# ORIGINAL ARTICLE

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# Phorophyte size and soil profiles differentially correlate with community structure among hemiepiphytes and nomadic vines

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# Abstract

Tropical non-self-supporting plants such as hemiepiphytes and nomadic vines are model organisms for disentangling biotic and environmental correlates which influence their occupancy patterns. We inventoried >4000 individuals from >3000 trees ranging from 1 to 200 cm diameter at breast height (DBH) in a northeastern Amazonian upland forest to address how tree (phorophyte) size, edaphic factors and recruitment strategy influence occupancy, diversity, and compositional patterns of two vascular non-self-supporting plant functional groups. Hemiepiphytes germinate on phorophytes prior to establishing soil connections, whereas nomadic vines initiate their life cycle on the forest floor and subsequently climb phorophytes for crown access, abandoning roots replaced by adventitious connections which may reach the ground. Our results show that larger phorophytes (≥30 cm DBH) supported more species for both hemiepiphytes and nomadic vines. However, nomadic vines' occupancy probabilities saturated faster at smaller stem sizes than that of hemiepiphytes indicating differential preferences for stem sizes among the two functional groups. For smaller phorophytes (<30 cm DBH), soil correlations were stronger with nomadic vines than hemiepiphytes, whereas no significant differences were detected among functional groups in relation to edaphic factors for larger ( $\geq$  30 cm DBH) ones. Finally, a small core group of species showed disproportionately greater abundances among large phorophytes suggesting that autogenic processes differentially promote survivability. Such interactions among phorophyte size and edaphic factors may result from the contrasting ecological requirements of hemiepiphytes and nomadic vines at the recruitment stage, demonstrating the necessity for elaborate demographic-based studies to better understand these complex plant-plant interactions.

Abstract in Spanish is available with online material

### KEYWORDS

Amazon, hemiepiphyte, life history, old growth, plant-plant interactions, rainforest, species richness, tree canopy, vines

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# 1 | INTRODUCTION

Plants which use other plants (phorophytes) for support may be classified into different functional groups according to their recruitment substrates, growth pattern and habitat preferences as either holoepiphytes, hemiepiphytes, or nomadic vines (Moffett, 2000; Zotz, 2016). Although a few epiphytic taxa may fit diffusely, a vast majority of taxa is classified, based on life history characteristics, into one of these three groupings. One important distinction between hemiepiphytes and nomadic vines compared to holoepiphytes is that members of the first two functional groups rely on shoot and/or adventitious root contact with the soil during growth (Zotz, 2013, 2016; Zotz et al., 2020). As a result, at some point in their growth patterns both hemiepiphytes and nomadic vines typically have contact with, and thus are influenced by, both phorophyte and soil. By contrast, nomadic vines start their life cycle in soil and only occasionally in suspended soil (Moffett, 2000), and it climbs phorophytes, loses roots, and potentially reconnects to the ground through adventitious roots (Caleño-Ruíz et al., 2018; Moffett, 2000). Hemiepiphytes may be distinguished from nomadic vines by the fact that germination occurs on the phorophyte itself, with their adventitious roots descending groundward only following successful establishment (Zotz, 2013).

Such contrasting demographic strategies are subject to different ecological challenges at the most vulnerable demographic phase: seedling recruitment (Mondragón et al., 2015; Silvertown & Charlesworth, 2009). Different life history strategies should indeed result in differential phorophyte and microsite preferences; however, such a prediction has rarely been tested, especially in tropical forests (Zotz, 2016). In summary, hemiepiphyte germination success is putatively influenced by phorophyte plant characteristics such as phorophyte bark quality, micro-architectural features (e.g., knotholes and bifurcations) (Laman, 1995; Tay et al., 2022; Zotz, Almeda, et al., 2021), and that of nomadic vine is limited by various factors associated with the understory such as solar radiation, leaf litter, and soil quality (Cockle, 2001). In light of these demographic contrasts, we predict that nomadic vines' occupancy is weakly related to phorophyte size (Orihuela & Waechter, 2010), and hemiepiphytes, due to their above-ground germination, should be favored on larger phorophytes which support conditions for the establishment of aboveground plants (Wagner et al., 2015).

Both hemiepiphytes and nomadic vines are important components of tropical lowland, sub-montane and cloud forests, as well as tropical savannas (Putz & Holbrook, 1986). In combination, these two functional groups represent more than two-thirds of all vascular non-self-supporting plant species across the Amazon Basin (Boelter et al., 2014; Irume et al., 2013; Obermüller et al., 2012). Furthermore, they provide shelter and food for insects and vertebrates (Gibernau et al., 2007; Madison, 1979; Vieira & Izar, 1999), stabilize soil moisture and nutrient levels (Clark et al., 1998; Stanton et al., 2014), and serve as bioindicators (Triana-Moreno et al., 2003).

