted epiphytes per tree: 1,699), while three other trees with a comparable dbh hosted fewer than 100 individuals. While the epiphyte accumulation curves with dbh of three of the focal tree species was quite similar, epiphyte abundance on one species (Aspidosperma) showed a markedly lower increase with increasing dbh.

3.3 | Tree growth rates and age estimates

Tree growth rates differed strongly between focal tree species, but were also highly variable among conspecifics. Calophyllum had by far the highest average annual diameter increment (0.21 ± 0.28 cm/year, mean ± SD, n = 159) while the average diameter increment of the other species was 30%–50% lower (Aspidosperma: 0.15 ± 0.22 cm/year, n = 595, Brosimum 0.11 ± 0.16 cm/year, n = 579, Manilkara: 0.12 ± 0.16 cm/year, n = 533). The high within-species variability is only partly explained by a change of diameter growth rate with tree size, as variability was high at any given dbh (Figure S1-2a). The interspecific differences in growth rates led to large differences in estimated tree age for a given size: A Calophyllum with a dbh of 100 cm is an estimated 223 years old, while a Brosimum with the same diameter is more than twice as old (588 years). The maximum ages of the sampled trees were 468 (Aspidosperma, dbh = 128 cm), 637 (Brosimum, dbh = 119 cm), 253 (Calophyllum, dbh = 111 cm) and 552 (Manilkara, dbh = 124 cm) years. Assuming that these are the maximum dbh values that can be attained by the respective tree species these figures can also be taken as first estimates of maximum tree longevity for this locality.

3.4 | Age–abundance relationships

Using tree age instead of dbh as predictor for epiphyte abundance results in quite different epiphyte accumulation curves (compare Figures 1 and 2). Now, Calophyllum has by far the fastest epiphyte accumulation rate, while accumulation on Brosimum is slowest.

**FIGURE 1** Epiphyte abundance as a function of the host tree’s diameter at breast height (dbh) and species identity. Data were fitted with a quasi-poisson generalized linear model and the minimum adequate model (abundance ~ dbh + tree species, Pseudo $R^2 = .69$) is depicted. Shaded bands indicate 95% confidence intervals.

**FIGURE 2** Epiphyte abundance as a function of host tree age and species identity. Data were fitted with a quasi-poisson generalized linear model and the minimum adequate model (abundance ~ age * tree species, Pseudo $R^2 = .70$) is depicted. Shaded bands indicate 95% confidence intervals. Tree age was estimated based on tree dbh using species-specific relationships between annual dbh increment and dbh (see Section 2).
3.5 | Do patterns change if abundant species are excluded?

To assess whether our results are fundamentally biased by common species (e.g., Christensonella uncata, which accounts for c. 20% of all individuals), we reran the above analyses, this time excluding all epiphyte species with >500 individuals from the dataset (11 species, accounting for 77% of the total). Interestingly, there were only minor changes in comparison to the patterns found for the whole dataset (compare Figure S1-3 to Figures 1 and 2).

3.6 | Influence of other dependent flora in the tree crown

Including liana and woody hemiepiphyte cover in the tree crown as a covariate improved the model fit significantly as compared to models using only dbh and tree species as explaining variables. Comparing model fit of quasi-poisson GLMs with all three variables (tree species, liana and hemiepiphyte cover, and tree dbh or tree age, respectively) with F-tests resulted in minimal adequate models including all variables and their interactions. Pseudo $R^2$ for the full model with tree dbh was .68, and .66 for the model with tree age - as compared to $R^2$ = .53 and .50 for the minimum adequate models fitted to the same dataset without liana and hemiepiphyte cover. Collinearity between liana and hemiepiphyte cover on the one hand and tree diameter or age on the other hand was not an issue, as the variables were almost completely independent (Pearson’s correlation: $R^2$ = .04 and .02, respectively). Interpreting the effect of a given variable in a model with a three-way interaction is difficult but liana and hemiepiphyte cover was generally positively correlated with epiphyte abundance and the effect was stronger in larger trees.

