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Comparing vascular epiphyte diversity hosted by the native *Cedrela dugesii* and the exotic *Annona cherimola* species in a cloud forest in central Mexico

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Abstract

Exotic species can significantly affect native species communities. However, there is a lack of studies comparing the communities of vascular epiphytes and their vertical stratification on native and exotic phorophytes coexisting within natural ecosystems. This study compares these aspects between the native phorophyte *Cedrela dugesii* and the exotic *Annona cherimola* within a fragment of cloud forest in central Mexico. We recorded all the epiphyte species present on every individual of each phorophyte species within 0.25 ha. We estimated and compared true diversities, relative abundance, and species composition, both total and per stratum: trunk (ZI), inner branches (ZII), and outer branches (ZIII) between phorophyte species. The association between epiphytes and phorophyte traits (branch diameter, inclination, and height; vegetation cover; and diameter at breast height) was also analyzed. The native phorophyte hosted a higher total (^{0}D:19) and per stratum ($^0D_{ZI}$:10; $^1D_{ZI}$:5.1; $^0D_{ZIII}$:15) diversity than the exotic one (^{0}D:10; $^0D_{ZI}$:3, $^1D_{ZI}$:3; $^0D_{ZIII}$:7), except in ZII. In both phorophytes, the most abundant species were *Pecluma ferruginea* in ZI (native:34 stands; exotic:15 stands) and *Tillandsia capitata* in ZII and ZIII (native:71, 168 stands; exotic:27, 25 stands). Species composition was similar between phorophytes, but different between ZI (associated with high vegetation cover and thick branches) and ZIII (associated with tall branches). Although both phorophytes host epiphytes, a higher diversity is hosted by the native species than the exotic one. To conserve and maintain this diversity of epiphytes and their functionality within the locality, continuous monitoring of both phorophyte species is necessary.

Keywords Introduced species · Phorophytes · *Pleopeltis* · Species composition · *Tillandsia* · Vertical stratification.

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Introduction

The increase of exotic species within natural ecosystems might represent a threat to the diversity and dynamics of communities (Pyšek et al. 2020; Gioria et al. 2023). When recently arriving at the new habitat, exotic species lack predators, thus they might grow and reproduce quickly, increasing their abundance in a short period (Gioria et al. 2023). Consequently, they might cause local extinctions of native species (Pyšek et al. 2020), decreasing diversity and changing species composition of the native communities (Bernard-Verdier and Hulme 2019; Rojas-Sandoval et al. 2022). Aggravated consequences might occur in strongly fragmented ecosystems (Rojas et al. 2011), due to the joint effects of fragmentation and exotic-native species interactions on the native community (Minor et al. 2009).

Cloud forests are strongly fragmented ecosystems covering around 0.4% of the world's surface and less than 1% of the Mexican territory (CONABIO 2010; Karger et al. 2021). They hold a high diversity of both species and interactions (Gotsch et al. 2016; Francisco et al. 2019). Interactions between phorophytes and epiphytes are particularly diverse within them. Because they have coexisted for a long time (Haro-Carrión et al. 2009; Wagner et al. 2015), phorophytes have developed morphological and chemical traits that favor the establishment of a diversity of epiphyte species (Valencia-Díaz et al. 2010; Vergara-Torres et al. 2010; Wagner et al. 2015). In general, perennial phorophytes of big size (height and diameter at breast height) with a well-developed canopy, fissured bark, with variation in the branching pattern (branch diameter, height and inclination) along the phorophyte, and lacking allelochemical production hold a greater diversity of epiphytes (Flores-Palacios and García-Franco 2006; Valencia-Díaz et al. 2010; Ramírez-Martínez et al. 2018; Victoriano-Romero and Figueroa-Castro 2025). However, the common phorophyte – epiphyte interactions within cloud forests are not exempt from the effects of exotic species (Alzate-Quintero et al. 2019).

Most studies comparing the diversity of vascular epiphytes between exotic and native phorophytes have been conducted at the forest level, in urbanized environments or in agroecosystems (Haro-Carrión et al. 2009; Boelter et al. 2011; Krömer et al. 2014; Bhatt et al. 2015; Nadège et al. 2016; Silva-Martins et al. 2020). In contrast, fewer studies compare the diversity of epiphytes hosted by single phorophyte types (exotic vs. native) in natural environments (Medeiros et al. 1993). In general, these studies have found that native phorophytes host higher species richness and abundance than the exotic ones, and that species composition is moderately different between phorophyte types (Medeiros et al. 1993; Haro-Carrión et al. 2009; Boelter et al. 2011; Krömer et al. 2014; Bhatt et al. 2015; Silva-Martins et al. 2020; Alvim et al. 2021). However, none of them describe the vertical stratification of epiphytes and how it varies between phorophyte types, except Silva-Martins et al. (2020). These authors found similar species richness, diversity, and species evenness across strata and between phorophyte types (Silva-Martins et al. 2020). Unfortunately, they used an uncommon tree stratification (main trunk lower half, main trunk upper half, and crown), which prevents comparisons with other studies and ignores the within-crown microenvironmental heterogeneity. Also, their comparisons are done between phorophyte types with contrasting phenology (perennial exotic vs. deciduous native). Hence, their results should be taken with caution.

