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RESEARCH ARTICLE

# Directional changes over time in the species composition of tropical vascular epiphyte assemblages

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## Abstract

1. Understanding the degree to which deterministic and stochastic processes drive community assembly is an ongoing focus of research in community ecology. This effort is strongly biased towards ground-rooted plants, resulting in a limited understanding of communities of other life-forms, such as structurally dependent plants. Vascular epiphytes are sessile organisms growing non-parasitically on three-dimensional dynamic patches, their host plants. Since negative biotic interactions are thought to play a minor role in vascular epiphyte assembly, in some forests, epiphytes are fascinating model organisms to understand the prevalence of environmental filtering in shaping community assembly.
2. We assessed the contribution of deterministic processes on the temporal dynamics of vascular epiphyte assemblages by tracking the direction of changes in composition, species richness and abundance in time at different ecological and spatial scales. We made use of a globally unique dataset from a lowland forest in Panama. We predict that if niche-based mechanisms dominate, (a) temporal changes will be directional and (b) differences in the species composition of epiphyte assemblages will be primarily related to host plant characteristics and, to a lesser degree, to the distance between host trees.
3. We show that temporal changes in vascular epiphyte assemblages were directional at different ecological scales, such as the forest patch, host species or individual tree assemblages. Epiphyte assemblages on host trees became more similar in their composition over time than expected by chance, and these changes were not due to homogenisation. While host characteristics were related to these directional changes, host structure rather than host identity was more strongly related to variation in assemblage dissimilarity, while spatial distance among trees was of minor importance. The observed directionality was primarily due to environmental filtering.
4. This study provides the first evidence that niche-based mechanisms dominate the dynamics of vascular epiphyte assemblages. Analysing temporal patterns of vascular epiphyte assemblages is a first important step towards understanding

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the relative importance of deterministic processes for diversity maintenance of one of the most diverse plant groups in the tropics.

5. *Synthesis*. Directionality in the temporal changes of epiphyte assemblages suggests that niche-based mechanisms dominate these temporal changes. Host size over host identity is the most important environmental filter for epiphyte assemblages establishment.

**KEYWORDS**
community dynamics, directional changes, determinism, environmental filtering, host species, host structure, temporal changes, long-term changes

## 1 | INTRODUCTION

Understanding variation in the relative importance of deterministic and stochastic processes in community assembly is an ongoing focus of research in community ecology (Shipley et al., 2012; Weiher & Keddy, 1995). Deterministic processes are species interactions and 'environmental filtering' (selection imposed by the abiotic environment), whereas stochastic processes are dispersal, disturbances and births and deaths (Chase & Myers, 2011). It has been suggested that the relative importance of each process type on community assembly varies for different taxa and across spatial and temporal scales (Chase, 2014; Chu et al., 2007; Farjalla et al., 2012). Consequently, temporal community dynamics emerging from deterministic and stochastic processes are likely to be different and thus provide a signature of the underlying processes (e.g. Maren et al., 2018; Stegen et al., 2013).

Vascular epiphytes are sessile organisms living non-parasitically on three-dimensional dynamic patches (i.e. host plants, Zotz, 2016). From an epiphyte perspective, newly establishing trees represent a new substrate sensu Platt and Connell (2003) in the context of natural disturbance and community assembly. As hosts grow, changes in their characteristics influence epiphyte assemblages development (Taylor & Burns, 2015). The production and ageing of a new substrate increases the habitable area and habitat heterogeneity (Zotz, 2016), which will increase species richness (Buckley, 2011; Flores-Palacios & Garcia-Franco, 2006; Hortal et al., 2009; Taylor & Burns, 2015) and abundance (Ockinger & Nilsson, 2010; Snäll et al., 2004; Spruch et al., 2019). The environmental heterogeneity (Stein et al., 2014) caused by structural enrichment (Zotz & Vollrath, 2003) resembles that created by a founder or pioneer species in the context of primary succession in terrestrial groups, thus rendering the differentiation of the ecological processes behind the observed dynamics challenging. Directional replacement of species is expected on new substrates; that is, an early successional species is replaced by late-successional species (see references within Platt & Connell, 2003), as in primary succession. In the case of vascular epiphytes, it is contested whether the concept of typical primary succession appropriately captures the nature of the ecological processes behind epiphyte assemblage dynamics (Zotz, 2016). Instead, it may rather be conceptualised as a facilitation cascade via successive habitat formation (during host ontogeny) and modification (Thomsen et al., 2010, 2018).

In contrast to ground-rooted plants, there is limited understanding of the processes driving vascular epiphyte assemblages. The composition of vascular epiphyte assemblages is assumed to be mainly defined by abiotic factors, for example, vegetative growth and spatial distribution are mainly limited by water availability as the major cause of mortality (Ding et al., 2016; Laube & Zotz, 2003; Olaya-Arenas et al., 2011; Rascher et al., 2012; Zuleta et al., 2016). However, the relative role of deterministic and stochastic processes in vascular epiphyte assemblage composition has yet to be established.

The relative importance of the processes driving community assembly may differ between epiphytes and ground-rooted plants (Zotz, 2016). This conjecture is primarily based on the structural dependency of epiphytes; they are physically dependent on host plants. Host tree species provide patches with distinct conditions for the development of vascular epiphyte assemblages (Wagner et al., 2015). Hosts can affect epiphyte assemblages via differences in architecture (Cardelus & Chazdon, 2005; Einzmann et al., 2014), physical and chemical bark characteristics (Benzing & Renfrow, 1974; Callaway et al., 2002), growth rate (Flores-Palacios & Garcia-Franco, 2006; Zotz & Vollrath, 2003), and canopy dynamics (Sarmento Cabral et al., 2015; Wagner & Zotz, 2020). Moreover, fundamental characteristics of these 'islands', such as substrate dynamics (Fahrig, 1992; Spruch et al., 2019; Taylor & Burns, 2015), change with time (Fahrig, 1992; Snäll et al., 2005). Thus, host age affects species richness, composition, abundance (Lie et al., 2009; Wagner & Zotz, 2020) as well as dynamics (Fedrowitz et al., 2012) of vascular and non-vascular epiphytes.

The absence of a species from a particular habitat may be due to lack of dispersal, habitat unsuitability (environmental filtering) and negative biotic interactions (Cadotte & Tucker, 2017). In general, negative biotic interactions (competition, herbivore pressure) are thought to play a minimal role in vascular epiphyte assembly (Burns & Zotz, 2010; Taylor et al., 2016; Zotz, 2016). Kraft et al. (2015) pointed out that a strict definition of environmental filtering refers to cases where the abiotic environment prevents establishment or persistence in the absence of biotic interactions;

therefore, epiphytes are interesting model organisms to understand the prevalence of environmental filtering in shaping community assembly.

Environmental filtering is most often inferred from the presence of non-random assemblage patterns (Cadotte & Tucker, 2017). For epiphytes, the increase in mean pair-wise compositional similarity over time for epiphyte assemblages on two different host species in lowland forests (Laube & Zotz, 2006a, 2007) provides tentative evidence for directional changes in assemblage composition (Mendieta-Leiva & Zotz, 2015). Using a unique new dataset, comprising consecutive epiphyte censuses from an old-growth lowland forest in Panama covering more than a decade, we investigate the relative importance of niche and neutral processes for assembly by examining species compositional changes, dispersal limitation, and the potential effect of host tree identity and host size. We use tree individuals as the sampling unit, treating them analogous to plots in terrestrial vegetation ecology. Trees are discrete habitable patches with delimited borders (Southwood & Kennedy, 1983) and can be conceptualised as habitat islands for epiphytes (Ellis, 2012; Taylor & Burns, 2015) with their own dynamics (Wagner & Zotz, 2020). Assuming dominance of neutral processes, we predict that (a) species composition of vascular epiphytes should not exhibit 'directional' change over time; (b) epiphyte species composition of epiphyte assemblages does not change with host tree species and host size; (c) differences in epiphyte species composition are related to the distances among trees, indicating the effects of dispersal limitation. In contrast, if niche-based mechanisms dominate, we predict directionality in changes of species composition and that differences in epiphyte species composition are related to differences in host plant properties but not to among host tree distance.