Disentangling the predictive factors of vascular epiphyte occurrences at individual-, phorophyte-, local- (100 m<sup>2</sup>), and/or regional-(>10 km) scales is a challenge particularly in forests of low vascular

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epiphyte densities (Burns & Zotz, 2010). Studies in the Amazon Basin have illustrated the importance of soil attributes in driving epiphyte composition (Boelter et al., 2014; Quaresma et al., 2017). Indeed, geographic variation in soil fertility and organic carbon have been documented across Amazonia (Quesada et al., 2020; Williams et al., 2002). Likewise, 60% of the variation in Amazonian tree biomass and mortality rates were explained by soil clay concentration and cation exchange capacity (CEC) (Toledo et al., 2017). Specifically, increasing clay concentration predicted lower tree mortality, higher tree biomass, longer-lived, and larger-sized phorophytes: all of which are positively correlated with epiphyte presence (Flores-Palacios & Garcia-Franco, 2006; Woods, 2017).

Soil phosphorus (P) is a limiting nutrient in tropical weathered soils and has a complex influence on epiphytes. Boelter et al. (2014) found a strong effect of soil P on nomadic vines in an old growth forest in Central Amazonia, with an increase of richness and abundance associated with higher soil P concentration. Soil P also influenced both directly and indirectly, through tree basal area, the abundance and richness of epiphytes in a tropical forest in Southern China (Ding et al., 2016). Although the influence of P on canopy epiphytes is far from clear, experimental evidence indicates that P fertilization of bark in the crown, and, independently, on soils in vicinity of focal trees increased the abundance and richness of holoepiphytes (Benner & Vitousek, 2007).

Phorophyte size is also an important predictor of epiphyte species richness as larger phorophytes provide larger surface areas (e.g., target effect sensu Lomolino, 1990), greater microhabitat variation through ontogenetic changes accompanying tree growth (Woods et al., 2015), and more temporally stable substrates thus increasing (re)colonization probabilities (Taylor & Burns, 2015). Increases in epiphyte species richness in relation to phorophyte stature are common (Flores-Palacios & Garcia-Franco, 2006; Zhao et al., 2015; Zotz & Vollrath, 2003). Likewise, primary forests composed of larger phorophytes tend to harbor more epiphytic species than smaller ones (Barthlott et al., 2001; Werner & Gradstein, 2009). However, studies at sites of high epiphyte density report weak (Zotz & Schultz, 2008), and even negative (Harrison et al., 2003) correlations with phorophyte size. Recently, a comparative study among two lowland Amazonian habitats of low epiphytic diversity, white-(varzea) and black- (igapó) water floodplain forests, reported contrasting richness-phorophyte size relationships among ecologically similar habitat types (Quaresma et al., 2020). Despite such disparity among relationships of phorophyte size and epiphyte community attributes, no study has yet attempted to disentangle phorophyte size from edaphic factors on occupancy, richness, and composition of non-self-supporting plant functional groups with contrasting ecological strategies.

Lowland northeastern Amazonia harbors the greatest concentration of large trees (Gorgens et al., 2021), making the Amapá National Forest (Figure 1) an ideal setting for evaluating determinants of non-self-supporting plant community structure. In light of the contrasting ecological requirements of hemiepiphytes and nomadic vines (Benner & Vitousek, 2007; Boelter et al., 2014), we



FIGURE 1 Map of the study area showing 11 plots (red dots) distributed on the research trail system (5×5 km) in the south part of the Amapá National Forest (ANF) at Amapá state, Brazil.

aimed to test the following predictions: (a) hemiepiphytes occurrence frequencies, when compared to nomadic vines, are skewed toward larger-stemmed phorophytes (>30 cm DBH) as hemiepiphytes recruitment and subsequent species accumulation are higher on larger phorophytes due to greater microhabitat heterogeneity (Woods et al., 2015), and longevity (Petter et al., 2021); (b) phosphorus, due to its rarity in the highly weathered soils, will best predict changes in abundance and richness of nomadic vines due to the importance of soil fertility at the vulnerable germination stage. To the contrary, we predict that hemiepiphytes are positively correlated with increased soil clay concentration as this edaphic characteristic contributes to phorophyte longevity and size (Toledo et al., 2017); and (c) compositional heterogeneity decreases with phorophyte size.

# 2 | METHODS

# 2.1 | Study area

In 2006, the Brazilian Program for Biodiversity Research (PPBio) installed a Long-Term Ecological Research (LTER) site composed by a grid trail system in 25 km<sup>2</sup> of *terra firme* (upland, non-seasonally

flooded) forest of the Amapá National Forest (ANF) in the extreme northeastern corner of the Brazilian Amazon near the Guiana Shield in Amapá state (0°55'29"N, 51°35'45"W) (Figure 1).