**FIGURE 3** Abundance of selected epiphyte species as a function of host dbh and species identity. The selected epiphyte species represent all unambiguously identifiable species with $n > 500$ individuals. Colour coding: red: Aspidosperma, green: Brosimum, blue: Calophyllum, purple: Manilkara. Data were fitted with a quasi-poisson generalized linear model (Pseudo $R^2$ are given in each panel). Full models (including tree species and dbh and their interaction) were simplified if the F-test upon single term deletion allowed for it. Depicted minimal adequate models include in all cases tree species and dbh and in the case of Dichaea panamensis, also their interaction. Shaded bands indicate 95% confidence intervals.
3.7 | Size–abundance and size–age relationships of single species

The accumulation patterns of the 10 most abundant epiphyte species with tree dbh or tree age, respectively, suggest that epiphyte species show differential host preferences (Figures 3 and 4). For example, while *Manilkara bidentata* seems to be the most suitable host for the orchid *Scaphyglottis behrii* and the fern *Elaphoglossum herminieri* (Figure 3c,f), this is not the case for the fern *Niphidium crassifolium* or the bromeliad *Tillandsia bulbosa* (Figure 3e,i). Filmy ferns (Hymenophyllaceae) occurred on 50% of the 80 large trees sampled in 2017. Interestingly, this group grew disproportionally often on *Brosimum* trees. While we found at least small patches on the majority of *Brosimum* and *Calophyllum* trees (90% and 70%, respectively), only few *Aspidosperma* and *Manilkara* trees hosted filmy ferns (25% and 15%, respectively). Accordingly, filmy fern abundance was significantly larger on *Brosimum* than on *Aspidosperma* or *Manilkara* (Kruskal–Wallis rank sum test, $\chi^2 = 36.09, df = 3, p < .001$, Figure S1-4).

Similar to the findings for overall epiphyte abundance, patterns for single species also depended strongly on the choice of predictor (compare e.g. abundance accumulation with dbh and age for *Elaphoglossum longicrure* (Figures 3 and 4d)).

3.8 | Composition of epiphyte assemblages

Although species composition of epiphyte assemblages did not strongly depend on tree species (Figure 5, NMDS ordination, centroids for tree species are close to each other and convex hulls are largely overlapping in all three dimensions), significant differences were found (MRPP, dissimilarity index: Bray–Curtis, 1,000 permutations, $A = 0.04, \delta = 0.82, p = .001$). These differences are not an artefact of spatial structure: the

**FIGURE 4** Abundance of selected epiphyte species as a function of host age and species identity. The selected epiphyte species represent all unambiguously identifiable species with $n > 500$ individuals. Colour coding: red: *Aspidosperma*, green: *Brosimum*, blue: *Calophyllum*, purple: *Manilkara*. Data were fitted with a quasi-Poisson generalized linear model (Pseudo $R^2$ are given in each panel). Full models (including tree species and dbh and their interaction) were simplified if the $F$-test upon single term deletion allowed for it. Depicted minimal adequate models include in most cases tree species, dbh and their interaction; exceptions (without interaction term) are *Elaphoglossum herminieri*, *Scaphyglottis behrii* and *Trichosalpinx orbicularis*. Shaded bands indicate 95% confidence intervals.
similarity of epiphyte assemblages on large trees did not increase with spatial proximity (Mantel test, \(r = .02, p = .31, 999\) permutations).

The indicator species analysis yielded 13 out of 44 tested epiphyte species with significant associations (Table S1-4). Of these, six species were associated with a single tree species, while seven species were associated with a combination of two or three tree species.

### 4 | DISCUSSION

Our first question was whether some tree species are better overall epiphyte hosts than others. Judging from the relationships of pooled epiphyte abundance per tree with dbh or estimated tree age, the answer to this question seems to be yes. However, the identification of the best host strongly depends on the used covariate (Figures 1

**FIGURE 5** Nonmetric multidimensional scaling (NMDS) ordination plots. Shown are all combinations of NMDS axes of the three-dimensional ordination of epiphyte abundances on sampled trees. Only occupied trees with dbh \(\geq 40\) (99 individuals) and epiphyte species with \(n \geq 30\) individuals (44 species) are included. Open circles: tree individuals. Lines represent convex hulls encompassing all trees of the respective species and connect the trees to the species’ centroid. Species scores of the most abundant epiphyte species \((n > 500)\) are added as weighted averages.