## 2 | MATERIALS AND METHODS

### 2.1 | Census and datasets

To quantify community dynamics, we followed the fate of vascular epiphyte assemblages on host tree individuals, the sampling unit, by means of repeated censuses within a lowland forest patch. Censuses were carried out at the Canopy Crane site in the San Lorenzo reserve (Figure S1), near the Atlantic coast of the Republic of Panama. This natural wet evergreen tropical forest (elevation 130 m a.s.l.) has a canopy height of 35–45 m. The crane was installed in 1997 with minimum disturbance, only two trees had to be removed and our study started 2 years later. The site is considered of very low human disturbance. Annual rainfall averages 3,400 mm (Wright et al., 2003).

We recorded the occurrence of all vascular epiphytes by inspecting every individual tree of a diameter breast height (DBH) ≥ 10 cm at all heights using a 54-m tall construction crane equipped with a small gondola. The accessible area is almost 1 ha. The census protocol was based on Zotz (2007); individuals with leaves or fronds smaller than 0.5 cm in length were not included. Individuals were counted as a survivor, recruit or dead by comparison with data from the previous census. This analysis focuses on epiphyte assemblages on a host tree and not at the plot scale. Thus, the number of trees included in each dataset was determined by the number of live and occupied trees at all censuses and data may sometimes differ from those reported in Laube and Zotz (2006a) and Zotz and Schultz (2008).

We analysed two datasets: The first consists of the data of two censuses spanning *c*. 10 years and will be referred to as 'FOREST' (compare Zotz & Schultz, 2008). Here, we recorded the fate of individuals and analysed the development of epiphyte assemblages on 207 tree individuals first recorded between 1998 to 2000 and again between 2010 to 2012, comprising 67 tree species within 32 families distributed in half of the crane area (0.4 ha, Figure S1). The second set consists of a series of five fine-grained censuses (shorter intervals) carried out about every other year (within 2–3 weeks) for 11 years (1999–2010) on 30 individuals of the host palm *Socratea exorrhiza*, which are scattered across the whole crane area (*c*. 1 ha, Figure S1), referred to as 'SOCRATEA' (compare Laube & Zotz, 2006a). Within the coarse-grained FOREST census, there are also 35 trees of *Socratea exhorriza* from which SOCRATEA is a subset.

*Socratea exhorriza* is a palm with stilt roots and arborescent habit (Rich, 1987), which in contrast to most Arecaceae increases in trunk diameter with height (Chave et al., 2008; Schatz et al., 1985). Although palms have neither branches nor a peeling bark, they lose their fronds, which causes disturbances throughout the trunk as the fronds fall down. Thus, like other trees, they are subjected to the dynamics of the forest, but when a nearby branch or tree falls, epiphytes growing on palms may be subjected to even harsher changes in microclimate as palms cannot offer a buffer, as trees do within their inner crowns.

We recorded the position of each individual epiphyte, height above ground, and in SOCRATEA a large proportion of individuals were also marked. In either database *c*. 4% of individuals could not be identified to species. These were excluded from our analyses. Analyses include only individuals of true epiphytes ('true' or obligate epiphytes are those that spend their entire life cycle in a host tree without making contact to the ground), hemi-epiphytes and nomadic vines were excluded (life-forms sensu Zotz, 2013, Table 1; Table S1). Species names follow the Tropicos® database (Tropicos.org., 2021).

We argue that in epiphytes, the combination of the three-dimensionality of their spatial location (within the tree individual), their vertical stratification (e.g. partitioning along the vertical gradient of the forest) and spatially non-random distribution (e.g. across host species or within the tree individual) produce inherent ecological scales, which can be potentially used as ecologically meaningful analytical scales (Mendieta-Leiva & Zotz, 2015). This is also done with non-vascular epiphytes (Ellis, 2012). For example, assemblages on individual host trees can be grouped (Figure 1) by single host tree species or a contiguous forest patch (Ellis, 2012; Mendieta-Leiva & Zotz, 2015). Therefore, we delimited tree and forest assemblages (Figure 1), according to host tree individuals, host tree species (Wagner et al., 2015) and a forest patch (Mendieta-Leiva & Zotz, 2015).

**TABLE 1** Changes in epiphyte assemblages between censuses (Figure 1a): a 10-year interval (FOREST, 207 host trees) and 2–3 year intervals (SOCRATEA, 30 palm trees of the species *Socratea exhorriza*). Vital rates were calculated: survival as the number of individuals remaining from the previous census, recruitment as the number of new individuals in a census and annual percentage mortality rates after Sheil and May (1996) using the number of individuals either not found or still in place and dead. Error terms are standard deviations. Species turnover rates were calculated after Bakker et al. (2003)

| DATASET | FOREST | | SOCRATEA | | | | |
|---|---|---|---|---|---|---|---|
| **Characteristic** | **2002** | **2012** | **1999** | **2002** | **2004** | **2007** | **2010** |
| Number of species | 93 | 92 | 47 | 44 | 44 | 39 | 43 |
| Number of individuals (% increase) | 11,490 | 13,983 (22) | 416 | 587 (41) | 639 (9) | 718 (12) | 1258 (75) |
| Average abundance per host tree (±*SD*) | 55 ± 214 | 68 ± 204 | 16 ± 16 | 23 ± 21 | 25 ± 254 | 28 ± 26 | 48 ± 50 |
| Average species number per host tree (±*SD*) | 6 ± 9 | 7 ± 9 | 5 ± 4 | 5 ± 3 | 6 ± 5 | 6 ± 4 | 8 ± 5 |
| Number of individuals dead between censuses (Annual % mortality rates) | | 8,870 (12) | | 182 (16) | 198 (20) | 342 (23) | 315 (18) |
| Number of individuals (recruitment %) | | 11,363 (81) | | 353 (60) | 250 (39) | 421 (59) | 855 (68) |
| Species turnover rates (range 0–1) | | 0.09 | | 0.18 | 0.10 | 0.13 | 0.15 |
| Pearson correlation $R^2$ between species richness and DBH (95% CI) | 0.74 (0.7–0.8) | 0.67 (0.6–0.7) | 0.34 (0–0.6) | 0.43 (0–0.7) | 0.41 (0–0.7) | 0.44 (0.1–0.7) | 0.60 (0.3–0.3) |
| Pearson correlation $R^2$ between abundance and DBH (95% CI) | 0.62 (0.5–0.7) | 0.60 (0.5–0.7) | 0.37 (0–0.7) | 0.46 (1–0.7) | 0.53 (0.2–0.8) | 0.54 (0.2–0.7) | 0.45 (0–0.7) |

## 3 | DATA ANALYSIS

### 3.1 | Epiphyte richness, abundance, mortality and recruitment

We characterised and compared the fine-grained censuses (SOCRATEA, censuses every other year for 11 years) and the coarse-grained censuses (FOREST, one interval of 10 years) as follows: (a) *Changes in epiphyte abundance at the tree level* were assessed by comparing epiphyte abundance per tree between censuses using linear mixed-effect models (LMEs). To account for temporal pseudoreplication and to deal with differences in abundance among host species, tree individuals and tree species were included as random effects in the case of the FOREST census. For SOCRATEA, only tree individuals were included as random effects and multiple comparisons were carried out with Tukey's posthoc test. Overdispersion was dealt with by log-transforming the response variable (abundance, natural logarithm), and normality was checked by inspecting model residuals (Crawley, 2005). We used the functions *'lmer'* for the models and *'glht'* for the posthoc tests from the R packages LME4 and MULTCOMP, respectively (Bates et al., 2012; Hothorn et al., 2008). (b) *Parameters* of epiphyte assemblages between censuses (mortality and recruitment) were calculated by dividing the number of remaining individuals by the original number of individuals (multiplied by 100) and dividing the number of new individuals by the total number of individuals observed per census (multiplied by 100), respectively. (c) *The general trend of increased species richness and abundance at the forest level* was evaluated using a GLMM to assess the changes in abundance or species richness, respectively, as a function of tree size and time. We used tree individuals as random effects to control for variability of the response variables across tree individuals and host tree species.

