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Vascular epiphyte assemblages in a Brazilian Atlantic Forest fragment: investigating the effect of host tree features

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Abstract This study investigates the relative importance of dispersal- and niche-related mechanisms structuring the assemblages of vascular epiphytes in a 10-ha secondary Atlantic Forest patch in São Paulo city, Brazil. We tested for the effect of characteristics of host trees (species, height, trunk diameter, presence of lianas, and distance to a near stream) and of space on epiphyte abundance, species richness, and species composition of vascular epiphytes. Inside a 0.2-ha plot, all 86 trees with diameter at breast height >13 cm (27 species) were recorded, as well as all epiphytes larger than 15 cm in length on those trees (380 individuals, 22 species). Twenty-eight trees (32.6 %) did not carry epiphytes. On individual trees, tree species showed a significant effect on epiphyte abundance, richness, and species composition. The bark-shedding *Piptadenia gonoacantha* carried less epiphytes than other tree species. Distance to the stream showed effects on abundance and species composition, with lower abundance farther from the stream. Tree height had a positive effect on abundance, richness, and species composition, but trunk diameter had none, supporting the importance of vertical stratification in controlling epiphyte richness. Variation partitioning analyses showed little or no effect of "pure space" on abundance, richness, and species composition (explaining 6.7, 4.5, and 0.7 % of variation, respectively), as compared to environmental effects (26, 30, and 14.5 %), generally supporting a higher importance of niche-based processes in structuring epiphytic assemblages on host trees in the plot.

Keywords Niche-assembly · Urban secondary forest · RDA · Forest fragment · Dispersal · PCNM

Introduction

There is an ongoing debate about the forces structuring plant assemblages, with two contrasting views about the most important processes involved.

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One of them considers communities as open, nonequilibrium assemblages structured mainly by dispersal, chance, and history ("dispersal-assembly") (Hubbell 2001). The other considers environmental variables as the main structuring force of communities, through the adaptation of each present species to specific ecological niches ("niche-assembly") (Silvertown 2004).

Data analysis techniques which partition variation of species data into environmental and spatial components have been used to investigate the relative importance of dispersal- and niche-related mechanisms (Peres-Neto and Legendre 2010; Chase and Myers 2011). Such methods have been widely applied to assemblages of trees (e.g., Legendre et al. 2009; Baldeck et al. 2013; Punchi-Manage et al. 2014) and terrestrial herbs (Jones et al. 2008), but only rarely to vascular epiphytes (Wolf 2005).

In quantitative studies of the epiphytic assemblage, the individual trees that carry the epiphytes (also known as host trees or phorophytes) present themselves as natural sampling units. The characteristics of host trees, as species, age, size, architecture, bark type, and leaf characteristics (Benzing 1990; Laube and Zotz 2006; Benavides et al. 2011) may influence the epiphyte species richness and composition on each tree.

The aim of this study is to contribute to the debate about niche-based versus dispersal-based processes structuring plant assemblages, by testing hypotheses about their importance in the assemblage of vascular epiphytes in an urban patch of Brazilian Atlantic Forest. Specifically, we tested if (1) characteristics of host trees (species, height, trunk diameter, presence of lianas, and distance to a near stream)—environmental variables from the point of view of epiphytes—have an effect on epiphyte abundance, species richness, and species composition on each tree, and if (2) spatial distances between trees have an effect on epiphyte abundance, richness, and composition. We used variation partitioning to compare the effect of the environmental and spatial components and to arrive at conclusions about the importance of niche-based versus dispersal-based mechanisms.

The study also provides a quantitative description of the epiphytic assemblage at the plot level, which may be used for future comparisons to other forests.

Materials and methods

Study site

This study was carried out in the Forest Reserve of the University of São Paulo (USP) (23°33′44″–23°34′02″S and 46°43′38″–46°43′49″W), inside the campus "Armando de Salles Oliveira," immersed in the western portion of the São Paulo metropolitan area. The Reserve occupies 10 ha, at 730–775 m altitude. It is crossed by a stream, which starts inside the Reserve and ends up in an artificial lake, at the Reserve boundary.

The soil is acidic, nutrient-poor, and aluminum-rich, with high-clay content (Varanda 1977). Mean annual temperature is 19.2 °C and mean annual rainfall is 1207 mm. Mean monthly temperatures range from 14 °C (June) to 23 °C (February) and mean monthly rainfall varies from 230 mm (January) to 40 mm (August), when soil goes through a water deficit (Gorresio-Roizman 1993). Air relative humidity is around 80 % and SE winds, coming from the ocean, prevail during the whole year (Varanda 1977).