---

**Tree species**

- Aspidosperma
- Brosimum
- Calophyllum
- Manilkara

**Stress = 0.18**

**Convergence after 466 tries**
and 2). In the case of dbh, epiphyte abundance increased fastest in *Manilkara*, more slowly in *Calophyllum* and *Brosimum* and slowest in *Aspidosperma* (Figure 1). This sequence changes with the use of tree age (2). Now, epiphytes accumulate fastest in *Calophyllum*, substantially slower in *Manilkara*, followed by *Aspidosperma* and *Brosimum*. In the past, those studies that accounted for the fact that epiphyte abundance increases with tree size and age when investigating epiphyte host specificity unanimously used some measure of tree size (such as dbh or basal area) as a covariate (Wagner et al., 2015). Our results demonstrate that, in many cases, this approach will lead to spurious conclusions as it ignores the often-large growth rate differences between tree species.

Although the overall trends are highly significant, the predictive power of the explaining variables ‘host species’ and ‘dbh’ or ‘age’, for a particular tree is low (Figures 1 and 2). As an extreme example, we counted 1,692 epiphytes on a *Brosimum* with dbh = 91 cm (estimated age = 560 years), but only three epiphytic plants on an even larger conspecific (dbh = 107 cm, age = 610 years). This variability is certainly partly due to the fact that the easily measurable dbh is an imperfect proxy for the two factors that are actually of interest: bark surface area and tree age. Regarding bark surface area, differences among trees of the same species and dbh can result from stochastic events (e.g. the loss of parts of the crown via branch breakage) but also from natural variation among tree individuals with regard to the number, length and diameter of branches. The fact that estimates of tree age based on dbh are fraught with uncertainty can be deduced from the large scatter in Figure S1-2a. Differences depend on genetic identity, growing site, but also temporarily changing conditions, for example, growth spurts after gap formation (Bowman et al., 2013; Brienen & Zuidema, 2006). However, even an exact determination of bark surface area and tree age would not allow precise predictions of epiphyte abundance. For one, stochastic processes (e.g. dispersal) cause variability and second, additional, unconsidered factors modulate the expected number of epiphytes per tree. For example, it is well established that epiphyte abundance is positively correlated with humidity (Gehrig-Downie, Obregón, Bendix, & Gradstein, 2011). Humidity, in turn, is higher close to water bodies (such as the brook running through our study site, Figure S1-1) or at the bottom of valleys, while it is decreased at the edge of a treefall gap or at the top of a ridge. Moreover, as indicated by our data, the microclimate in a tree crown may also be modified by lianas and large, woody hemiepiphytes (e.g. species of the genus *Clusia* occurring at our study site). While liana and hemiepiphyte cover was uncorrelated with tree species, it significantly contributed to the remaining variance in per tree epiphyte abundance. Of course, this result could be explained in two, not mutually exclusive, ways: lianas and hemiepiphytes might modify the microclimatic conditions in the tree crowns or they might prefer the same conditions as epiphytes.

Given the large intraspecific variability in annual dbh increments, the calculated tree ages can only represent rough estimates for each individual tree. Especially for the largest trees, age estimates based on population averages of annual dbh increment may easily be too high because these trees are probably those that had above average growth rates, while many of the slow growing small trees in a population, which contribute to low average increment rates, may eventually die from shade-induced carbon starvation without reaching maximum tree sizes. To address the intraspecific variability in growth rates, bootstrapping methods have been developed (Bullock et al., 2004; Lieberman & Lieberman, 1985). However, this caveat does not affect our conclusion that the identification of good and poor hosts depends on the choice of tree age or size as explanatory variable. Our estimates of longevity (up to 637 years for *Brosimum*) are within the range of previously published estimates for tropical rainforest trees: three studies using tree ring analyses or stochastic simulations report maximum longevities between 427 and 661 years (Brienen & Zuidema, 2006; Fichtler et al., 2003; Lieberman, Lieberman, Hartshorn, & Peralta, 1985), while a radiocarbon-based study indicated that some tree individuals in the Brazilian Amazon attain >1,200 years (Chambers, Higuchi, & Schimel, 1998), although these extreme values have been contested (Worbes & Junk, 1999).