Therefore, there is still a lack of studies addressing the effects of phorophyte type (native vs. exotic) on the epiphyte community and its vertical stratification (Medeiros et al. 1993; Bhatt et al. 2015; Nadège et al. 2016; Silva-Martins et al. 2020). Specifically, there is a gap in the study of epiphyte vertical stratification between native and exotic phorophytes within natural ecosystems. Here, we compare the diversity and vertical stratification of the communities of vascular epiphytes associated with the exotic phorophyte *Annona cherimola* and the native *Cedrela dugesii* in a fragment of cloud forest in central Mexico. We were particularly interested in analyzing if: (i) species richness, abundance, dominance, and composition of the community of vascular epiphytes differ between the two phorophyte types (exotic vs. native); (ii) the epiphyte community changes across vertical strata; and (iii) the epiphyte community is associated with particular morphological traits of phorophytes (vegetation cover; branch height, inclination and diameter, and diameter at breast height). We hypothesize that the native phorophyte will host higher species richness and abundance of epiphytes than the exotic one (Medeiros et al. 1993; Haro-Carrión et al. 2009; Boelter et al. 2011; Krömer et al. 2014; Alvim et al. 2021), but that composition and dominance will be relatively similar (Boelter et al. 2011; Silva-Martins et al. 2020; Alvim et al. 2021). Also, we expect a heterogeneous vertical distribution of epiphytes in both phorophyte types (Krömer et al. 2014), but similar between them (Silva-Martins et al. 2020).

Materials and methods

Study site

The present study was conducted at the Amatlán de Quetzalcóatl locality (18º58'28" N, 99º01'29" W; 1,702.4 m above sea level), within the Morelos State in central Mexico (Figure S1; INEGI 2010). Located within the "Chichinautzin Biological Corridor", Amatlán is near the "El Tepozteco"

protected natural area. Its climate is temperate subhumid with a mean annual temperature of 18–20 °C. The mean annual precipitation is 1222–1279 mm, with a rainy season from June to September (Bilbatúa-Navarrete 2019). Different vegetation types are distinguished within the locality, including temperate forest (composed of conifers and species within the *Quercus* genus) and tropical dry forest. The cloud forest is highly fragmented and has a restricted distribution to the slopes of wet canyons (CONABIO 2010; Hernández-Cárdenas et al. 2014; INEGI 2015). At the locality of study, *Eugenia crenularis* Lundell (Myrtaceae), *Cedrela dugessi* S. Watson (Meliaceae), *Annona cherimola* Mill. (Annonaceae), *Urera caracasana* (Jacq.) Gaudich. ex Griseb. (Urticaceae), *Prunus samydoides* Schltdl., and *P. ferruginea* Steud. (Rosaceae), figure among the most abundant tree species. As for the epiphyte community, it is dominated by bromeliads and ferns, but orchids and peperomias are also found (Victoriano-Romero and Figueroa-Castro 2024).

Study species

We conducted this study with the native (Mexico) *Cedrela dugesii* S. Watson (Meliaceae) (IPNI 2025), and the exotic *Annona cherimola* Mill. (Annonaceae) (Villaseñor and Espinosa-García 2004; IPNI 2025) as the focal phorophyte trees (Figure S2). We chose these two species because they have a similar abundance (*C. dugesii*: 13 individuals in 0.25 ha; *A. cherimola*: 11 individuals in 0.25 ha) within the fragment of cloud forest (Victoriano-Romero and Figueroa-Castro 2024); their height is relatively similar at the locality [*C. dugesii*: 13.46 ± s.e. 1.57 m; *A. cherimola*: 12.82 ± 1.28 m; $t_{22} = 0.31$, $P = 0.76$]; both species have similar branch length, canopy volume (Calderón and Germán 1993; Ramírez-Martínez et al. 2018) and leaf phenology (*i.e.*, deciduous; Calderón and Germán 1993; Ortiz-Rodríguez et al. 2015). A brief description of each phorophyte species is provided within the supplementary information.

Epiphyte community field sampling

In order to determine how the vascular epiphyte community is affected by phorophyte nature (native vs. exotic), we sampled all the epiphytes growing on all the individuals of *C. dugesii* (13) and *A. cherimola* (11) found in 0.25 ha within the study site. Epiphyte sampling was conducted by climbing to the canopy of the trees. In each phorophyte, we identified and quantified all the epiphytes found and the vertical stratum of the tree in which they were growing. We considered three strata (Vergara-Torres et al. 2010; Ruiz-Cordova et al. 2014): zone I (ZI) is the main trunk of the tree; zone II (ZII) includes the inner branches, and zone III (ZIII) corresponds to the outer branches. Epiphytes were classified as accidental, facultative, and holoepiphytes (Kress 1986; Benzing 1990). Accidental epiphytes were used to describe the community, but they were excluded from any statistical analysis. Because facultative and holoepiphytes can complete their life cycle in the canopy (Kress 1986; Benzing 1990), they were included in all statistical analyses. In order to establish if different epiphytes were associated with particular phorophyte morphological traits, we measured height, slope and diameter of the branches on which each epiphyte stand was established. In addition, we measured vegetation cover above each epiphyte and the diameter at breast height (DBH) of each sampled tree. A detailed description of epiphyte sampling is provided within the supplementary information.