The regional climate is classified by Köppen-Geiger as Equatorial monsoon (Kottek et al., 2006). Mean annual temperature varies between 22°C and 32°C, and average annual rainfall is ca. 2284 mm with a rainy season from December to July, and precipitation often exceeding 60mm per month even in the driest months (ICMBio, 2014). Altitude varies between 100 and 200m a.s.l with slopes attaining 7% inclination. Ultisols and oxisols are the predominant soil types in ANF, with clay concentration varying from 2% to 48%, and sand from 35% to 82%, average CEC around 10 cmol kg<sup>-1</sup>, and low available phosphorus at 2 mg dm<sup>-3</sup> (PPBio, unpublished data): typical of the low soil fertility of Guiana Shield (Quesada et al., 2011). Canopy trees typically reach heights of 25-35 m with frequent larger trees reaching 50m in height (ICMBio, 2014). The most abundant tree families in the area are Lecythidaceae, Fabaceae, Sapotaceae, Burseraceae, and Annonaceae, and the dominant species are Vouacapoua americana Aubl. (Fabaceae), Eschweilera ovata (Cambess.) Miers, E. coriacea (DC.) S.A. Mori, Lecythis chartacea (O. Berg) Eyma (all three are Lecythidaceae), and Eugenia cupulata Amshoff (Myrtaceae) (JJT, unpublished data).

# 2.2 | Field sampling

The survey was conducted in 11 out of the 30 previously established plots in the ANF according to guidelines established by the Rapid Assessment for LTER (RAPELD) methods (Magnusson et al., 2005). The 11 plots ( $250m \times 20m$ ) were divided in 25 sections ( $10m \times 20m$ ), out of which 10 from each plot were selected for this study (110 sections). We selected one phorophyte  $\geq$ 30 cm DBH from each section in the following form: Firstly, we marked all phorophytes  $\geq$ 30 cm DBH and subsequently chose the third phorophyte listed for each section. The selected phorophyte ( $\geq$ 30 cm DBH) was used as the center point for the establishment of circular subplots of 6 m radius (113 m<sup>2</sup>).

From March to September 2017, all non-self-supporting plants on phorophytes of DBH  $\geq 1$  cm (within the circular subplots) were surveyed from the ground using binoculars in combination with crown access using traditional tree climbing methods, and single rope climbing techniques (Anderson et al., 2015). We counted all plant individuals on the phorophytes to estimate abundance, assuming as an individual a leaf bundle for ferns and Gesneriaceae, and a group of stems for Araceae, Clusiaceae, Cyclanthaceae, Marcgraviaceae, and Orchidaceae. An individual was defined as an entity which was entire physically separated from other individuals of the same species or by individuals of other species.

Observations were made as to the habit, vertical position, and presence/absence of soil connections to evaluate whether individuals were connected to the soil through adventitious roots, aerial root feeders, and/or stem basal connections (Moffett, 2000; Zotz, 2013). When the plant was connected to the soil or showed any vestigial sign of rupture, it was classified as a nomadic vine. When no soil connection by root or stem was observed, information from the literature, on previously reported life history traits, was used to supplement our classifications (Massa, 1996; Zotz et al., 2020; Zotz, Weigelt, et al., 2021). Field identifications were made using regional guides (e.g., Ribeiro et al., 2002; Zuguim et al., 2008), and botanical vouchers were collected for comparison with material deposited in regional herbaria: Amapaense herbarium (HAMAB) at the Instituto de Pesquisas Científicas e Tecnológicas do Amapá, and the João Murça Pires Herbarium (MG) at the Museu Paraense Emílio Goeldi in Belém do Pará, Brazil. Circumscriptions of fern taxonomy followed PPG I (Pteridophyte Phylogeny Group, 2016) and angiosperms followed APG IV (Angiosperm Phylogeny Group, 2016).

Superficial (0-5 cm deep) soil samples were collected every 50m (first sample at 0 m) along the plot's 250m long central line with the 6 total samples pooled to make a composite for each plot. Soil analyses were conducted at the soil laboratory of the Brazilian Agricultural Research Corporation (EMBRAPA) of Amapá to be analyzed following protocols established by EMBRAPA (1997): Clay concentration (soil particles <0.002 mm) was determined by the hydrometer method; the available phosphorus was estimated by the ammonium molybdate-ascorbic acid method, which produces a blue color complex read photometrically at 660nm; K<sup>+</sup> and Na<sup>+</sup> were extracted by 1-Molar Mehlich solution and measured by atomic absorption; Ca<sup>2+</sup>

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and  $Mg^{2+}$  were extracted by 1-Normal KCL solution and also measured by atomic absorption;  $K^+$ ,  $Na^+$ ,  $Ca^{2+}$ , and  $Mg^{2+}$  were summed to obtain total base cation (BC).

# 2.3 | Data analysis

Species richness for hemiepiphytes and nomadic vines was estimated using the Chao index (Chao, 1984). Abundance and richness of hemiepiphytes and nomadic vines were related to phorophyte size (DBH) using generalized linear model (GLM; *glm* function), assuming a Poisson distribution for abundance and Gaussian distribution for richness. To estimate the probability of occurrence of hemiepiphytes and nomadic vines in relation to DBH, we used logistic regression with a maximum likelihood estimator. The presence/absence of nonself-supporting plants was related to DBH and functional group (hemiepiphytes and nomadic vines) and the interaction between DBH and functional group.

The effect of soil P, BC, and percentage of clay on species abundance and richness (Chao index) was tested also using GLM (abundance/richness = soil+functional group+functional group×soil) assuming a Poisson distribution for abundance and Gaussian distribution for richness data. Models were run for small- (<30 cm DBH), and large- ( $\geq$ 30 cm DBH) tree size classes with subplot as sample unit.