We further asked whether epiphyte species differ regarding their preferences for tree species. To answer this question, we used several approaches: we assessed changes in abundance with dbh and age, respectively, for the most abundant epiphyte species at the study site, we ran an indicator species analysis and we compared the dissimilarity of epiphyte assemblages on large individuals of the focal tree species using multivariate methods (NMDS, MRPP). The first approach produced evidence for differential host preferences, since not all abundant species showed the same ranking of host preference. Not surprisingly, preference patterns depended on the covariate: for example, none of the species had a clear preference for *Calophyllum* when dbh was used as a covariate, while in 70% of the cases such a preference emerged when using tree age as a covariate (Figures 3 and 4). However, in some cases, the distributional biases are so strong that conclusions are unaffected by the covariate. For example, according to both perspectives, the most preferred host of the fern *Elaphoglossum herminieri* is *Manilkara* (Figures 3 and 4c).

Even though our dataset indicates that epiphyte species differ from each other regarding their accumulation rates on the four tree species the observed patterns are only correlative and as such do not prove causation. Take, for example, the orchid *Scaphyglottis behrii* (Figures 3 and 4f), which is, on average, strongly underrepresented on *Brosimum*. However, on one medium-sized *Brosimum* tree it was as abundant as on similar sized *Manilkara* trees. To test rigorously whether the overall pattern truly indicates ‘avoidance’, one should transplant commonly grown *Scaphyglottis behrii* on *Manilkara* and *Brosimum* trees and compare their fitness (e.g. relative growth rates and survival).

The indicator species analysis identified about a third of the epiphyte species as significantly associated with one or several of the four tree species. The differential associations with tree species (among the associations with one tree species, one with *Brosimum*, two with *Calophyllum* and three with *Manilkara*) yield additional evidence for the existence of differential host specificity and the indicator species lend themselves for informed experiments. The
fact that the tree species were not clearly separated in the NMDS ordination suggests differential host specificity to be rather weak (Figure 5), although species-specific host biases were sufficient to translate into significant differences of epiphyte species composition among the focal tree species (MRPP). Differential host preferences are necessary for tree diversity to contribute to the diversity of vascular epiphytes. Our results yield evidence that they exist but indicate at the same time that many epiphyte species have parallel host preferences. The potential importance of tree diversity as a driver for epiphyte diversity seems thus relatively small but existent. Moreover, we focused here on only four tree species. Although the focal species differed in some traits (see Appendix S2), trait differences could have been more extreme if other focal species had been chosen (e.g. deciduous vs. evergreen species). Thus, clearer signals of differential host specificity might emerge if a different or larger set of host species were studied.

So far, we have treated tree age and size as covariates that possibly confound our conclusions from field studies regarding host specificity. On the one hand, this is necessary as all trees are inherently growing and ageing organisms. On the other hand, tree longevity and maximum size are also species-specific traits which, as such, can cause host specificity. For example, although Figure 2 identifies Calophyllum as the host species that accumulates epiphytes fastest, this species is relatively short-lived. Thus, poorer hosts in terms of lower accumulations rates (like Manilkara or Brosimum) are available for much longer periods for epiphytic colonization and population growth. Thus, it clearly depends on the chosen perspective which tree species is called good or poor host. Long-lived tree species should be especially critical for epiphyte species that are slow colonizers and need a long time to reach maturity. If long-lived tree species are missing, for example, in tree plantations with short rotation periods, such epiphyte species will probably be unable to form viable (meta-)populations, even if the tree species offer otherwise favourable traits (Einzmann & Zotz, 2016). Available data suggest that in comparison to terrestrial herbaceous plants, epiphytes have generally low population growth rates and long life cycles, which underlines the importance of long-lived tree species (Zotz, 2016). Compilations of studies on bromeliads and orchids indicated very low relative growth rates and the estimated age at first reproduction ranged between 6 and 20 years (Zotz, 2016). Only little is known about epiphyte longevity but anecdotal evidence from cultivated plants indicates that orchids can live for more than 100 years (Anonymous, 1968) and a few in situ observations on bromeliads and orchids also indicate that longevity is often in the range of several decades (Schmidt & Zotz, 2002 and G. Zotz, unpublished). As exceptions to the rule, some twig orchids, for which high turnover times are arguably crucial in sight of the instability of their substrate, may reach maturity in less than a year (Chase, 1986). In our study system, the overrepresentation (according to the indicator species analysis, Table S1-4) of several orchid species on the longer-lived tree species (Brosimum and Manilkara) as compared to the much shorter lived Calophyllum might be explained by differences in tree longevity.