Data analyses

Total and per vertical stratum epiphyte diversity was compared between phorophytes through true diversities at three orders of q (0, 1, 2) and their 95% confidence intervals (CI; Jost 2006; Chao et al. 2014). In addition, we estimated the proportion of common species ($EF_{0,1}$) and rare species ($1\text{-}EF_{0,2}$), as well as sampling completeness (C_m; Jost 2006). Species composition between phorophyte types and per vertical stratum were compared with non-metric multidimensional scaling analyses (NMDS), and a non-parametric similarity analysis (ANOSIM; Clarke et al. 2014). Moreover, to establish if epiphyte abundance across vertical strata was higher, lower, or as expected by random, we conducted χ^2 tests and Haberman residuals analyses (Haberman 1973). Finally, in order to establish the association between phorophyte traits (*i.e.*, diameter at breast height; branch diameter, height and inclination, and vegetation cover) and the epiphyte communities, principal component analyses (PCA) were conducted; one using epiphyte groups (bromeliads, ferns, orchids, and peperomias), and the other at the species level. In addition, to explore if the variation in morphological traits (branch diameter, height and inclination; and vegetation cover) along the phorophyte influence mean species richness per zone within individual trees, we applied a hierarchical generalized additive model (HGAM; Pedersen et al. 2019). True diversities, NMDS, ANOSIM and HGAM analyses were conducted in R v. 4.3. (R Core Team 2023). PCAs were conducted in Past 3.21 (Hammer et al. 2001). χ^2 and Haberman residuals were estimated in Excel. A detailed description of the analyses is provided within the supplementary information.

Table 1 Epiphyte species associated with the exotic *Annona cherimola* and the native *Cedrela dugesii* phorophyte species at a fragment of cloud forest in Central Mexico

Epiphyte species	Epiphyte type	Phorophyte species	
		A. cherimola (exotic)	*C. dugesii* (native)
Pteridophytes			
Nephrolepidaceae			
Nephrolepis undulata (Afzel. ex Sw.) J. Sm.	F	0	1
Polypodiaceae			
Pecluma ferruginea (M. Martens & Galeotti) M. G. Price	F	18	34
Pleopeltis acicularis (Weath.) A. R. Sm. & T. Krömer	H	39	55
Pleopeltis furfuracea (Schltdl. & Cham.) A. R. Sm. & Tejero	H	22	65
Pleopeltis polylepis var. *interjecta* (Weath.) E. A. Hooper	H	0	2
Pteridaceae			
Adiantum andicola Liebm.	F	0	1
Spermatophytes			
Araliaceae			
Oreopanax peltatus Linden	A	3	3
Bromeliaceae			
Tillandsia achyrostachys É. Morren in Baker.	H	2	6
Tillandsia capitata Griseb.	H	52	245
Tillandsia caput-medusae É. Morren	H	0	3
Tillandsia circinnatioides Matuda	H	0	5
Tillandsia hubertiana Matuda	H	7	14
Tillandsia ionantha Planch.	H	0	4
Tillandsia makoyana Baker	H	0	39
Tillandsia recurvata (L.) L.	H	0	17
Tillandsia schiedeana Steud.	H	3	11
Tillandsia spp.*	H	41	150
Viridantha atroviridipetala (Matuda) Espejo	H	0	1
Myrtaceae			
Eugenia crenularis Lundell	A	0	6
Orchidaceae			
Prosthechea linkiana (Klotzsch) W. E. Higgins	H	1	12
Piperaceae			
Peperomia tetraphylla Hook. & Arn.	H	32	22
Poaceae			
Oplismenus burmanni (Retz.) P. Beauv.	A	1	1
Polemoniaceae			
Bonplandia geminiflora Cav.	A	0	1
Total		221	698

Epiphyte types: A= accidental, F= facultative, H= holoepiphyte. Epiphyte abundance for each phorophyte species is shown. *= stands belonging to the *Tillandsia* genus that lacked reproductive structures needed for identification at the species level

Table 2 Diversity of the communities of vascular epiphytes associated to the exotic (*Annona cherimola*) and the native (*Cedrela dugesii*) phorophytes

Diversity metric	Phorophyte	
	Annona cherimola (exotic)	*Cedrela dugesii* (native)
^0D	10 (10–13.7)	19 (19–33)
^1D	6.8 (6.4–7.5)	7.6 (7.0–8.4)
^2D	6 (5.6–6.7)	5 (4.6–5.5)
$EF_{0,1}$	0.68	0.40
$1 - EF_{0,2}$	0.39	0.73

True diversities at three orders of q (^0D, ^1D, ^2D) and uniformity factors (EF) are provided for each zone within each phorophye species. ^0D: species richness; ^1D: number of species with similar abundance; ^2D: number of species with the same dominance; $EF_{0,1}$= proportion of common species; $1 - EF_{0,2}$= proportion of rare species. Within ^0D, ^1D, ^2D cells, the true diversity value and the 95% CI (lower-upper) are provided

Results

Communities of vascular epiphytes hosted by different phorophytes (native and exotic)

A total of 919 stands, from 23 species (including the group *Tillandsia* spp.) and 10 families, were recorded across the 24 phorophyte individuals sampled (Table 1). Out of these, four species were accidental (17%). The remaining species were either holoepiphytes (16 species, 70%) or facultative epiphytes (3 species, 13%). Bromeliaceae had the highest species richness (10), followed by Polypodiaceae (4 species). All other plant families were represented by a single species. *Tillandsia capitata* had the highest abundance in the community, and the second most abundant was the group *Tillandsia* spp. *Pleopeltis acicularis* was the third most abundant species in the community (Table 1; Figure S3A).