### 3.2 | Temporal dissimilarity of tree-assemblages

Temporal changes in the species composition of epiphyte assemblages on individual trees (individual tree-assemblages, Figure 1 B2) were assessed using a temporal beta-diversity index (Legendre, 2019) for both presence/absence (Sorensen) and abundances-per-species (Bray-Curtis). The beta-diversity index decomposes dissimilarities (turnover) into loss and gain components (of species or abundances-per-species, Legendre, 2019). Pair-wise dissimilarities were computed between assemblages at time 1 and time 2 (T1 and T2) on each tree individual (as analogous to a 'site' or plot, Figure 1 B2). The index also tests for significance in the difference between gains and losses of species (or abundances-per-species). Consistent, significant gains or losses in time indicate the overall direction of change in assemblages (Legendre, 2019). To calculate temporal beta-diversity indices, we used the function '*TBI*' (Legendre & De Caceres, 2013) from the package ADESPATIAL (Dray et al., 2019). Given that the index calculates dissimilarities, analyses were carried out only for trees that were populated at all censuses. Temporal differences were assessed for both datasets, the coarse-grained and fine-grained censuses (FOREST and SOCRATEA).

### 3.3 | Changes of within-census mean dissimilarity

To evaluate changes in dissimilarity within-census, that is, of the forest patch and among host tree-assemblages, we calculated the mean dissimilarity of tree epiphyte assemblages for the FOREST, SOCRATEA and host species assemblages per census (Figure 1 B1). For 17 host species with at least three individuals (out of 65), the dissimilarity of epiphyte assemblages was calculated using the Chao index implemented in the '*vegdist*' function from the R package VEGAN (Oksanen et al., 2019). Differences in mean dissimilarity between censuses were assessed using Wilcoxon signed-rank test.

Dissimilarity, as assemblage dissimilarity independent from differences in alpha diversity, was assessed using the Raup-Crick metric (βrc) for presence/absence data (Chase et al., 2011). This was done for the FOREST, SOCRATEA and nine host tree species assemblages (i.e. host species with at least three tree individuals hosting at least five epiphyte individuals at any census, to avoid spurious results, Figure 1a; Table S2) using 999 randomisations, following Chase et al. (2011). To assess whether compositional dissimilarity of vascular epiphyte assemblages, as variation in assemblage dissimilarity independent from differences in alpha diversity, was related to differences in host tree sizes (DBH), we ran a mantel test (function '*mantel.test*') using the R package APE (Paradis & Schliep, 2019), with 999 permutations. The Raup-Crick dissimilarity matrix was correlated with a distance matrix of DBH values for each host tree for the first and second census, using Euclidean distance. To assess whether compositional dissimilarity of epiphyte assemblages was spatially structured, we ran a mantel correlogram (function '*mantel.correlog*') using the R package NCF (Bjornstad, 2020). The Raup-Crick dissimilarity matrix was correlated with a distance matrix with Euclidean distances between host trees. We used 5-m increments for a total range from 20 to 100 m of distance.

## 3.4 | The relative importance of deterministic or stochastic processes in compositional changes of vascular epiphyte assemblages

To find out whether deterministic or stochastic processes dominate changes in dissimilarity, we used a null model approach. We calculated an expected null distribution of dissimilarity (betadiversity) using the Raup-Crick metric (βrc) for presence/absence data (Chase & Myers, 2011). βrc creates this null dissimilarity based on random assembly processes, using a given alpha- and gamma-diversity (Chase et al., 2011). The βrc indicates if and how strongly the observed dissimilarity between epiphyte assemblages deviates from null expectation with values ranging from −1 to 1. A 0 indicates that assemblages are as dissimilar as expected by chance and highly stochastic likely due to relatively unimpeded dispersal among assemblages (no difference between observed dissimilarity and null expectation). Negative values indicate that assemblages are less dissimilar than expected by chance, possibly due to deterministic environmental filters shared across sites that create highly similar assemblages. Positive values indicate that

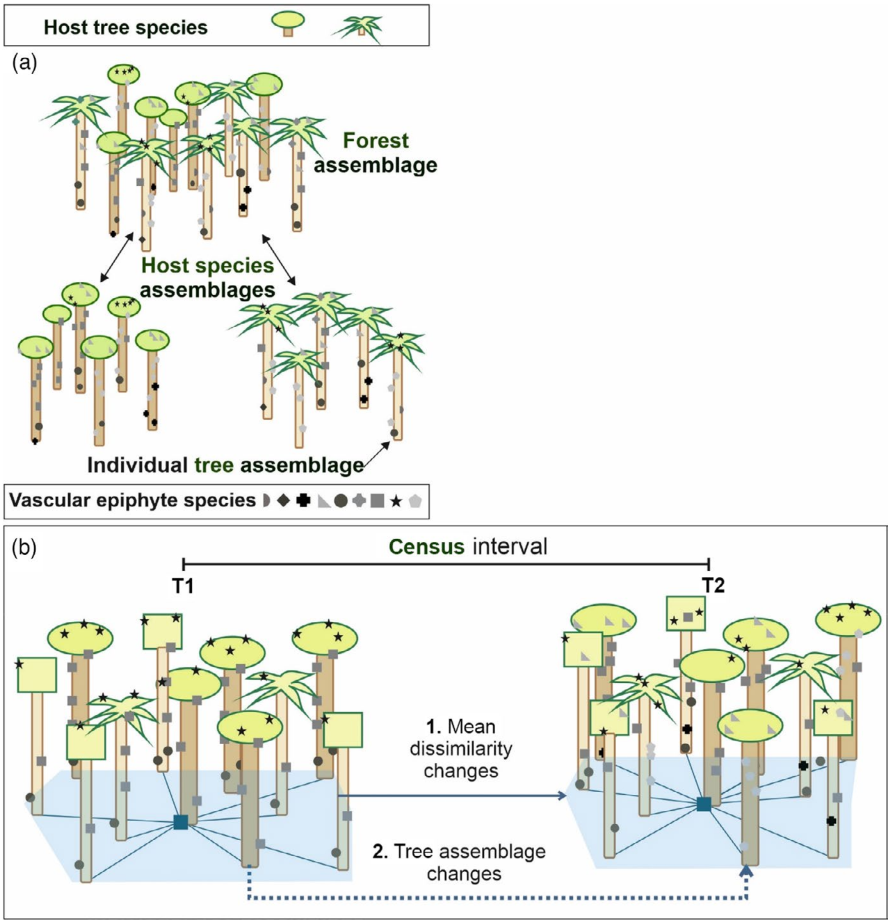

**FIGURE 1** (a) Illustration of the ecological scales used in the analysis of dynamics of vascular epiphytes assemblages. Tree species are indicated by different crown shapes, different symbols represent different epiphyte species. Given the dimensionality of vascular epiphytes the host tree individual is the most intuitive and spatially explicit reference of a vascular epiphyte assemblage. Scales may decrease or increase in grain, from the individual tree-assemblage, to host species assemblages and to the forest assemblage (Mendieta-Leiva & Zotz, 2015). (b) Illustration of the analytical roadmap to assess the dynamics of assemblages at different scales. (1) Changes in mean dissimilarity (within census) and (2) Changes in individual tree-assemblages

assemblages are more dissimilar than expected by chance, probably due to deterministic environmental filters favouring dissimilar species composition, i.e. strong biotic structuring forecast creating very different communities in adjacent sites (Chase et al., 2011). The 'regional' species pool of an assemblage was defined as the total species richness and alpha-diversity as the species richness of individual assemblages (e.g. forest assemblage species richness and tree assemblage species richness). We ran the Raup-Crick metric for the FOREST, SOCRATEA and host tree species assemblages (on host species with at least three tree individuals and at least five epiphyte individuals) using 2,000 randomisations according to Chase et al. (2011). To test whether mean Raup-Crick values deviated significantly from 0, we used the sign-test and the command '*SIGN.test*' from the R package BSDA (Arnholt & Evans, 2017). For host species assemblages, we corrected for multiple testing using the Benjamini and Hochberg method (command *'p.adjust'*, Benjamini & Hochberg, 1995). All analyses were carried out in R software version 4.0.4 (R Core Team, 2021).