The influence of phorophyte size on functional group attributes (beta diversity, heterogeneity and composition) was analyzed at plot level. Firstly, data were pooled into eight phorophyte size classes of 10 cm (DBH:  $\geq 1 - < 10$ , ...,  $\geq 70$  cm), and average DBH for each size class was used as predictor. The influence of forest structure on group attributes was analyzed at the subplot level. This format was also used to estimate tree density (N) and average DBH for size class. A scaling function (InN = a + b InDBH; with In at base 10) was fitted and the slope – b (hereafter named scaling exponent) was extracted to represent forest structure. This is a numerical continuous variable, for which high negative values indicate higher density of small trees and lesser negative values indicate an increase in density of large trees.

We analyzed beta diversity by calculating turnover rate as Simpson dissimilarity index ( $\beta_{sim}$ ) (Baselga, 2010), and as Bray–Curtis dissimilarity index ( $\beta_{BC,BAL}$ ) (Baselga, 2017) for presence/absence and abundance data (respectively), at plot and subplot spatial scales. Heterogeneity was estimated by calculating dissimilarity matrices with the indices versions of Sorensen ( $\beta_{sor}$ ) and Bray–Curtis ( $\beta$ BC) for multiple sites (Baselga, 2010, 2017), with principal coordinate analysis (PCoA) subsequently applied on these matrices. The axes of PCoA were used to calculate average Euclidean distances between objects and group centroids as a measure of group heterogeneity. PCoA was also run using Bray–Curtis dissimilarity matrices, and the first axis was used to represent species composition.

Analysis of covariance (ANCOVA) was used to test for the influence of phorophyte size (averaged DBH per size class), forest structure (scaling exponent), and functional group (hemiepiphytes and WILEY bioTROPICA

nomadic vines) on turnover rates, heterogeneity, and compositional variation of non-self-supporting plants. Functional group was treated as a factor in ANCOVA, and average DBH and the scaling exponent were used as covariables in separate models: community property = DBH or scaling exponent+functional group+DBH×functional group.

Additionally, the influence of average DBH and the scaling exponent on composition of hemiepiphytes and nomadic vines was tested by permutational multivariate analysis of variance (PERMANOVA) using Bray-Curtis as dissimilarity metrics (Magurran, 2004). The adonis2 function available in the vegan package, version 2.5-7 (Oksanen et al., 2020), was used to run PERMANOVA. This function supports the use of continuous explanatory variables, running a regression to analyze the relationship between species matrix centroids and the continuous independent variables.

Vegan was also used to estimate alpha diversity and to calculate distances from centroids in community data. The ape package version 5.0 (Paradis & Schliep, 2019) was used to run PCoA, and the Betapart package version 1.4-1 (Baselga, 2017) was used for partitioning of beta diversity. All analyses were performed using the R platform version 3.4.2. (R Core Team, 2017).

#### 3 RESULTS

# 3.1 | Phorophyte stem size and community attributes

A total of 3412 phorophytes (1-200 cm DBH) were inventoried, and nomadic vines were vastly more abundant and with greater species richness (4226 individuals and 36 species) than hemiepiphytes (687 individuals and 11 species; Table S1). We found a total of 11 genera (three of hemiepiphyte species and nine of nomadic vine species) and seven families (three of hemiepiphyte species and five of nomadic vine species). Abundance and species richness increased significantly with phorophyte size for both nomadic vines (GLM: slope- $b_{abundance} = 0.01$ ; slope- $b_{richness} = 0.03$ , p < .001) and hemiepiphytes (GLM:  $b_{abundance} = 0.02$  and  $b_{richness} = 0.01$ , p < .001), although with low predictability ( $\leq 11\%$ ) (Figure S1).

In support of the first prediction, occurrence probabilities reached asymptote on significantly larger-sized phorophytes for hemiepiphytes (DBH >100 cm) when compared to nomadic vines (DBH >40 cm) demonstrating a significant shift in distributional patterns among the two functional groups in relation to phorophyte size (Figure 2). Nomadic vines also had a significantly higher occurrence probability (48%) on smaller (DBH <10 cm) trees when compared to hemiepiphytes (7%). Overall, nomadic vine abundances were greater than those of hemiepiphytes (GLM: intercept- $a_{\text{functional group}} > 1.3, p < .005$ ) for all phorophyte sizes. Nomadic vine species richness was greater than that of hemiepiphyte in smaller-stemmed phorophytes (GLM:  $a_{\text{functional group}} > 8$ , p < .001); however, no differences were detected among larger ones ( $a_{\rm functional\ group}$  <1.2, p >.05) unless when clay was included as a covariable ( $a_{\text{functional group}} = 9.6, p < .005$ ) (Figure 4; Table S2).