The maximum size of a tree species will also have direct consequences for two reasons. For one, smaller trees offer less surface for colonization. In our study system, the largest sampled Calophyllum trees were substantially smaller than the largest sampled individuals of the other species (Figure 1). Thus, if our criterion for host quality was epiphyte abundance on the largest encountered individuals, Calophyllum would perform badly. The second reason why maximum tree size could cause (differential) host specificity is due to the fact that in the forest environment, the microclimate in a tree crown is determined by the relative position of the tree in the forest canopy. Understorey tree species, that is, those that never reach the forest overstorey will be completely avoided by epiphyte species that are restricted to exposed growing conditions (unless a tree grows at the edge of a forest stand). In our study system, all focal tree species all reach the forest’s overstorey prompting the null expectation that species composition in mature individuals is similar. However, as in our system tree growth rates and longevity differ, exposed growing sites might be available for different time spans with consequences for the abundance of heliophile species.

5 | CONCLUSIONS

The outcome of studies on epiphyte host specificity critically depends on the inclusion of species-specific tree growth rates. Studies on epiphyte distributions among different tree species in systems where data on tree growth rates are unavailable may still yield valuable results. However, in such cases researchers should be aware that tree longevity is an unquantified species-specific trait that may easily mask the effect of other traits such as bark characteristics.

This study also conveys an impression of the complexity of the studied system. Given the large number of potentially relevant tree characteristics, the high species diversity and the difficulty to adequately consider confounding covariables, studies that correlate epiphyte abundance to host tree species can only serve as starting points to identify potential host biases. They are a necessary first step leading to informed experiments. However, to unequivocally corroborate putative host associations, field experiments (e.g. transplanting epiphytes, systematically sowing seeds on different tree species, etc.) are indispensable. Moreover, to disentangle the relative influence of covarying tree traits, we need to experimentally manipulate potential proximate factors (e.g. light or water). It is thus now time to take the next step and move into the modern age of experimental ecology.

ACKNOWLEDGEMENTS

This study would not have been possible without the dedicated help of many persons. The following persons helped with assembling the 2017 dataset and the tree trait data: Christian Göbel, Florian Masche, Paula Morales, Lilisbeth Rodríguez, Sebastian Schäfer and Tizian Weichgrebe. The census dataset has been
assembled in collaboration with Glenda Mendieta Leiva. We were supported in the field by Ruth Arias, Maritza Moya, María Vega, Rousmery Bethancourt and Eduardo Sánchez. We thank CTFS-ForestGeo for providing the permanent plot data and the Republic of Panama for making its natural resources available (research permits: SE/P-32-09, SE/P-14-10, SC/P-26-10, SE/P-3-11, SE/P-32-16, and SC/P-3-18). This work was funded by the DFG (ZO 94/5-1 and WA 3936/1-1).

AUTHORS’ CONTRIBUTIONS
K.W. and G.Z. conceived the ideas and designed the methodology; K.W. collected and analysed the data; K.W. led the writing of the manuscript with input by G.Z.

DATA AVAILABILITY STATEMENT
Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.1jwstqiqs (Wagner & Zotz, 2019).

ORCID
Katrin Wagner https://orcid.org/0000-0003-4326-1086
Gerhard Zotz https://orcid.org/0000-0002-6823-2268