## 4 | RESULTS

### 4.1 | Epiphyte richness, abundance, mortality and recruitment

A total of 101 epiphyte species belonging to 61 genera in 13 families were observed in the two FOREST censuses (Table 1, Table S1). More than half of these species also occurred within the SOCRATEA dataset in the periodic censuses (63 species, 39 genera, 11 families), although *S. exorrhiza* only represents 11% of the total number of trees. In the FOREST dataset, the initial 2002 census yielded *c.* 11,500 individual epiphytes from 93 species; 10 years later, these numbers had increased to *c.* 14,000 (+22%) from 92 species, with a significant increase in mean abundance per tree (LME, *F* value = 10.2, $p = 0.001$, Table 1). Epiphyte abundance in the SOCRATEA dataset in the periodic censuses increased by 193% in 11 years. However, only at the fourth census mean abundance per tree was significantly different from the first (LME, Tukey test $p = 0.03$, Table 1), and in the last census mean abundance per tree was significantly different from that of all previous censuses (LME, Tukey test $p < 0.01$, Table 1). Although mortality between the two FOREST surveys was high (77%), recruitment was even higher (81%). Mortality between SOCRATEA surveys averaged 45%. The cumulative mortality in assemblages on SOCRATEA over 8 and 11 years (86% and 90%, respectively) exceeded the mortality over 10 years in the FOREST dataset (Table 1). Furthermore, at the forest level, there was a significant change in total abundance (Table S3). A noteworthy change at the forest level was an increasing dominance of shade-loving ferns (e.g. *Ananthacorus angustifolius*, *Elaphoglossum sporadolepis*, *Dicranoglossum panamense*, *Asplenium serratum* and *Elaphoglossum doanense*, Table S1). Moreover, in SOCRATEA, there were significant changes in time when comparing abundance changes of the ten most abundant species (from the last census, $\chi^2 = 446$, $df = 36$, $p > 0.001$, Table S1, five of these species were ferns).

### 4.2 | Temporal dissimilarity of tree-assemblages

In the FOREST dataset, temporal turnover of individual tree-assemblages ranged from 33% to 100% for presence/absence (mean 85%) and from 0% to 100% for abundance (mean 74%, Figure S2); turnover was generally due to gains (Figures 2 and 3). The degree of gains or losses seemed contingent on the size of the hosts (Figures 2 and 3; Figure S2), and assemblages on larger hosts with smaller changes in DBH evidenced lower turnover overall (Figure S2). Temporal changes in individual tree-assemblages, independent of the census (either coarse or fine-grained), were characterised by a signal of directionality, i.e. turnover was mainly characterised by gains in both the number of species and epiphyte individuals per species; as they were significantly more common in tree-assemblages than losses (Figures 2 and 3). Gains were most common in smaller trees with large changes in DBH (for both presence/absence and abundance, Figure S2; Figures 2 and 3), although differences were not significant (Table S6). In the SOCRATEA dataset, species gains also exceeded species losses in the majority of palms (Figure 3, presence/absence) as did increases in epiphyte abundance per species (Figure 3, abundance). These trends increased with time so that by the fourth census, the number of trees with gains was significantly larger than the number of trees with losses (Figure 3). The maximum percentage of species losses (60%) was much lower than the maximum percentage of gains (*c.* 95%).

### 4.3 | Changes of within-census mean dissimilarity

Mean Chao dissimilarity slightly decreased after 10 years in the FOREST (blue dot, Figure 4; Figure S3a; Table S4), SOCRATEA (Figure S3b) and in most host species assemblages (in 11 out of 17 host species, black and red dots, Figure 4; Table S4). A significant reduction in dissimilarity was found in tree-assemblages of the three host-species *S. exorrhiza*, *Lozania pittieri* and *Marila laxiflora*, whereas a significant *increase* was found in only one case, in assemblages on *Brosimum utile* (Figure 4; Table S4).

When controlling for the effect of different alpha diversity on dissimilarity, changes in Raup-Crick dissimilarity in time were similar to those of Chao dissimilarity: the mean Raup-Crick dissimilarity showed a general trend of reduced dissimilarity. Mean Raup-Crick dissimilarity of assemblages in FOREST, SOCRATEA and assemblages on seven (out of nine) host tree species were negative, indicating a lower dissimilarity than null expectation at all points in time (Figure 5; Figure S4; Table S5).

### 4.4 | The relative importance of deterministic or stochastic processes in compositional changes of vascular epiphyte assemblages

Mean Raup-Crick values were negative at all points in time and significantly different from null expectation at all points in time in FOREST and in two out of five SOCRATEA censuses, i.e. individual

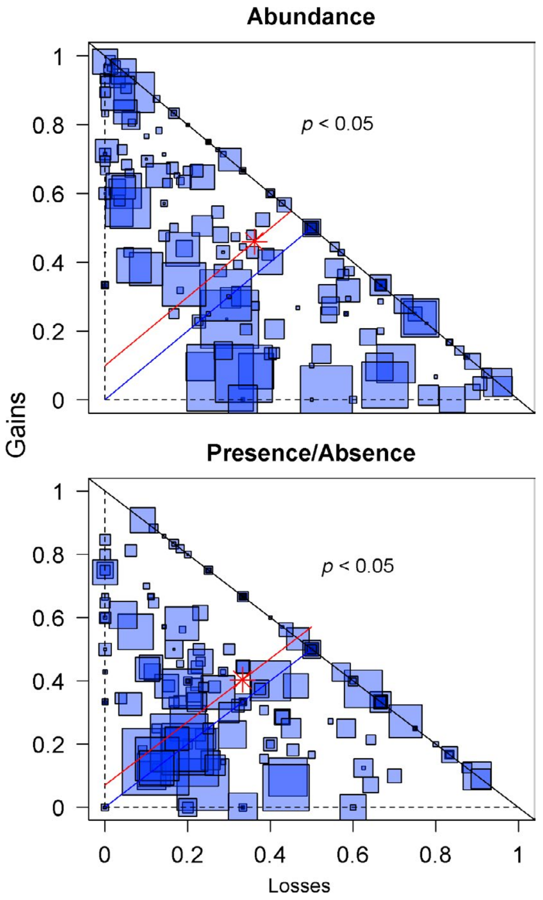

**FIGURE 2** Plots depicting temporal dissimilarity, turnover decomposed into gains and losses, between FOREST censuses. Each tree (squares) position represents turnover percentage is composed by the percentage of losses in the *x*-axis and gains in the *y*-axis. The 207 individual tree-assemblages are plotted according to the degree of losses and gains computed from the species abundance (upper) and species occurrence data (lower). The size of the square represents the DBH of the tree individual. Tree individual assemblages located in the blue line (with a slope of one) are similar in time because they had as many gains as losses, while those located on the dotted vertical and horizontal lines have experience either only gain and no loss or the way around. The red line drawn parallel to the blue line (i.e. with slope 1) passes through the spatial centroid (asterisk) of all squares, its position above the green line indicates that, on average, species gains dominated losses. The *p* value in the upper right corner indicates whether differences between species gains and losses were significant or not based on a permutation paired *t*-test. The number of tree-assemblages with mostly losses, gains or that registered neutral changes were significantly higher on 'small' than on 'big' host trees, for both species and abundance. The classification of size was according to first census DBH data, trees below the mean were classified as 'small' and those above as 'big'. Temporal changes in abundance per species were (33) losses, (29) gains and (4) neutral for big trees and (44) losses, (75) gains and (22) neutral for small trees, $\chi^2 = 8$, $df = 2$, $p = 0.01$. For presence/absence they were (30) losses, (27) gains and (9) neutral for big trees and (33) losses, (72) gains and (36) neutral for small trees, $\chi^2 = 11$, $df = 2$, $p = 0.003$. The change in colour tone of squares is merely due to overlapping, and has no further meaning