#### 3.2 Interactions among phorophyte size, edaphic correlates, and functional groups

Abundance was positively related to soil P but negatively related to BC and clay (Table 1 and Table S2). Specifically, for small-stemmed phorophytes, variation in hemiepiphyte abundance was not correlated with soil P, whereas nomadic vine abundance varied significantly in relation to all soil variables. In support of the second prediction, soil P was significantly and positively correlated with nomadic vine abundance (Figure 3a) (ANCOVA:  $b_{\text{interaction}} = 0.251$ ; p = .006) for the small stem size class, whereas both nomadic vine and hemiepiphyte abundances declined in relation to clay (slopeb = -0.04; p = .001) and BC (b = -3.039;  $p \le .001$ ) concentrations (Figure 3b,c). For larger phorophytes, only soil P was positively correlated with variation in abundance of both hemiepiphytes and nomadic vines (b = 0.373; p = .001 for both groups) (Figure 3d), but BC, and clay concentration was not (Table 1, Figure 3e,f). Overall, nomadic vine abundances were more strongly correlated with the measured soil properties than those of hemiepiphytes, and this influence was most pronounced among smaller phorophytes (Table 1).

Richness was related only to BC and clay on small-stemmed phorophytes (Table 1 and Table S2). In contrast to the second prediction, variation in soil P was not correlated with species richness for either hemiepiphytes and nomadic vines (Figure 4a,d), and nomadic vine species richness declined significantly on smaller phorophytes ( $b_{\text{interaction}} = -18.029, p = .004$ ) in relation to increasing BC (Table 1, Figure 4b,e). Increased clay concentration, however, was also negatively associated with nomadic vine species richness but only for small phorophytes ( $b_{interaction} = -0.215, p = .02$ ) (Figure 4c). No measured soil variables were significantly correlated with variation in hemiepiphyte species richness (Table 1).

#### 3.3 **Compositional trends**

For individual phorophytes, compositional heterogeneity decreased significantly (Figure 5c; ANCOVA: slope-b = -0.002, p = .01) for both functional groups in relation to phorophyte size (Table 1 and Table S3). Likewise, spatial turnover (e.g., beta diversity) marginally decreased among large phorophytes only for nomadic vines (Figure 5a; b = -0.003, p = .08) independent of whether abundance or presence/absence data were analyzed (Table S3). At the subplot scale, neither turnover nor heterogeneity were correlated (b = -0.096, p = .5, and b = -0.10, p = .3) with either group in relation to increased densities of larger than average stem sizes (Figure 5b,d). Variation in species composition for both nomadic vines and hemiepiphytes differed significantly with phorophyte size at the individual- ( $b_{\text{interaction}} = 0.007$ , p < .001), and subplot- ( $b_{\text{interaction}} = -0.70$ , p = .003) scales (Figure 5e,f) independent of whether abundance (Figures S2a,b and S3a,b) or presence/absence (Figures S2c,d and S3c,d) data were analyzed (Table 1 and Table S3).

A core group of species, those which contributed to >1% abundance for each functional group, were represented by 14 nomadic



TABLE 1 Summary of relations of functional group (hemiepiphytes—H and nomadic vines—NV) attributes with soil and forest properties: Abundance and richness (Chao Index) are related to soil phosphorus (P), total base cation (BC), and clay concentration for small ( $1 \le DBH < 30 \text{ cm}$ ) and large (DBH  $\ge 30 \text{ cm}$ ) phorophytes; turnover ( $\beta_{Bray-curtis}$  and  $\beta_{Simpson}$ ), heterogeneity (distance from PCoA centroid), and composition (PCoA Axis 1) are related to mean phorophyte DBH and forest structure (scaling exponent) calculated on abundance and presence/absence data. Detailed results of these analyzes are in Tables S2 and S3

	Predictors	Dependent variables					
	Soil	Abundance		Richness			
Phorophyte size	properties	н	NV	н	NV		
Small	Р	ns	+	ns	ns		
	BC	-	-	ns	-		
	Clay	-	-	ns	-		
Large	Р	+	+	ns	ns		
	BC	ns	ns	ns	ns		
	Clay	ns	ns	ns	ns		
	Forest	Turnover		Heterogeneity		Composition	
Data type	properties	н	NV	н	NV	н	NV
Abundance	Mean DBH	ns	ns	-	-	ns	+
	Structure	ns	ns	ns	ns	ns	-
Pres./abs.	Mean DBH	ns	ns	-	-	ns	+
	Structure	ns	ns	ns	ns	ns	+

Note: ns: non-significant relation; +: positive significant relation; -: negative significant relation.



**FIGURE 3** Correlations of soil fertility [(a and d) phosphorus and (b and e) total base cation], and (c and f) soil texture (percent clay) with hemiepiphyte and nomadic vine abundances as distributed in two phorophyte size classes [(a-c) small: Trees with  $1 \le \text{DBH} < 30 \text{ cm}$ ; and (d-f) large: Trees  $\ge 30 \text{ cm}$  DBH]. Abundances were pooled by subplot (n = 110). Generalized linear models (GLM) using Poisson distribution were used to test for the effects of soil, functional group, and their interaction (abundance = soil + functional group + soil × functional group) on abundance. Confidence intervals were estimated through bootstrapping. GLM results are presented in Table S2.

vine and 9 hemiepiphyte species (Figures 6a and S4a). Only two species (14%) of core nomadic vines (*Philodendron guianense* Croat & Grayum and *P. cremersii* Croat & Grayum) were highly abundant (>20% of total individuals) on larger phorophytes, compared to more than half of core hemiepiphyte (*Marcgravia* sp. 1, *P. linnaei* Kunth, *P. melinonii* Brongn. ex Regel, *P. megalophyllum* Schott, *P. solimoesense* A. C. Sm., and *P. callosum* K. Krause). Furthermore, half of nomadic vines and two-thirds of hemiepiphytes were equitably distributed across the forest structure gradient in the studied subplots. The remaining species exhibited a bimodal distribution at high densities for both small and large phorophytes (Figure 6b and Figure S4b).