REFERENCES
Anonymous. (1968). How old is an orchid plant? American Orchid Society Bulletin, 37, 405.
Benavides, A. M., Vasco, A., Duque, A. J., & Duivenvoorden, J. F. (2011). Association of vascular epiphytes with landscape units and phorophytes in humid lowland forests of Colombian Amazonia. Journal of Tropical Ecology, 27, 223–237. https://doi.org/10.1017/S0266467410000726
Blüthgen, N., Menzel, F., Hovestadt, T., Fiala, B., & Blüthgen, N. (2007). Specialization, constraints, and conflicting interests in mutualistic networks. Current Biology, 17, 341–346. https://doi.org/10.1016/j.cub.2006.12.039
Bowman, D. M. J. S., Brienen, R. J. W., Gloor, E., Phillips, O. L., & Prior, L. D. (2013). Detecting trends in tree growth: Not so simple. Trends in Plant Science, 18, 11–17. https://doi.org/10.1016/j.tplants.2012.08.005
Brienen, R. J. W., & Zuidema, P. A. (2006). Lifetime growth patterns and ages of Bolivian rain forest trees obtained by tree ring analysis. Journal of Ecology, 94, 481–493. https://doi.org/10.1111/j.1365-2745.2005.01080.x
Brown, J. H. (2014). Why are there so many species in the tropics? Journal of Biogeography, 41, 8–22. https://doi.org/10.1111/jbi.12228
Bullock, S. H., Turner, R. M., Hastings, J. R., Escoto-Rodriguez, M., Ramírez Apud López, Z., & Rodríguez-Navarro, J. L. (2004). Variance of size-age curves: Bootstrapping with autocorrelation. Ecology, 85, 2114–2117. https://doi.org/10.1890/03-3115
Callaway, R. M., Reinhart, K. O., Moore, G. W., Moore, D. J. M., & Pennings, S. C. (2002). Epiphyte host preferences and host traits: Mechanisms for species-specific interactions. Oecologia, 132, 221–230. https://doi.org/10.1007/s00442-002-0943-3
Chambers, J. Q., Higuchi, N., & Schimel, J. P. (1998). Ancient trees in Amazonia. Nature, 391, 135–136. https://doi.org/10.1038/34325
Chase, M. W. (1986). A monograph of Leuchloss (Orchidaceae), Systematic Botany Monographs, 14, 1–97. https://doi.org/10.2307/25027638
Chown, S. L., & Gaston, K. J. (2000). Areas, cradles and museums: The latitudinal gradient in species richness. Trends in Ecology & Evolution, 15, 311–315. https://doi.org/10.1016/S0169-5347(00)01910-8
Colwell, R. K., & Hurtt, G. C. (1994). Nonbiological gradients in species richness and a spurious rapoport effect. The American Naturalist, 144, 570–595. https://doi.org/10.1086/285695
Condit, R. (1998). Tropical forest census plots. Berlin, Germany: Springer.
Condit, R., Aguilar, S., Hernandez, A., Perez, R., Lao, S., Angehr, G., ... Foster, R. B. (2004). Tropical forest dynamics across a rainfall gradient and the impact of an El Niño dry season. Journal of Tropical Ecology, 20, 51–72. https://doi.org/10.1017/S026646740001081
Condit, R., Perez, R., Aguilar, S., & Lao, S. (2009). Sherman 6 ha forest census plot data. Retrieved from http://ctfs.si.edu/webatlas/data_sets/sherman/
De Cáceres, M., Legendre, P., & Moretti, M. (2010). Improving indicator species analysis by combining groups of sites. Oikos, 119, 1674–1684. https://doi.org/10.1111/j.1600-0706.2010.18334.x
Dufrene, M., & Legendre, P. (1997). Species assemblages and indicator species: The need for a flexible asymmetrical approach. Ecological Monographs, 67, 345–366. https://doi.org/10.2307/2963459
Ehrlich, P. R., & Raven, P. H. (1964). Butterflies and plants: A study in coevolution. Evolution, 18, 586–608. https://doi.org/10.1111/j.1558-5646.1964.tb01674.x
Einzmann, H. J. R., Beyschlag, J., Hofhansl, F., Wanek, W., & Zotz, G. (2015). Host tree phenology affects vascular epiphytes at the physiological, demographic and community level. AoB Plants, 7, plu73. https://doi.org/10.1093/aobpla/plu073
Einzmann, H. J. R., & Zotz, G. (2016). How diverse are epiphyte assemblages in plantations and secondary forests in tropical lowlands? Tropical Conservation Science, 9, 629–647. https://doi.org/10.1177/194008291660090205
Fichtler, E., Clark, D. A., & Worbes, M. (2003). Age and long-term growth of trees in an old-growth tropical rain forest, based on analyses of tree rings and 14C. Biotropica, 35, 306–317. https://doi.org/10.1111/j.1744-7429.2003.tb00585.x
Flores-Palacios, A., & García-Franco, J. G. (2006). The relationship between tree size and epiphyte species richness: Testing four different hypotheses. Journal of Biogeography, 33, 323–330. https://doi.org/10.1111/j.1365-2699.2005.01382.x
Gehrig-Downie, C., Obregnón, A., Bendix, J., & Gradstein, S. R. (2011). Epiphyte biomass and canopy microclimate in the tropical lowland cloud forest of French Guiana. Biotropica, 43, 591–596. https://doi.org/10.1111/j.1744-7429.2010.00745.x
Hillebrand, H. (2004). On the generality of the latitudinal diversity gradient. The American Naturalist, 163, 192–211. https://doi.org/10.1086/381004
Johansson, D. (1974). Ecology of vascular epiphytes in West African rain forests. Acta Phytogeographica Suecica, 59, 1–129.
Laube, S., & Zotz, G. (2006). Long-term changes of the vascular epiphyte assemblage on the palm Socratea exorrhiza in a lowland forest in Panama. Journal of Vegetation Science, 17, 307–314. https://doi.org/10.1111/j.1654-1103.2006.tb02450.x
Leigh, E. G., Davidar, P., Dick, C. W., Puyraudeau, J. P., Terborgh, J., ter Steege, H., & Wright, S. J. (2004). Why do some tropical forests have so many species of trees? Biotropica, 36, 447–473. https://doi.org/10.1111/j.1744-7429.2004.tb00342.x
Lieberman, D., Lieberman, M., Hartshorn, G., & Peralta, R. (1985). Growth rates and age-size relationships of tropical wet forest trees in Costa Rica. Journal of Tropical Ecology, 1, 97–109. https://doi.org/10.1017/S026646740000016X
Lieberman, M., & Lieberman, D. (1985). Simulation of growth curves from periodic increment data. Ecology, 66, 632–635. https://doi.org/10.2307/1940415
McKenna, D. D., & Farrell, B. D. (2006). Tropical forests are both evolutionary cradles and museums of leaf beetle diversity. Proceedings of the National Academy of Sciences of the United States of America, 103, 10947–10951. https://doi.org/10.1073/pnas.0602712103
Merwin, M. C., Rentmeester, S. A., & Nadkarni, N. M. (2003). The influence of host tree species on the distribution of epiphytic bromeliads in experimental monospecific plantations, La Selva, Costa Rica. Biotropica, 35, 37–47. https://doi.org/10.1111/j.1744-7429.2003.tb02060.x