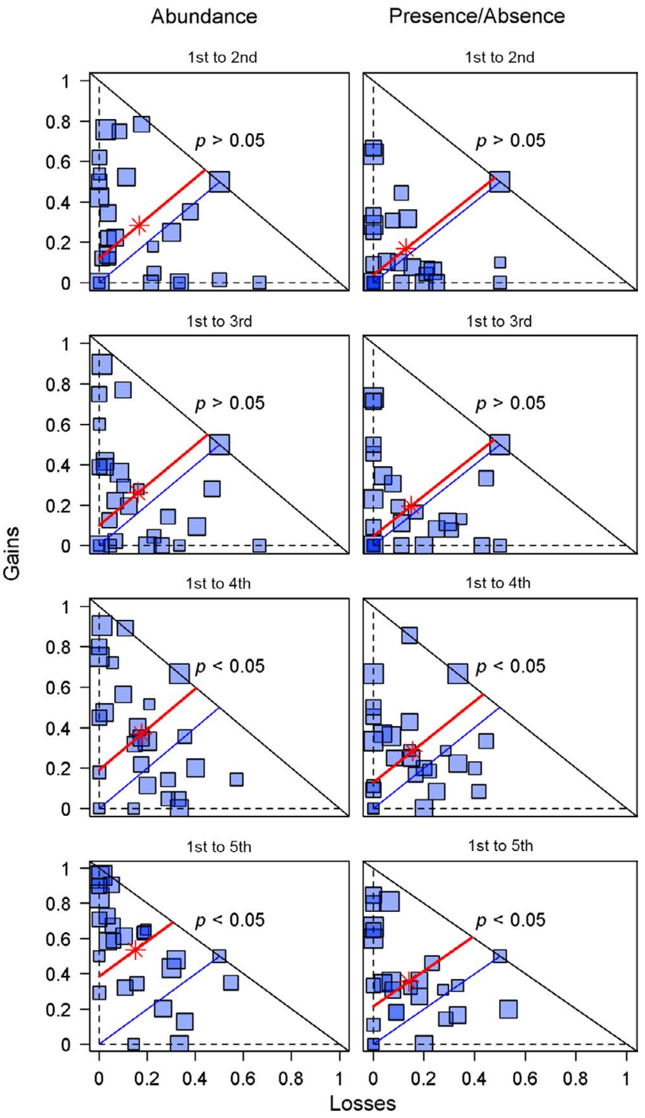

**FIGURE 3** Plots depicting temporal dissimilarity, turnover decomposed into gains and losses, comparing SOCRATEA censuses, where each consecutive census is compared with the first (e.g. first to second, first to third and so on). The position of each tree (squares) represents turnover percentage, which is composed of the percentage of losses in the *x* axis and gains in the *y* axis. The 25 individual host palms are plotted according to the degree of losses and gains computed from the species abundance (left column) and species occurrence data (right column). The size of the square represents the DBH of the palm individual. Tree individual assemblages located in the blue line (with slope of one) had as many gains as losses, while those located on the dotted vertical and horizontal lines indicate either only gain and no loss or the way around. The position of each tree (squares) is defined by the percentage of losses in the *x* axis and gains in the *y* axis. The red line drawn parallel to the green line (i.e. with slope = 1) passes through the spatial centroid (asterisk) of all squares, its position above the blue line indicates that, on average, species gains dominated losses. The *p* value in the upper right corner indicates whether differences between species gains and losses were significant or not based on a permutation paired *t*-test.

tree-assemblages shared, on average, more species than expected by chance (Figure 5; Figure S4). In four out of nine host species assemblages mean Raup-Crick values were significantly different from null expectation at both points in time (*S. exorrhiza*, *Perebea xanthochyma*, *M. laxiflora*, Figure 5; Table S5) or became significantly different from null expectation in time (*L. pittieri*). Change in epiphyte assemblages in *Brosimum utile* and *Poulsenia armata* differed in the former, assemblages changed from more similar than expected to more dissimilar than expected over 10 years, while in the latter, assemblages were more different than expected by chance in both censuses (Figure 5; Table S5).

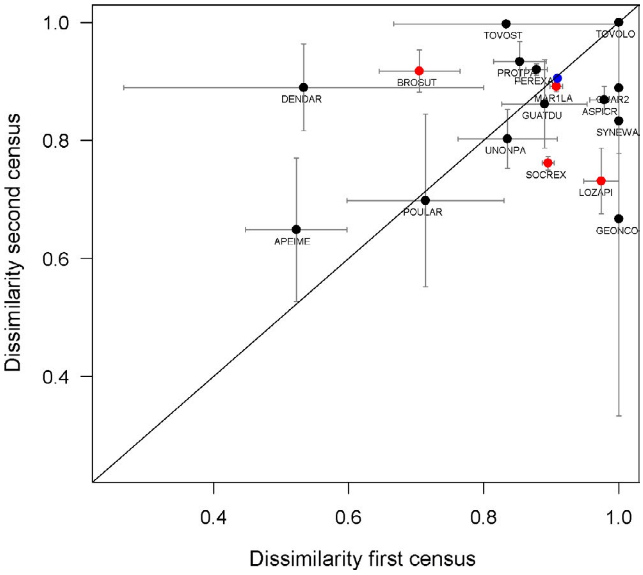

**FIGURE 4** Changes in mean dissimilarity (Chao index) in time of host tree species assemblages (included are 17 host tree species, those with at least three tree individuals, see Section 2). The blue dot represents the mean dissimilarity of the entire FOREST (207 tree individuals, $p < 0.05$, non-parametric Wilcoxson test, Table S4). The *x*-axis represents dissimilarity among host tree assemblage within the first census, the *y*-axis within the second census. The crosses in grey represent the standard error according to census, horizontal for the first census and vertical for the second census, they can vary according to census. Host epiphyte assemblages with significantly different mean dissimilarity between censuses are indicated with colour red ($p < 0.05$, non-parametric Wilcoxson test, Table S4)

Taken together, these results indicate the directionality of changes in the composition in epiphyte assemblages, which supports the first prediction that niche-based mechanisms dominate temporal changes of vascular epiphyte assemblages. Trends were observed at the level of FOREST, SOCRATEA, and specific host-species assemblages (although assemblages in SOCRATEA showed some temporal variation, mean βrc differed from 0 in the first and fifth SOCRATEA census, Figure S4). Notably, the directionality observed in assemblages on *S. exorrhiza* was consistent with that in the fine-grained SOCRATEA dataset (Figure 5; Table S5).

The second prediction, which implies that under niche-based mechanisms, differences in species composition of epiphytes assemblages would be related to hosts characteristics, was also supported, although for host species it was not entirely consistent, unlike for host size with a clear trend. Directionality was observed in epiphyte assemblages of four host species (*P. xanthochyma*, *L. pittieri*, *S. exorrhiza* and *M. laxiflora*, Figure 5). Together, these species comprise 45% of the tree individuals represented by the nine host tree species (Figure 5; Tables S2 and S5). Among the host species assemblages showing directionality, the most consistent signal was found in assemblages of *P. xanthochyma*, *M. laxiflora* and *S. exorrhiza*. The consistent signal with small confidence intervals around the mean Raup-Crick values in both censuses suggests that the characteristics of these host species may impose strong habitat filtering on their epiphyte assemblages (Figure 5; Table S5). Changes in the opposite direction (from more