The USP Forest Reserve comprises a patch of secondary forest, considered by Rossi (1994) as being a mosaic of areas in different disturbance and regeneration stages. This author estimated the forest to be at least 90-year old, based on the species present in its intermediate stratum. It belongs to the domain of the Brazilian Atlantic Forest and has similar floristic composition as the Atlantic Dense Ombrophilous Forest and the Semideciduous Seasonal Forest (sensu Veloso et al. 1991). Thirty-seven species of vascular epiphytes (Dislich and Mantovani 1998) and more than 120 native woody species (Rossi 1994) have been identified in this forest patch, which represents one of the few fragments of the regional native vegetation in the city of São Paulo.

Data collection

A 0.2-ha plot was established inside the Reserve, with its longer (60 m) side parallel to the stream. The plot corresponds to "Area 2" of Dislich et al. (2001). A complete census of the trees with trunk diameter at breast height (dbh) >13 cm, measured at 1.30 m height, was made inside the plot. Prior observation showed that trees with dbh <13 cm only very rarely carried epiphytes. The dbh of every live stem was measured, and the rooting position of every tree was mapped. For each tree, the total height and presence or absence of lianas were also recorded. Taxonomic identification of trees was made using the key published by Rossi (1994) and comparing plant material with exsiccates from the herbarium of the Instituto de Botânica de São Paulo (SP). Tree species were classified, according to their light regeneration strategies, into one of three successional groups: “climax,” “secondary,” or “pioneer,” based on the literature (Gorresio-Roizman 1993; Tabarelli 1994; Knobel 1995) and on the second author’s experience.

All trees were climbed, using appropriate climbing techniques (Nadkarni 1988; Oliveira and Zaú 1995). After climbing each tree to the highest possible point, we measured the tree’s height using a weighted marked line to measure length to the ground and a measuring pole to measure remaining distance to the tree’s top. On each tree, all epiphyte individuals found were recorded and identified to the species level. The term “epiphyte” is here used in its wider sense, including holoepiphytes, facultative epiphytes, and also (primary) hemiepiphytes (Benzing 1990) and nomadic vines (Moffett 2000). Ephemeral (Benzing 1989) or accidental (Bøgh 1992) epiphytes were not considered. An individual was considered as being “a group of plants spatially separated from other group of the same species by an area of the trunk without plants or occupied by another species” (Bøgh 1992). Only the individuals with more than 15 cm length were recorded. Due to the great variety of growth forms featured by the epiphytes, no measure related to cover or biomass of individuals was made. Epiphytes were surveyed from May to October 1995. Taxonomic identification was made using the key provided by Dislich and Mantovani (1998).

Species names of trees and epiphytes were checked for synonymy and recent taxonomic changes at the Plant List database (The Plant List 2013) and corrected accordingly. For both trees and epiphytes, the classification of angiosperm families follows the recommendations of APG III (Bremer et al. 2009), and those of pteridophytes follow Smith et al. (2008).

Data analysis

All statistical analyses were performed in the statistical environment R, version 3.1.1 (R Core Team 2014) using packages *vegan*, *reshape*, *MASS, BaylorEdPsych*, and *visreg*.

To test for effects of environmental and spatial variables on epiphyte abundance and species richness, we used generalized linear models (GLM), following the recommendations of Zuur et al. (2009). As response variables, we considered the number of individuals (abundance) and the number of species (richness) on each tree. These are count variables, which indicate the use of a Poisson GLM. However, our response variables fitted better a negative binomial distribution, so we used GLM with negative binomial error distribution and a log link function (negative binomial GLM).

We performed GLMs to test for (1) the effects of environmental variables, (2) spatial effects, and (3) joint effects of environment and space. Variable selection to find the most parsimonious (“best”) model was performed applying a forward procedure, by sequentially including those variables which led to a lower Akaike’s “an information criterion” (AIC). Variation explained by each model was measured by the adjusted McFadden pseudo R^2 ($\overline{R}^2_{\mathrm{MFd}}$) (Long 1997). These results were used to conduct a variation partitioning analysis, as outlined by Borcard et al. (2011). The method allows partitioning the variation of response variable data into four complementary components: [a] “pure environment” (nonspatial environmental variables), [b] “spatially structured environment,” [c] “pure space” (spatial autocorrelation independent of environmental variables), and [d] “undetermined” (Legendre et al. 2009).

The environmental explanatory variables considered were tree species, dbh, tree height, and presence of lianas, as well as the geographic coordinate y inside the plot. As the plot is parallel to the stream, the y coordinate corresponds to distance to the stream plus a constant. Analysis of residuals led to the inclusion of a quadratic y term as explanatory variable in the GLM. Most of the tree species were represented by only a few individuals, so we pooled species with four or less individuals into two groups: early-successional (pioneer and secondary species) and late-successional (climax species).

Spatial patterns were modeled using principal coordinates of neighborhood matrix (PCNM, also called distance-based Moran’s Eigenvector Maps dbMEM) (Legendre and Legendre 2012) as explanatory variables in the GLM. We used only the 22 PCNM variables with significant ($p < 0.05$) positive spatial autocorrelation, as measured by Moran's *I*. These were labeled V1–V22, variables with lower numbers representing variation at broader spatial scales.