Total epiphyte species richness (^0D) was significantly higher in the native phorophyte than in the exotic one (Table 2; Fig. 1). The number of epiphyte species with similar abundance (^1D) was not significantly different between phorophytes. The number of species with similar dominance (^2D) was significantly higher in the exotic phorophyte than in the native one. The exotic phorophyte hosted a higher proportion of common epiphyte species ($EF_{0,1}$) than the native one. The opposite pattern was found for the proportion of rare species ($1\text{-}EF_{0,2}$; Table 2). Sampling coverage was 99% for both phorophyte species. Epiphyte species composition was similar between phorophyte types (NMDS: stress = 0.2 with two dimensions; ANOSIM: $R = 0.09$, $P = 0.08$; Figure S4); 53% of the epiphyte species were shared by both phorophytes (9 species and the group *Tillandsia* spp.; Table 1). In both phorophytes, the first and second most abundant species were *Tillandsia capitata* (native: 245 stands, 35%;

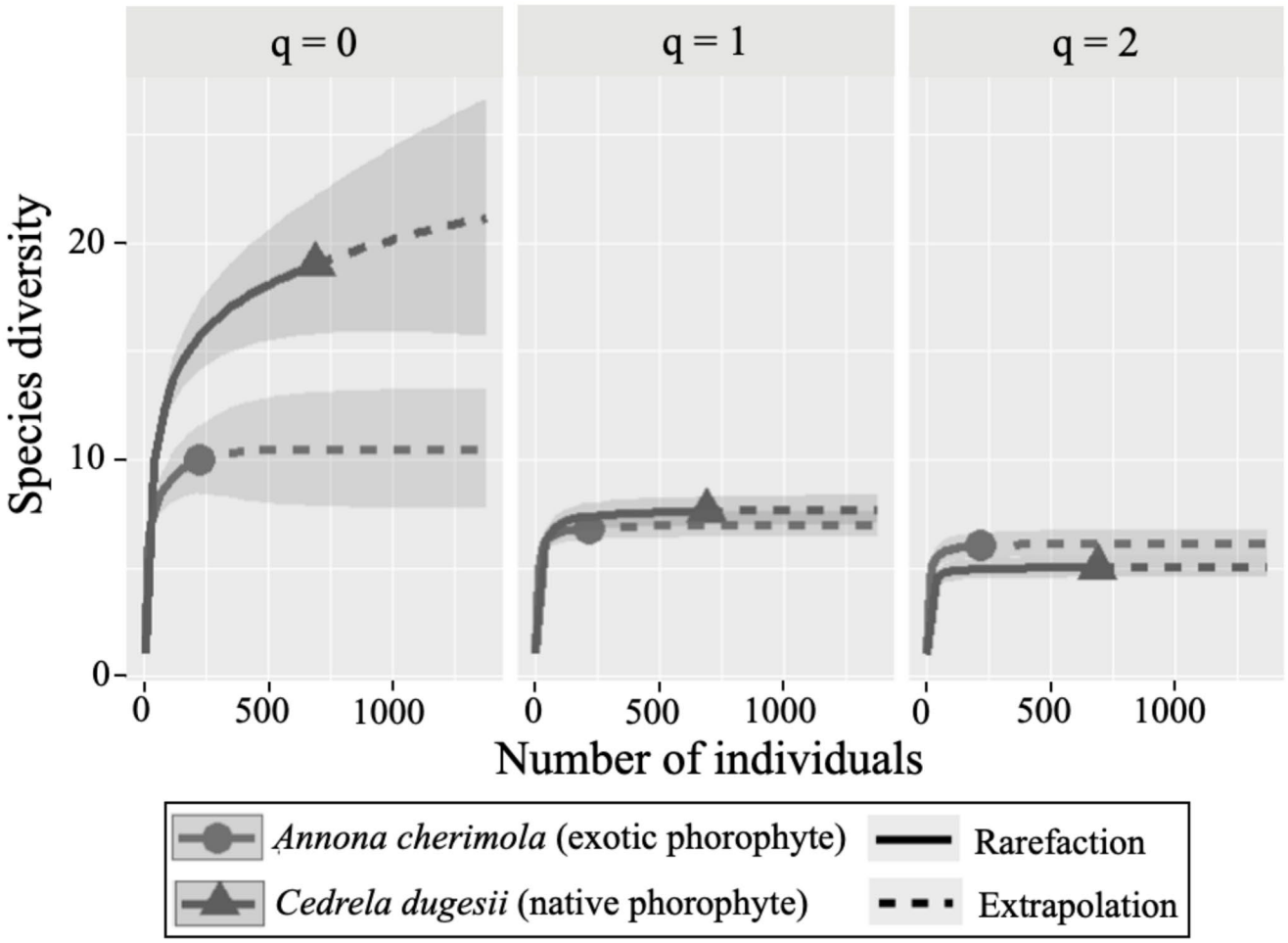


Fig. 1 Total true diversities at three orders of q (0 = species richness, 1 = number of common species, 2 = number of species with similar dominance) of vascular epiphyte species associated with an exotic (*Annona cherimola*, dots) and a native (*Cedrela dugesii*, triangles) phorophyte. Rarefaction (from observed data; continuous line) and extrapolation curves (dashed line) are shown

exotic: 52 stands, 24%; Table 1; Figure S3 B, C), and *Tillandsia* spp. (native: 150 stands, 21%; exotic: 41 stands, 19%; Figure S3B, C). *Pleopeltis furfuracea* and *P. acicularis* were the third most abundant species hosted by the native (65 stands, 9%) and the exotic (39 stands, 18%) phorophyte, respectively. The fourth epiphyte species most abundant in the exotic and native phorophytes were *P. tetraphylla* (32 stands, 15%) and *P. acicularis* (55 stands, 8%), respectively (Table 1; Figure S3 B, C).