Mittelbach, G. G. (2012). Community ecology. Sunderland, UK: Sinauer Associates.

Naranjo, C., Iriondo, J. M., Ríofrio, M. L., & Lara-Romero, C. (2019). Bioclimatic and biodiversity. Learning to estimate epiphytic species diversity in two upper Amazonian forests. Journal of Ecology, 111, 1115–1118. https://doi.org/10.1111/1365-2745.13333

Sotala, M., & Zotz, G. (2017). How old are tropical trees? The persistence of a myth. International Association of Wood Anatomists Journal, 20, 255–260. https://doi.org/10.1163/22941932-90000689

Worbes, M., & Junk, W. J. (1999). How old are tropical trees? The persistence of a myth. International Association of Wood Anatomists Journal, 20, 255–260. https://doi.org/10.1163/22941932-90000689

Wright, D.H. (1983). Species-energy theory – An extension of species-area theory. Oikos, 41, 496–506. https://doi.org/10.2307/3544109

Wyse, S. V., & Burns, B. R. (2011). Do host bark traits influence trunk epiphyte communities? New Zealand Journal of Botany, 39, 296–301.

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. Basel, Switzerland: Springer International Publishing.

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 – Correlates with tree size, tree age and bryophyte cover. Journal of Tropical Ecology, 19, 81–90. https://doi.org/10.1017/S026647403003092

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). Mixed effects models and extensions in ecology with R. New York, NY: Springer.

SUPPORTING INFORMATION

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

How to cite this article: Wagner K, Zotz G. Including dynamics in the equation: Tree growth rates and host specificity of vascular epiphytes. J Ecol. 2020;108:761–773. https://doi.org/10.1111/1365-2745.13333