We detected significant compositional changes (PERMANOVA: F > 7.50, p = .001) for hemiepiphytes and nomadic vines along a phorophyte size gradient, although variation was weakly explained ( $R^2 < 0.15$ ) (Table S4). Forest structure was related to species composition of nomadic vines (F > 4, p = .001) and hemiepiphytes (F = 2.6, p = .05), but also with low predictability ( $R^2 < 0.07$ ) (Table S4).

# 4 | DISCUSSION

# 4.1 | Indirect effects: Interactions among phorophyte stem size and soils

This study showed that meso-scale distributional patterns of two functional groups of non-self-supporting plants (hemiepiphytes and nomadic vines) with contrasting ecological strategies have distinct relations with phorophyte size and soil properties in an old growth Amazonian forest. Phosphorus (a rare soil nutrient in lowland Amazonia) showed stronger correlations with nomadic vine abundances, than with hemiepiphytes. Both correlative (Boelter et al., 2014; Ding et al., 2016) as well as experimental (Benner & Vitousek, 2007) studies indeed point to phosphorus (P) as a strong predictor of local abundance and richness among epiphytes. For example, Benner and Vitousek (2007) showed that canopy P availability increased with soil P fertilization and possibly, P-rich phorophyte



FIGURE 4 Correlations of soil fertility [(a and d) phosphorus and (b and e) total base cation], and (c and f) soil texture (clay concentration) with species richness (Chao index) of hemiepiphytes and nomadic vines as distributed in two phorophyte size classes [(a-c) small: Trees  $1 \le DBH < 30$  cm; and (d-f) large: Trees  $\ge 30$  cm DBH). Abundances were pooled by subplot (n = 110) to estimate richness. Generalized linear models using Gaussian distribution were used to test for the effect of soil, functional group, and its interaction (richness = soil + functional group + soil × functional group) on richness. Confidence intervals were estimated through bootstrapping. Results from GLM are presented in table S2.

tissues release P into stemflow and throughfall, increase P-supply for epiphytes. Extractable soil P is considered an important indicator of its availability for plants (Quesada et al., 2010). In the weathered and acidic clayey tropical soils, phosphorus is mostly bound to aluminum (Al) and iron oxides, thus limiting its extractability by plants (Sollins et al., 1988). In ANF, Al was positively correlated with clay (r = 0.58, p < .001) suggesting that soil P is complexed to oxides, inhibiting its availability for uptake in clayey soils.

Generally, total soil P in lowland Amazonia increases with clay concentration (Quesada et al., 2010), but depending on the measurement technique employed, as is the case with extractable soil P, it increases disproportionately in sandier soils. At ANF, extractable soil P was indeed inversely related to clay (r = -0.61, p < .001) and positively related to sand concentration (r = 0.55, p = .001). However, we do not have information on total soil P reserves of the ANF soil profiles, therefore limiting the scope of our conclusions with regard to correlations among soil P and hemiepiphytes. Most likely, nomadic

vines disproportionately benefit from the higher concentration of extractable soil P in sandy soils as, by definition, this functional group maintains soil connections throughout its entire growth program (Rains et al., 2003; Zotz, 2016). This prediction was supported in part by the fact that nomadic vine abundance and extractable soil P were significantly and positively correlated. Experimental studies of the effects of soil P on germination and growth are needed to further elucidate the role of this nutrient in the population dynamics of non-self-supporting plants.

Lowland Amazonia is geologically old with considerable heterogeneity in soil texture: an edaphic feature which directly influences water, nutrient, and carbon retention capacity (Quesada et al., 2010, 2011, 2020). In this study, soil clay concentration was negatively correlated with hemiepiphyte abundance and richness. Clay-rich soils offer greater support for larger statured trees by reducing mortality caused by uprooting (Nelson et al., 1994; Toledo et al., 2012), which contributes to the demonstrably greater densities of larger trees



FIGURE 5 Correlations of mean phorophyte size (DBH) per size class per subplot (a, c and e), and forest structure (b, d and f) with (a and b) turnover ( $\beta$ Bray-Curtis), (c and d) PCoA centroid distances and (e and f) composition (PCoA Axis 1) based on abundance data. Mean diameter per size class (tree DBH: 1-10 cm; 10-20 cm; ...; ≥70 cm) was calculated for each plot, and the scaling exponent was calculated by subplot. See Table S3 for the results of the analyzes.