PCA results showed that the first two components explain most of the variance in the distribution of epiphyte species for both phorophytes at the group (exotic: 63.23%; native: 71.7%) and at the species level (exotic: 64.27%; native: 72.89%). In both analyses, branch height was negatively correlated with the first component, whereas branch diameter was positively correlated with that same component for both phorophyte species. Moreover, in both analyses with the native phorophyte, a positive correlation was found for vegetation cover with the first component and DBH with the second one. In the ordination space of both phorophytes, the heterogeneous distribution of groups and species of epiphytes along the tree is evident. Bromeliads showed an association with tall and thin branches and low vegetation cover (Fig. 2). This pattern is particularly evident for *T. capitata* (Figure S5B, C) and *T. makoyana* (Figure S5F). In contrast, *Peperomia tetraphylla* in both phorophytes (Figs. 2, S5A, D), and the fern *P. ferruginea* in the native phorophyte (Figure S5E) and orchids are associated with low, thick branches and high vegetation cover (Fig. 2). The fern *P. furfuracea* showed an association with tall, thin branches and low vegetation cover (Figure S5B, E).

Vertical distribution of epiphytes along a native and an exotic phorophyte

In zone I, species richness (^{0}D) and number of species with the same abundance (^{1}D) were significantly higher in the native phorophyte than in the exotic one (Table 3; Figure

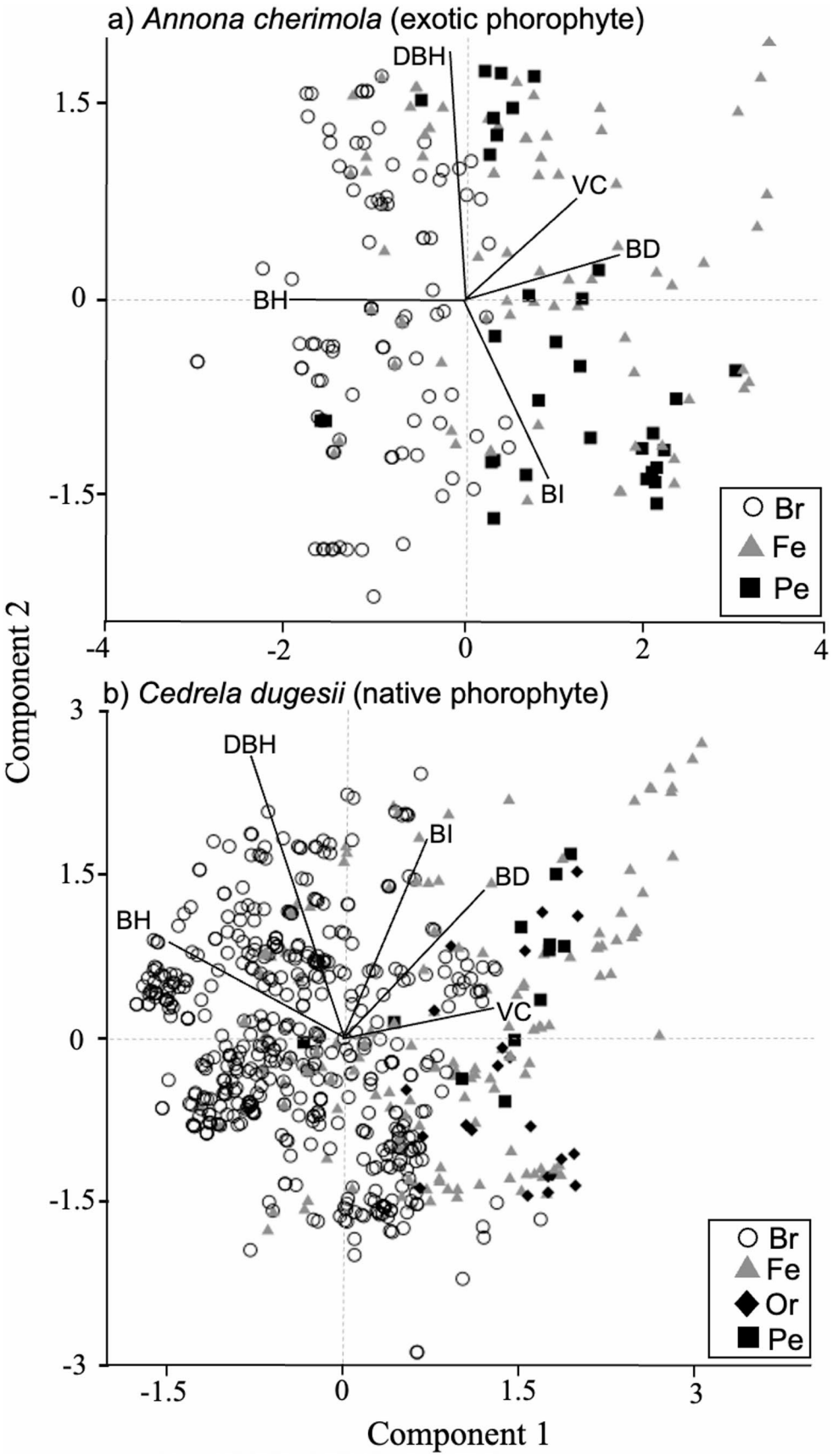


Fig. 2 Principal component analyses conducted to find out the association between *Annona cherimola* (a) and *Cedrela dugesii* (b) traits with the abundance of vascular groups of holoepiphytes and facultative epiphytes (Br: Bromeliads, Fe: Ferns, Or: Orchids, Pe: Peperomias). DBH: diameter at breast height; BD: branch diameter; BH: branch height; BI: branch inclination; VC: vegetation cover