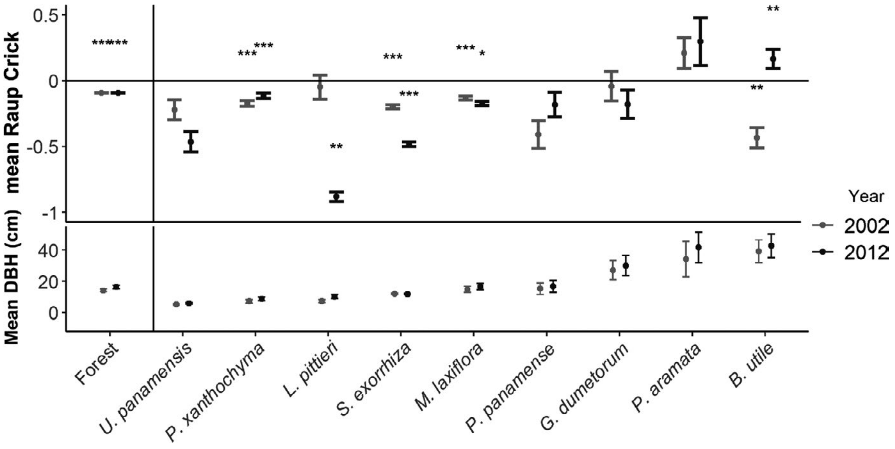

**FIGURE 5** Mean Raup-Crick values and confidence intervals organised according to different ecological scales showing whether epiphyte assemblages were more or less dissimilar than null expectation (complement with Figure S3). Census sequence is indicated by increasingly darker symbols. Below these values is the corresponding mean DBH (in cm) of host tree individuals and respective confidence intervals are shown. Confidence intervals were calculated with a randomisation test (999 repetitions). Upper asterisks above each census represent significant deviation of mean βrc from 0. Significance levels are <0.05*, <0.01**, <0.001***. The nine host tree species differ in the number of individuals and make up *c*. 70% of the total FOREST census (Table S2)

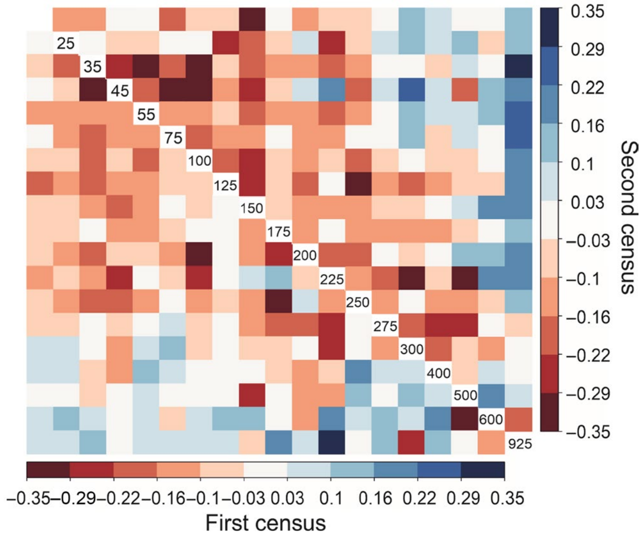

**FIGURE 6** Mean Raup-Crick values grouped according to host trees DBH classes per FOREST census (*x*-axis 2002 and *y*-axis 2012). Raup-Crick values were averaged according to DBH classes, which were organised in steps of 10, 25 and 100 cm according to the frequency of tree individuals per DBH class, e.g. category 25 includes individuals with DBH between 10 and 25 cm. In contrast, the last category 925 contains tree individuals with a DBH from 601 to 925 cm (Figure S5). The colours represent the range of RC values, where red represents negative values and blue positive values

similar to more dissimilar than expected by chance, i.e. positive βrc values) were observed in a single host tree species (*B. utile*, Figures 4 and 5). The association between βrc dissimilarity and DBH dissimilarity (among host tree individuals) yielded a clear trend: host species assemblages with smaller diameters were more similar to each other than expected (negative βrc values, Figure 6; Figure S5), and tree-assemblages with larger diameters (positive βrc values) were more dissimilar than expected by chance at both censuses (Figure 6; Figure S4, $R^2 = 20$, Mantel test $p < 0.001$ for both censuses). Given that trees are growing 'islands', it is expected that host size and epiphyte species richness correlate positively. The observed correlation between composition dissimilarity and DBH (Figure 6) would be unsurprising if epiphyte species on smaller trees were a subset of those on bigger ones. However, this was not the case as the epiphyte assemblages of smaller host trees were not particularly nested within the assemblages of the larger ones (Figure S6).

Finally, the last prediction indicating that dissimilarity will be related to geographical distance reflecting the dominance of neutral processes in temporal changes was not supported. There was no sign of spatial structure in βrc dissimilarity at any point in time (Figure 7).

## 5 | DISCUSSION

Analysing a unique dataset covering more than a decade in a pristine lowland forest, we observed directional epiphyte community dynamics. An increased similarity among tree-assemblages over time was not due to homogenisation of assemblages or decreasing species numbers but instead more likely due to environmental filtering. Although the directional changes seemed to be explained by host identity, we found that host size was the strongest driver of changes in composition and assemblage dissimilarity, while spatial distance among trees was of minor importance. Our results suggest that deterministic processes mainly drive temporal compositional changes in vascular epiphyte assemblages.

### 5.1 | Epiphyte richness, abundance, mortality and recruitment

By contrasting the long-term changes in vascular epiphyte assemblages in a lowland forest across scales (FOREST, SOCRATEA, host species assemblages and individual tree assemblages), temporal patterns of epiphyte assemblages at the forest scale emerge: high turnover of individual plants with increasing abundance over time. Fine-grained censuses covering more than a decade (SOCRATEA*)* revealed gradual changes that cumulatively are consistent with those of the coarse-grained censuses in the FOREST. Long-term changes result from a gradual process, not from stasis with infrequent punctuations. This consistency between different temporal grains suggests that the observed directionality is not merely due to chance. Noticeable changes at the forest level included a significant change in abundance and the increasing dominance of shade-loving ferns, which may reflect the structural development of the forest at the study site (Table S3). Finally, we note that the censuses SOCRATEA and FOREST may not be fully comparable due to the particularities of the palm *S. exorrhiza*. For example, *S. exorrhiza* is structurally simpler than other trees, but in contrast to most Arecaceae, it increases in trunk diameter with height (Chave et al., 2008; Schatz et al., 1985). Similarly, its trunk with a smooth bark is quite distinct from most tree branches of similar diameter, but its stability as substrate is partially countered by regular disturbances when large fronds fall down (pers. obs.). As any other tree, this palm is affected by normal forest dynamics, but a tree fall of a neighbour will subject epiphytes on a palm to harsher changes in microclimate than on other trees that offer more shade with their crowns. Taken together, a palm clearly cannot encompass the range of potential substrates for epiphytes in a forest, but this is true for any tree species in a diverse tropical forest.

The trend of increasing abundance over time is an inherent characteristic of epiphytes at the tree scale, given the continuously increasing availability of colonisable substrate throughout the ontogeny of host trees (Spruch et al., 2019). This continuous increase in abundance over time has been observed for both vascular (Schmit-Neuerburg, 2002; Laube & Zotz, 2006a; Einzmann & Zotz, 2017; Laube & Zotz, 2007) and non-vascular epiphytes (Ellis, 2012). The high turnover of individuals, i.e. high mortality and recruitment rates, shows that epiphyte assemblages are much more dynamic than net changes alone suggest. Epiphytes are subjected to frequent natural disturbances of varying intensity, e.g. tree falls,