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(Gorgens et al., 2021), and above-ground biomass stocks (Castilho et al., 2006) of Amazonian forests of high clay concentration. Curiously, at ANF large tree (>30 cm DBH) densities are inversely correlated with clay concentration (r = -0.5, p < .001), as areas with large trees are generally located in sandier sites in proximity to water courses. The negative relation of non-self-supporting plant abundance and richness with clay may be an indirect influence of higher density of smaller-statured trees, whereas increased abundance and richness in relation to sandy soils may simply be auto-correlative effects that sandier soils are located in greater proximity to water courses as humidity is a fundamental limiting factor for epiphytes (Obregon et al., 2011). However, without evidence from experimental studies, we are unable to disentangle the effects of humidity from soil types on hemiepiphytes and nomadic vines, in this study.

#### 4.2 Direct effects and phorophyte size

Phorophyte size, as inferred by stem diameter, was positively related to non-self-supporting plant richness and abundance while negatively related to turnover. Biotic filters in the form of autogenic processes such as facilitative interactions, inter-specific competition

(Ellis & Ellis, 2012), and abiotic filters such as changes in local microclimates in relation to phorophyte size/age (Woods et al., 2015) directly contribute to epiphyte community assembly dynamics. In this study, neither ontogenetic processes in community development, nor microclimatic variables were directly measured. However, the information culled from the distributional patterns of non-selfsupporting plant functional groups in relation to phorophyte size, and related metrics of forest structure allow us to respond to some predictions. Specifically, two predictions confirmed in this correlative study are that non-self-supporting plant species richness increased while spatial turnover decreased in relation to phorophyte stem size.

Species turnover decreased and compositional similarity increased with greater phorophyte-size suggesting repeatability of non-self-supporting plant assemblages among large phorophytes. Woods et al. (2015) showed that epiphyte species accumulate as more microhabitats are formed with crown growth, with a corresponding decrease in turnover as nested epiphyte assemblies repeat in niches unique to larger crowns. Large trees are disproportionately exposed to wind, light, higher temperatures, and drier conditions (Gorgens et al., 2021), factors which contribute to species filtering for xerophyllic plants (Hao et al., 2011). Branch loss may also



FIGURE 6 Species-level abundance (standardized by maximum) histograms of hemiepiphytes (red bars) and nomadic vines (blue bars) related to gradients of (a) phorophyte size and (b) forest structure. Data were pooled into phorophyte size classes (DBH: 1-10 cm; 10-20 cm;...; ≥70 cm) by each plot to allow ordination along mean diameter of phorophyte and pooled into subplots for ordination along the gradient of forest structure using the scaling exponent. The vertical dashed lines in (a) divide trees smaller and larger than 30 cm DBH. Core species with >1% contribution to abundance are, for nomadic vines: Evodianthus funifer (Poit.) Lindm, Heteropsis flexuosa (Kunth) G. S. Bunting, H. steyermarkii G. S. Bunting, Philodendron cremersii Croat & Grayum, P. duckei Croat & Grayum, P. guianense Croat & Grayum, P. platypodum Gleason, P. surinamense (Miq.) Engl., P. ecordatum Schott, P. panduriforme (Kunth) Kunth, P. pulchellum Engl., P. ushanum Croat & Moonen, Trichomanes ankersii C. S. Parker ex Hook, & Grey., and Araceae 42; and for hemiepiphytes; Marcgravia sp.1 and sp.2, Philodendron callosum K. Krause, P. linnaei Kunth, P. pedatum (Hook.) Kunth, P. hylaeae G. S. Bunting, P. megaphyllum Schott, P. melinonii Brongn. ex Regel and P. solimoesense A. C. Sm.

contribute to local epiphyte extinctions in larger crowns (Sarmento Cabral et al., 2015) also explaining lower species richness than expected in larger trees. When Petter et al. (2021) included branch fall even at low rates in a simulation model, reductions in species alpha diversity were significant. Mortality of large trees in ANF is expected to be lower than average for Amazonia as climate, topography, and soil are favorable for the persistence of very high-statured trees (>70m in height) (Gorgens et al., 2021). A combination of crown microclimates and branch mortality dynamics may contribute to explaining decreased beta diversity and augmented compositional similarity among hemiepiphytes and nomadic vines of larger phorophytes.

Likewise, increased non-self-supporting plant turnover in forest stands with a higher proportion of small trees indicates that other properties such as trait functional diversity (e.g., bark type and bark water potential) may act as determinants of community structure.

Indeed, trees with higher bark water potential support higher epiphyte diversity than those with lower water retention values (Callaway et al., 2002). However, lowland Amazonian epiphytes have yet to show affinities at either species- or family level in relation to bark type (Boelter et al., 2014).

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The larger phorophytes of mixed-age class forests may act as "stepping stones" in epiphyte dispersal processes, thus increasing colonization rates, and rescue effects in the sub canopy (Ruchty et al., 2001). For example, a simulation study (Petter et al., 2021) showed that forests with low turnover rates (2.2% of stem substitution) accumulate more individuals and species of epiphytes due to substrate longevity.

Inter-specific phorophyte habitat heterogeneity may also influence epiphyte community structure (e.g., Barbosa et al., 2020; Marcusso & Kamimura, 2019; Woods et al., 2019). However, at ANF an oligarchy of four phorophyte species-Manilkara huberi (Ducke) A.