Table 3 Diversity of vascular epiphytes hosted within different vertical strata by the native *Cedrela dugessi* and the exotic *Annona cherimola* phorophytes

Diversity metric	Native phorophyte			Exotic phorophyte		
	Zone I	Zone II	Zone III	Zone I	Zone II	Zone III
^{0}D	10 (10–33)	12 (12–14.4)	15 (15–20)	3 (3–3)	9 (9–18.2)	7 (7–11.9)
^{1}D	5.1 (4.1–7.2)	6.0 (5.5–6.8)	5.1 (4.5–5.9)	3 (2.9–3.3)	5.9 (5.3–7.2)	4.1 (3.9–5.4)
^{2}D	3.9 (3.1–4.9)	4.7 (4.3–5.3)	3.3 (2.9–3.3)	3 (2.9–3.3)	5.36 (4.9–6.2)	3.3 (2.6–4.2)

True diversities at three orders of q (^{0}D, ^{1}D, ^{2}D) are provided for each zone within each phorophye species. ^{0}D: species richness; ^{1}D: number of species with similar abundance; ^{2}D: number of species with the same dominance. Within each cell, the true diversity value and the 95% CI (lower-upper) are provided

S6A). In contrast, the number of species with the same dominance (^{2}D) was similar for both phorophyte types. In zone II, true diversities at the three orders of q did not differ between the exotic and the native phorophyte (Table 3; Figure S6B). In zone III, the native phorophyte hosted a significantly higher species richness than the exotic one. The number of species with the same abundance and dominance (^{2}D) was similar between the exotic and the native phorophyte (Table 3; Figure S6C). In both phorophytes, *P. ferruginea* was the most abundant species in zone I, whereas *T. capitata* was the most abundant species in zones II and III (Figure S7). *Pleopeltis acicularis* was also an abundant species in zones I and II of both phorophytes (Figure S7); whereas the *Tillandsia* spp. group had a high abundance in ZIII of the exotic phorophyte (Figure S7A), and in zones II and III of the native one (Figure S7B). *Peperomia tetraphylla* figured as an abundant species in ZI and ZII of the exotic phorophyte (Figure S7A), and ZI of the native one (Figure S7B).

Epiphyte composition was different across vertical strata within each phorophyte (NMDS: stress = 0.2 with two dimensions; ANOSIM: $R = 0.34$, $P = 0.001$). Results from the NMDS showed that epiphyte composition of ZI in both phorophytes was significantly associated with thick branches ($r^2 = 0.64$; $P < 0.01$, coefficient = -0.99), and high vegetation cover ($r^2 = 0.33$, $P < 0.01$, coefficient = -0.99; Figure S8). In contrast, epiphyte species composition in ZIII of both phorophytes was significantly associated ($r^2 = 0.51$; $P < 0.01$, coefficient = 0.93) with branch height (Figure S8). In both phorophytes, branch inclination did not affect epiphyte composition among zones ($r^2 = 0.11$; $P = 0.07$, coefficient = -0.91; Figure S8).

Vascular epiphytes were heterogeneously distributed along both phorophytes. The frequency of all the epiphyte species analyzed was significantly different from the frequency expected by random (Fig. 3). In both phorophytes, *P. tetraphylla*, *P. ferruginea*, and *P. acicularis* were overrepresented in ZI and subrepresented in ZIII. Moreover, *Tillandsia capitata* was subrepresented in ZI of both phorophytes but overrepresented in ZIII of the native phorophyte. The abundance of the fern *P. furfuracea* was as expected by random in all strata of the exotic phorophyte but overrepresented in ZII and subrepresented in ZIII of the native one. The orchid *P. linkiana* was overrepresented in ZI but subrepresented in ZIII of the native phorophyte. Finally, in the native phorophyte *T. makoyana* was overrepresented in ZIII, but subrepresented in ZI and ZII; Fig. 3).

The HGAM model explained 38.5% of deviance; it was fitted (restricted maximum likelihood: 105.1, K-S test: $P = 0.89$), with not overdispersed data ($P = 0.9$) nor outliers ($P = 1$). The model revealed that mean species richness per zone within trees was significantly affected by the intercept, branch height (Figure S9D) and vegetation cover (Figure S9H), but not by phorophyte type. Branch diameter, branch inclination and zone did not have a significant effect on mean species richness per zone within the tree (Figures S9, S10).