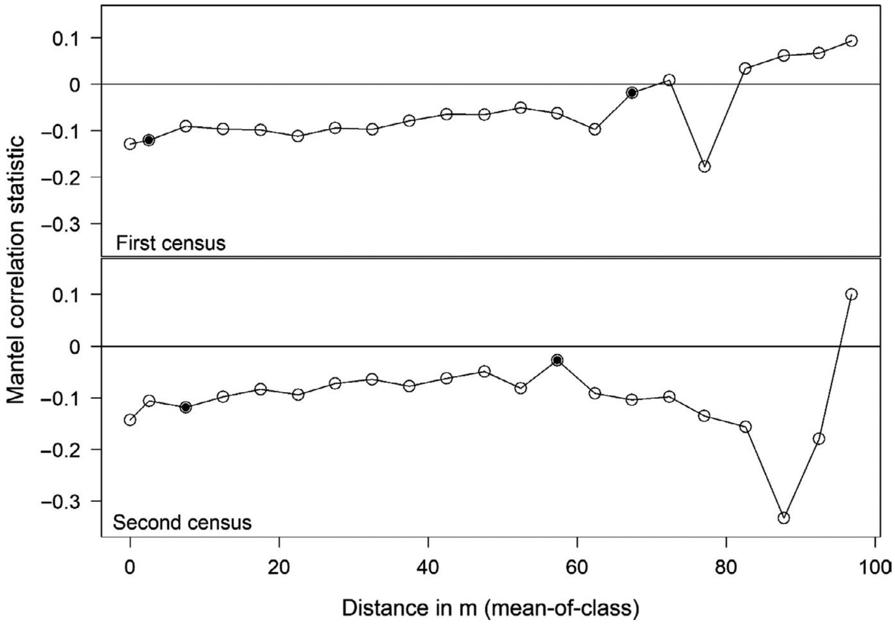

**FIGURE 7** Plots depicting multivariate Mantel correlogram results for both censuses to discern whether dissimilarity of epiphyte assemblages was spatially structured, i.e. whether differences in composition were due to spatial distance (Legendre & Legendre, 2012). These correlograms show the correlation between composition dissimilarity (Raup-Crick) of epiphyte assemblages in individual trees with a matrix of spatial distance of each individual tree-assemblage using distance increments of 5 m. The *x*-axis represents distance in a range of 0 to 100 m, whereas the *y*-axis represents the direction and degree of correlation between distance and dissimilarity. The mantel test results are shown by black points, which indicate significant correlations ($p < 0.05$)

branch breakage (Hietz, 1997; Sarmento Cabral et al., 2015), mechanical stripping of mats by mammals (Nadkarni, 2000). These mechanical stressors may cause much more mortality than physiological causes like desiccation (Zuleta et al., 2016). Desiccation may occur due to drought or herbivory or a combination of both and typically affects primarily juveniles, given that their surface-volume ratios are much larger than those in larger conspecifics (Zotz, 2016). At a regional scale, evapotranspiration may indirectly exacerbate forest disturbance by increasing the partial or total drying of branches and trunks Zuleta et al. (2016). This could be a likely explanation for the elevated mortality in our study area too, since Sarmento Cabral et al. (2015) found - in our study site- that the majority of epiphytes on the floor were still attached to branches (65%). Such disturbances and the continuous production of new substrates by growing trees provide the basis for constant change in the species composition of epiphyte assemblages. The high turnover resulting from mortality and recruitment makes us confident that the time frame of this study was sufficiently long to detect meaningful temporal patterns.

## 5.2 | Directional changes

Temporal changes showcased trends of directionality, as predicted if niche-based mechanisms dominated temporal changes of vascular epiphyte assemblages. Directional trends were observed at the level of individual tree-assemblages, mean-census dissimilarity and within-census dissimilarity.

Temporal changes in individual tree-assemblages were largely due to increased richness and abundance rather than homogenisation. At the same time, individual tree-assemblages became increasingly similar with time. Dissimilarity results were comparable when using both dissimilarity metrics and a null model (Chase et al., 2011). Although seemingly diverging, these trends support the idea of environmental filtering behind the temporal changes in vascular epiphyte assemblages, suggesting that some epiphyte species may be filtered thus conforming a 'habitat-specific' species pool.

The fine-grained changes in SOCRATEA supported the coarse-grained changes in FOREST. Although we have previously noted that these censuses may not be fully comparable due to the particularities of the palm *S. exorrhiza*, we concluded that *Socratea* is not entirely unrepresentative of the average tree in the forest matrix. This justification also applies for the temporal changes on epiphyte assemblages.

The overall trend from the null model showed that most individual tree-assemblages were more similar than expected by chance within a census and remained so over time, both when analysed together or when grouped by host species. However, when individual tree-assemblages were grouped by host species, a moderate degree of variability was observed. When epiphyte assemblages are significantly more similar than expected by chance, assemblages probably occupy similar microhabitats (Chase & Myers, 2011). Only tree-assemblages belonging to *Brosimum utile* changed from more similar than expected to more different than expected by chance in 10 years (Figure 5; Table S5). If assemblages occupy considerably different microhabitats or species interactions change, checkerboard distributions are expected (Chase & Myers, 2011). One particular observation about *Brosimum utile* is that unlike other local host species, some conspecifics of regular size can be found almost devoid of vascular epiphytes (per. obs.).

Combining the results of the changes in mean dissimilarity (based on dissimilarity metrics) and within-census dissimilarity (based on the null model) allows us to highlight the consistency of the results. Some of the variability of the results among host species may be due to differences in the number of tree individuals and perhaps epiphyte species numbers per host species, which simply reflect the natural heterogeneity of the system. Also, the low number of tree individuals in some host species may preclude us from finding a consistent pattern or significant differences for some of the host species, given sufficient stochastic noise. Out of the four host species where assemblages were significantly more similar than expected by chance, *L. pittieri* had only five trees and the lowest species richness (Table S2). On *U. panamensis*, with slightly more trees (12), species richness was also low, assemblages being also more similar than expected, but the suggestive trend was not significant (Table S2).

The host species with the largest number of trees and the most consistent signal of directionality were *S. exorrhiza*, *M. laxiflora* and *P. xanthochyma*. These species grow under similar conditions in the forest (midstory) and have relatively small DBH (range from 10 to 20 cm; Figure 5). The consistent signal of directionally in assemblages of these host species agrees with a previous observation, although in a different host species, *Annona glabra*, a multi-stemmed species of four to seven meters height growing in monotypic stands restricted to marshy areas, with little vertical differences in microclimate. Here, a similar decrease in mean dissimilarity (within census) was observed over a period of 8 years (Laube & Zotz, 2007). These stands, unlike the host species assemblages in our study, are not subjected to the effect of the forest matrix. For instance, the conditions in the forest understorey, which are generally more favourable in terms of temperature stability and water relations, may facilitate germination and possibly the early establishment of a wide array of species (Krömer et al., 2006), thus counteracting the effect of habitat filtering by these host species in comparison to the *Annona glabra* monotypic stand. Alternatively, disturbance, dispersal, colonisation and mortality may re-set the input of stochasticity in the system, as observed in the fine-grained censuses (SOCRATEA, Figure 5; Figure S4), where there was temporal fluctuation of within-census similarity.

## 5.3 | The relative importance of deterministic or stochastic processes in compositional changes of vascular epiphyte assemblages

Host characteristics better explained the reduced dissimilarity in species composition within-census instead of spatial distance among trees at any point in time. This result agrees with the expectation that niche-based mechanisms dominate temporal changes of vascular epiphyte assemblages. It also indicates that dispersal limitation may not play an essential role in the composition of epiphyte assemblages. Amongst host characteristics, host size rather than host species identity best explained the patterns of reduced dissimilarity within-census, and these relationships were consistent through time.

Host species identity is a proxy for a specific combination of structural, physical and chemical characteristics defining a set of diverse microhabitats (Wagner et al., 2015). We observed marked variation in the dissimilarity of tree-assemblages and in how this dissimilarity differed from null expectation across host species (Figure 5; Table S5). This observation highlights the varying degrees of environmental heterogeneity within and across host species, suggesting it may have a differential effect on vascular epiphyte assemblages' structure and temporal changes. Burns and Zotz (2010) and Laube and Zotz (2006b), analysing different subsets of our dataset, suggested that epiphyte species are differentially adapted to using different host species, and epiphyte distribution was indistinguishable from random in the majority of species. Most recently, Wagner and Zotz (2020) showed that tree species-specific changes in epiphyte abundance strongly depend upon the response variable, that is, whether host size or host age are used. While growth rate differences of host species have a clear effect on the speed of accumulation of epiphytes over time (Wagner & Zotz, 2020), it is unknown how these differences would affect species composition dissimilarity. Additionally to the intrinsic factors of the hosts, such as substrate dynamics and the inter- and intra-specific variation in host tree characteristics (Wagner et al., 2015), extrinsic factors such as the location of individual trees within the forest matrix create gradients of environmental heterogeneity. The way these gradients affect epiphyte assemblage composition is also highly related to the ecophysiology of epiphyte species. The differences between-taxa may be reflected in the distinctive response of functional traits to environmental conditions (Petter et al., 2016), which in turn will determine the effect of the environmental heterogeneity on compositional differences.