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Chev. (Sapotaceae), Vouacapoua americana Aubl. (Fabaceae), Dinizia excelsa Ducke (Fabaceae), and Sextonia rubra (Mez) van der Werff (Lauraceae)—contribute to nearly half of the large trees (≥70 cm DBH) (JJT, unpublished data). Therefore, heterogeneity of bark types, bark water potential and crown architecture are expected to be lower among large trees due to the relatively low number of species which make up the large trees at ANF.

# 4.3 | Pitfalls: Assumptions in relation to phorophyte size, specificity, and growth programs

In this study, we assume "phorophyte neutrality" (Wagner et al., 2015); that is, phorophyte species type nominally influences non-self-supporting plant assembly structure. We offer two supporting reasons. Firstly, two studies, one from Amazonia (Boelter et al., 2014) and another from the Brazilian Atlantic Rainforest (Rogalski et al., 2016), suggest that hemiepiphytes and nomadic vines (particularly Aroids) do not show phorophyte specificity. Secondly, we suggest that it would be remotely advantageous for Amazonian non-self-supporting plants to have co-evolved with select phorophyte species because a vast majority of Amazonian tree species occur at densities of <1 adult individual/hectare (Pitman et al., 2002; ter Steege et al., 2013). Considering the sheer bottleneck in conspecific phorophyte numbers dispersal limitation would act as a nearly insuperable barrier thus rendering this coadaptation unlikely in Amazonian forests. Bark characteristics, also not measured in this study, may be an important determinant of epiphyte distributions. Rugosity has been shown to have a positive effect on epiphyte presence in many tropical regions (Callaway et al., 2002; Wagner et al., 2015), but null models based on a study from central Amazonia revealed weak associations among bark types (Boelter et al., 2014).

Another potential pitfall in our premise is the assumption that DBH is an accurate index for phorophyte biomass, height, secondary branching complexity, and longevity combined. Results from long term demographic studies and dendrochronological surveys of Amazonian trees do offer support that DBH is a reliable indicator of overall biomass (Chave et al., 2005), and of time since initial establishment (Chambers et al., 1998; Laurance et al., 2004; Schöngart et al., 2005). Nonetheless, snap-shot sampling designs assume a "space for time substitution" (Pickett, 1989) which are limited by the fact that neither the importance of ontogenetic changes nor that of forest dynamics, in relation to inter-specific variation in phorophyte growth rates (Petter et al., 2021), are considered. For example, intra-specific temporal variation in bark quality (see Wagner & Zotz, 2020) open the possibility that phorophyte specificity may change over time.

Phorophytes with greater stem size, generally used as a proxy for phorophyte stature, typically harbor higher species richness and abundance (Flores-Palacios & Garcia-Franco, 2006; Hirata et al., 2008; Taylor & Burns, 2015; Wagner & Zotz, 2020). One of three possible mechanisms are typically invoked to account for this relationship. Firstly, target effects, that is greater surface area offers greater capture potential and subsequent recruitment from the epiphytic seed rain by chance alone. Secondly, rescue or longevity effects result in a greater species accumulation on longer-lived substrates due to the increased chance of (re)colonization over time. Finally, ontological effects may favor changes in phorophyte quality over time as the density and variety of microsite quality increases (Taylor & Burns, 2015; Woods, 2017). However, a recent study of epiphyte communities in Amazonian flooded forests reported variable correlations among phorophyte size and community attributes (Quaresma et al., 2020).

In general, changes in phorophyte quality in relation to age would predict that the epiphytic flora occupying smaller trees represents a subset of those from larger trees (Rasmussen & Rasmussen, 2018). However, this was not the case here. Uniquely, a shift linking divergent ecological strategies at early demographic phases suggests a discontinuity in non-self-supporting plant floristic similarities in relation to phorophyte stem size.

Few demographic studies (sensu Laman, 1995) exist for non-selfsupporting plants. To our knowledge, the only reported works on epiphytic post reproductive biology have been conducted on holoepiphytes (reviewed in Mondragón et al., 2015), the one functional group not included in this study. Indeed, factors which influence in vivo germination, and seed to seedling success are under studied for epiphytes; however, the few published works point to hydric stress as the principal bottleneck (Pereira-Dias & Santos, 2015). The role of soil nutrient concentration and/or substrate quality on recruitment success of non-self-supporting plants remains understudied. Experimentally based demographic studies focusing on how local environment affects early life-cycle phases (i.e., recruitment and germination) (Mondragón & Calvo-Irabien, 2006) are sorely needed.

# AUTHOR CONTRIBUTIONS

E.R.C.A. and J.J.T designed the research and performed statistical analyses. E.R.C.A. and L.R.T.R. collected the data, and M.V.I. helped with functional group classification. C.E.Z, E.R.C.A., and J.J.T wrote the manuscript. R.R.H. contributed to the early drafts.

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# CONFLICT OF INTEREST

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

# DATA AVAILABILTIY STATEMENT

The data that support the findings of this study are openly available in DataOne at https://www.dataone.org/, reference number PPBioAmOc.648.9.

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