Discussion

The study revealed that the native phorophyte hosts up to twice the total species richness (^{0}D) and diversity (^{1}D) of vascular epiphytes with lower dominance (^{2}D) than the exotic one. This provides clear evidence of the influence of phorophyte nature (native vs. exotic) on the vascular epiphyte communities. Three non-mutually exclusive factors might explain these results. First, it has been found that the longer the coexistence time of species within ecosystems, the greater the number of interactions established (Fenster et al. 2004). Native trees provide a mosaic of environmental factors (availability of specific micorrhycic fungi, lack of allelochemical production; Kartzinel et al. 2013; Ochoa-Bonilla et al. 2024) that have evolved in coexistence with epiphytes through long periods of time, favoring their establishment (Alvim et al. 2021; Ochoa-Bonilla et al. 2024). In contrast, because the interaction between epiphytes and exotic phorophytes is relatively recent, the micro-environment provided by *A. cherimola* might limit epiphyte establishment. For instance, it has been acknowledged that

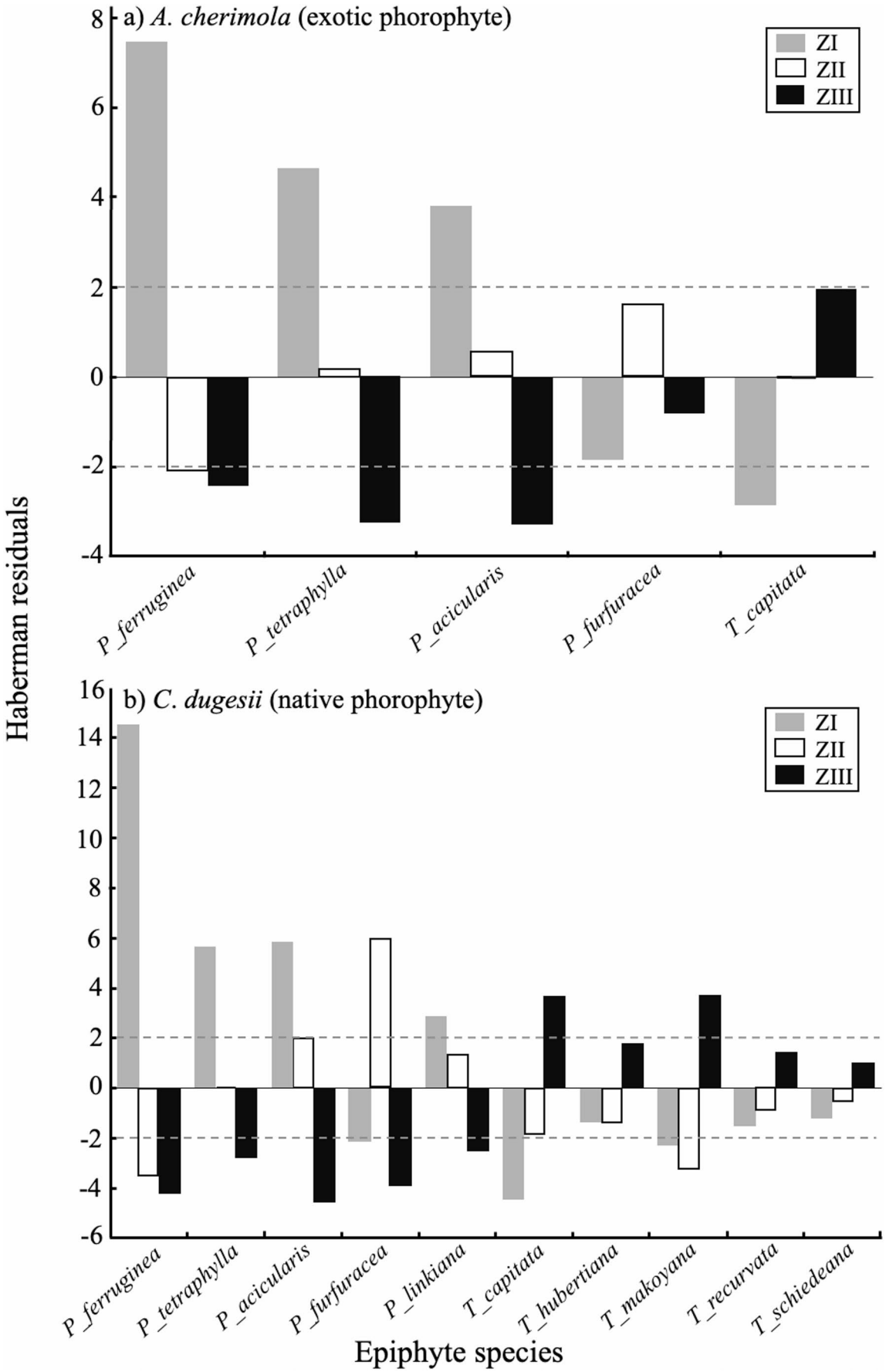

a) A. cherimola (exotic phorophyte)
ZI
ZII
ZIII
8
6
4
2
0
-2
-4
P_ferruginea
P_tetraphylla
P_acicularis
P_furfuracea
T_capitata
b) C. dugesii (native phorophyte)
ZI
ZII
ZIII
16
14
12
10
8
6
4
2
0
-2
-4
-6
P_ferruginea
P_tetraphylla
P_acicularis
P_furfuracea
P_linkiana
T_capitata
T_hubertiana
T_makoyana
T_recurvata
T_schiedeana
Haberman residuals
Epiphyte species