Host species identity is often used to explain spatial variation of vascular epiphyte assemblages (Wagner et al., 2015; Zotz, 2016). However, this is the least likely explanation since most trees analysed belong to the host species *S. exorrhiza* and *P. xanthochyma* which are distributed in the sub canopy and *M. laxiflora*, distributed in the understorey of the forest (Table S2). These tree species are generally small, and with individuals consistent in their sizes, based on their DBH; thus, they are somewhat sheltered within the forest matrix. Therefore, the vertical gradient in these trees may encompass only a small subset of microhabitats along the vertical gradient of the forest, for example, exposed microsites in the outer crown of the canopy are missing. These host species may offer a combination of low microhabitat diversity due to their structure (Zotz, 2007), and a high degree of stability due to their location within the forest matrix; this may impose a strong habitat filter. We found out that assemblages on host tree species with larger DBH were more dissimilar than expected by chance, likely due to microhabitat differences, because larger size leads to a greater number of microhabitats, and more diverse species interactions (Chase & Myers, 2011, Figure 5; Figures S5 and S6). The coarse trend indicating that individual tree-assemblages on host species with a smaller and more consistent DBH were significantly more similar than expected by chance, and vice versa, was further explored.

We found that individual tree-assemblages that were significantly more similar than expected by chance were found mostly on trees with generally small DBH, and this pattern was accentuated after 10 years. It can be argued that this pattern may be largely driven by assemblages on tree individuals that are still young and/or those belonging to host species which are typically small. In the first case, temporal changes due to the increase in species richness and abundance may be considered some kind of 'succession' of epiphyte assemblages on young trees in development. For vascular epiphytes, the concept of typical primary succession may not adequately capture the nature of the ecological processes behind epiphyte assemblage dynamics (Zotz, 2016). The establishment of epiphytes occurs on both new and old empty substrates. New substrates are rarely found in nature, where theoretically a directional replacement of species is expected, that is, early successional species are replaced by late-successional species (see references within Platt & Connell, 2003), as in primary succession. As a substrate for epiphytes, the tree has its dynamics and is a living and constantly expanding organism; this process results in structural enrichment, which increases environmental heterogeneity (Stein et al., 2014; Zotz & Vollrath, 2003).

Similarly to terrestrial pioneer species, during primary succession, epiphyte species already established may serve as facilitators for newcomers (Jian et al., 2013). Nonetheless, the previous process is counterbalanced by the constant production of new substrate and the availability of new habitats as the new substrates arise. Therefore, the dynamics of vascular epiphytes could be conceptualised as a facilitation cascade via successive habitat formation and modification (Thomsen et al., 2010, 2018). Combining these particularities is likely to result in temporal changes driven mainly by the accumulation of species and, to a lesser degree, by species replacement. Species accumulation predominance has been previously observed in some studies of epiphylls, which also occur on an expanding habitat, such as the leaves, although probably more dynamic and ephemeral than trees (Mežaka et al., 2020).

Taken together, the evidence suggests that not host species identity but tree size, quantified here by DBH, seems to determine the compositional dissimilarity of vascular epiphyte assemblages largely and that this relationship remains stable in time, as distance did not seem to play a role. The observed temporal fluctuation in the difference of mean dissimilarity from null expectation (SOCRATEA) suggests that early phases of community assembly may be primarily influenced by stochasticity (e.g. colonisation and extinction events), while eventually, determinism (environmental filtering) dominates. The relative importance of these processes in community assembly should be explored across different life stages (e.g. Yang et al., 2016), both of the epiphyte and the host species (Laube & Zotz, 2006a; Wagner & Zotz, 2020). In a deterministic framework, lower heterogeneity should lead to reduced dissimilarity and vice versa (Fukami, 2010). Our results are more consistent with the predictions of niche theory than those of the neutral theory (Chase & Myers, 2011). Although we advocate the concept of environmental filtering determining vascular epiphyte assemblages, a more precise demonstration would require proof of independence from biotic factors (Kraft et al., 2015). Apart from the role of the host tree, the importance of biotic interactions for vascular epiphyte assemblages, for example, fungi in orchids, herbivory, pollinators and dispersal, is mainly unexplored (Zotz, 2016).

Patterns and processes underlying *terrestrial* vegetation dynamics are far better known. The role of niche-based processes is the predominant one with dispersal and demographic stochasticity playing a lesser role, with these mechanisms operating in parallel (e.g. Chisholm et al., 2014; Kraft et al., 2008; Rees et al., 2001). Examples from lowland forests indicate habitat filtering. Variance in environmental drivers as well as topography are important determinants of community composition. Comparisons cannot be made directly, as for terrestrial vegetation, even functional diversity is used to understand temporal dynamics. However, the analysis of functional traits in assemblages has kicked off recently (Wagner et al., 2021). The single closest study we can compare our research with that of Legendre and Condit (2019) who assessed temporal dissimilarity in the BCI dynamics plot. Previously, directional compositional changes were identified in different lowland forests along the Panama Canal (Condit et al., 2004), likely caused by climatic factors. Legendre and Condit (2019) showed that the spatial structure of the forest changed considerably in time, similarly to the changes identified in our tree-assemblages. However, there is one main difference: while the general tendency in epiphyte tree-assemblages was towards the gain of individuals per species and species in time, all but one of the habitats studied by Legendre and Condit (2019) showed species losses. The exceptional case was a swamp, which, similar to epiphyte tree-assemblages, reacted differently to occasional droughts. The authors noted that drought-created gaps in the forests canopy favoured species that established in these empty or new niches, thus changing the species composition of the entire system. This suggests a surprising similarity between a swamp and epiphyte assemblages: ecological niches needed by 'alien' species are created in the swamp as is new substrate constantly made available for vascular epiphytes by the growing tree.

In previous research in the study area, checkerboard patterns were detected for data of the first census (Burns & Zotz, 2010). Because in lowland forests, trees may die before epiphytes fully cover them, it was argued that neutral processes might have generated these patterns (Burns & Zotz, 2010). While competition is known to play a complementary role determining terrestrial vegetation (e.g. Pillet et al., 2018; Taubert et al., 2015), it is entirely unknown whether that is the case for vascular epiphytes. This highlights the importance of long-term surveys of epiphyte assemblages in different ecosystems types, such as those at intermediate elevations in the Andes, where the highest epiphyte diversity can be found (Krömer et al., 2005). In these ecosystems, vascular and non-vascular epiphytes co-exist in a much more complex fashion. In our system, we can only ascertain that while many small-sized tree assemblages seem to become more similar in time, we cannot predict which direction these changes will take, whether increased similarity will be accentuated or a different directional change will take place.

This study is the first one of its kind, not only because it documents the temporal changes of epiphyte assemblages in a natural forest over a decade but also because it explores emergent patterns in their dynamics to infer the relative importance of processes influencing community assembly. However, given its observational nature, these analyses only allow us to produce hypotheses about the underlying mechanisms. Epiphyte assemblages from other forests have to be studied to assess the generality of our findings. Finding similar temporal patterns in other geographical areas and forest types would have exciting implications for epiphyte research, for example, the possibility of establishing general patterns in the dynamics of vascular epiphyte assemblage dynamics. We have observed that the dynamics of epiphyte assemblages are relatively fast. Thus, we hope that our research will encourage the establishment of other long-term studies or the re-census of previously studied epiphyte assemblages.

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## CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

## AUTHORS' CONTRIBUTIONS

G.M.-L. conceived the manuscript and analysed the data; G.Z. devised the census protocol; G.M.-L. and G.Z. collected data; G.M.-L. and G.Z. wrote the paper with input from H.L.B.

## DATA AVAILABILITY STATEMENT

Data are available from Zenodo https://doi.org/10.5281/zenodo.5645775 (Mendieta-Leiva et al., 2021).

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