Fig. 3 Haberman residuals for epiphyte species recorded on different vertical strata (ZI= main trunk, grey bars; ZII= inner branches, white bars; ZIII= outer branches, black bars) along the exotic *Annona cherimola* (a) and the native *Cedrela dugesii* (b) phorophytes. Bars within the horizontal dashed lines indicate that the observed frequency of the species was as expected by random. Bars above or below the horizontal dashed lines indicate that the observed frequency of the species was different from random (above: more frequent than expected by random; below: less frequent than expected by random)

heterogeneous and complex tree crowns (with numerous branches; Hernández-Pérez et al. 2018) provide a stable microenvironment (low variation in light incidence and moisture) that favors epiphyte diversity (Callaway et al. 2002; Hernández-Pérez et al. 2018; Ramírez-Martínez et al. 2018). Crowns in plants within the *Annona* genus have few branches (Younes 2016), whereas those in *Cedrela* species have numerous branches (Menalled and Kelty 2001; Delagrange et al. 2008). The positive relationship between mean species richness per zone within individual trees with vegetation cover and branch height found in *C. dugesii* shows that complex tree crowns host a higher epiphyte diversity (Menalled and Kelty 2001; Delagrange et al. 2008; Hernández-Pérez et al. 2018).

Second, phorophytes with fissured crusts retain high amounts of water, favoring epiphyte establishment (Mehltreter et al. 2005; Wagner et al. 2015). The native *C. dugesii* has a more fissured crust (Calderón and German 1993; Pennington et al. 2010) than the exotic *A. cherimola* (Luna-Vega 1999; Ortiz-Rodríguez et al. 2015). Therefore, *C. dugesii* might offer a humid microenvironment proper for epiphyte germination and survival, not present in *A. cherimola*. Finally, the production of allelochemicals in phorophyte tissues might limit epiphyte germination, development, and establishment (Valencia-Díaz et al. 2010, 2013; Fernández-García 2014; Flores-Palacios et al. 2015; Hernández-Álvarez 2021). Previous studies have shown that allelochemicals produced by different Annonaceae species inhibit seed germination, radicle growth, shoot length, and root length in non-epiphyte plant species (Fujii et al. 2003; Novaes et al. 2016).

Species composition was heterogeneous along the phorophytes and moderately similar between phorophyte species. This agrees with results from a previous study in which 52% of epiphyte species were shared between exotic and native phorophytes (Silva-Martins et al. 2020). Moreover, epiphytes within the genera *Tillandsia* and *Pleopeltis* were common in both types of phorophytes, as it was previously recorded (Boelter et al. 2011; Alvim et al. 2021). Lack of contrasting differences in species composition between phorophytes might be attributed to the anemochoric dispersion of most of the epiphytes recorded (Bromeliaceae and Polypodiaceae) and to the reduced size of the forest (Hernández-Cárdenas et al. 2014). Across strata, the most pronounced differences in species composition were detected between ZI and ZIII in both phorophytes (only 26% and 10% of shared species in the native and the exotic phorophyte, respectively). Bromeliads predominated in thin and tall branches, whereas peperomias were associated with high vegetation cover.

The heterogeneous distribution of epiphytes along phorophytes has been previously recorded (Krömer et al. 2014; Silva-Martins et al. 2020). Differences in specific microenvironmental requirements and adaptations of each epiphyte species (Wagner et al. 2013; Ruiz-Cordova et al. 2014; Nardy et al. 2024) explain such distribution. While in ZI, humidity and vegetation cover are high, but temperature and solar radiation are low; in ZIII, the opposite pattern occurs (Cardelús and Chazdon 2005; Woods et al. 2015). Therefore, epiphyte species will not distribute in both zones. For instance, the peperomia *P. tetraphylla* predominated in ZI, since it has thin cuticles and it requires a high level of humidity (Mickel and Smith 2004; Suwanphakdee et al. 2024). In contrast, the bromeliads *T. capitata* and *T. makoyana* were mostly distributed in ZIII, since they have tank rosettes, absorbent trichomes, and CAM metabolism, which favor their survival in relatively dry conditions (Reyes-García et al. 2022). Therefore, both phorophyte morphological traits and epiphyte adaptations determine the vertical distribution of vascular epiphytes (Wagner et al. 2013; Ruiz-Cordova et al. 2014; Reyes-García et al. 2022).

In conclusion, our results showed that the native phorophyte hosts a total epiphyte community more diverse (^{0}D, ^{1}D) than the exotic one. Across vertical strata, species composition differs similarly in both phorophytes. Epiphytes showed a heterogeneous distribution along the phorophytes according to their particular associations with morphological traits of each phorophyte species (branch diameter and height, vegetation cover). Therefore, both the time of coexistence between epiphytes and each phorophyte type, as well as the morphological traits of each phorophyte, play an important role in the communities of vascular epiphytes. Conservation of the native phorophyte *C. dugesii* will assure the maintenance of a diverse community of vascular epiphytes. In addition, continuous monitoring of populations of the exotic phorophyte *A. cherimola* will limit possible negative impacts of this phorophyte on the plant community, including epiphytes and native phorophytes (Fujii et al. 2003). Future studies must evaluate the impact of phorophyte type (native vs. exotic) on the epiphyte communities. This will increase our understanding of the epiphyte-phorophyte interaction in biodiverse natural ecosystems, particularly those strongly fragmented, where species introduction might be common, as the cloud forest (Williams-Linera et al. 2022).

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Declarations

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