The collinearity among explanatory variables was analyzed with variance inflation factors (VIF), using 3 as the cutoff value (variables with VIF >3 were excluded from the analysis). Conditional plots showing partial residuals were drawn using the R package *visreg*, to show the effects of each variable retained in the best model. We also tested for spatial structure in the Pearson residuals of the best model in order to verify any spatial correlation not explained by the environmental variables. This was done by testing the significance of Moran's *I*, a spatial correlation coefficient, using the Holm correction for multiple testing (Borcard et al. 2011).

To analyze the effect of environmental and spatial variables on epiphyte species composition, we performed redundancy analyses (RDA), based on the number of individuals of each species on each tree, after Hellinger-transformation, as suggested by Borcard et al. (2011). Spatial patterns in species composition variation were modeled using the significant positively autocorrelated PCNM variables. As environmental explanatory variables we considered tree species/groups, dbh, tree height, presence of lianas and *y*.

In all RDA analyses, the effect of explanatory variables was tested by means of permutation tests (number of permutations = 100,000). To determine the proportion of the variability in the data explained by the explanatory model, we calculated an adjusted and unbiased coefficient of multiple determination (R^2_{adj}) (Peres-Neto et al. 2006). In order to identify the best model, we first ran a global test with all environmental variables, and if significant, applied a forward selection procedure of explanatory variables with the Blanchet et al. (2008) double stopping criterion, as implemented by function *ordiR2step* of the R package *vegan*. VIFs were used to assess collinearity among explanatory variables, using 3 as the cutoff value.

Variation partitioning was used to analyze the contributions of [a] "pure environment," [b] "spatially structured environment," [c] "pure space," and [d] "undetermined" to species composition variation, based on R^2_{adj}.

Results

Host trees

We recorded 86 trees, belonging to 27 species of 25 genera and 17 families (Online Resource 1). The plot featured a total basal area of 23.9 $\mathrm{m}^2\ \mathrm{ha}^{-1}$ and total density of 430 ind ha^{-1} of trees with dbh >13 cm. Three secondary species (11 % of total)—*Alchornea sidifolia* Müll. Arg., *Croton floribundus* Spreng., and *Piptadenia gonoacantha* (Mart.) Macbr.—responded for 55 % of recorded individuals and for 65 % of total basal area (Online Resource 1). Fifteen species of trees (55.6 % of total) were represented by only one individual.

Tree dbh ranged from 13.05 to 51.88 cm (median 24.91) and tree height ranged from 5.5 to 20.5 m (median 13.75). Lianas were found on 73 % of the trees.

Epiphytes

The 380 epiphytic individuals recorded in the plot belonged to 22 species in 11 genera and six families. Among the 22 epiphytic species, 15 were holophytes, five were primary hemiepiphytes, and two were nomadic vines (Online Resource 2). No facultative epiphytes were found.

Four species (18 % of total) accounted for almost 2/3 of the total number of individuals (Online Resource 2): *Microgramma squamulosa* (Kaulf.) de la Sota, a creeping fern; *Rhipsalis grandiflora* Haw., a pendent cactus; *Pleopeltis astrolepis* (Liebm.) E. Fourn., also a creeping fern; and *Aechmea bromeliifolia* (Rudge) Baker, a tank bromeliad. Five species, or 23 % of the number of recorded species, were represented by only one individual.

Most species of epiphytes, especially the most abundant ones, inhabited a lower number of tree species than would be expected from random draws taken from the tree population (Online Resource 3), indicating some preference for particular species of trees. Some epiphytic species, like *M. squamulosa* and *A. bromeliifolia*, appeared on a relatively high number of individual trees, as compared to their total number of individuals, while others, like *R. grandiflora* and *Pleopeltis hirsutissima* (Raddi) de la Sota, showed the opposite pattern (Online Resource 4), indicating a more clumped distribution of the latter two species in comparison to the former ones.

Abundance on individual trees

Epiphytes were present on 58 of the 86 recorded trees (67.4 %). Half of the recorded trees carried none or just one epiphytic individual. The mean number of epiphytic individuals per tree (abundance) was 4.42 (standard deviation SD = 6.44). The maximum number of individuals on one tree was 36 (Fig. 1b).

The best general model, after variable selection on both environmental and PCNM variables, retained dbh, tree height, tree species/groups, y (including a quadratic term y^2), and the PCNM variables V8 and V11. However, dbh and V11 were not significant ($p > 0.05$) (Table 1). Presence of lianas and all other PCNMs were excluded in the variable selection process. We also found no significant two-way interactions among the environmental variables. The best model explained 34 % of the variation in abundance ($\overline{R}^2_{\mathrm{MFd}} = 0.3357$).

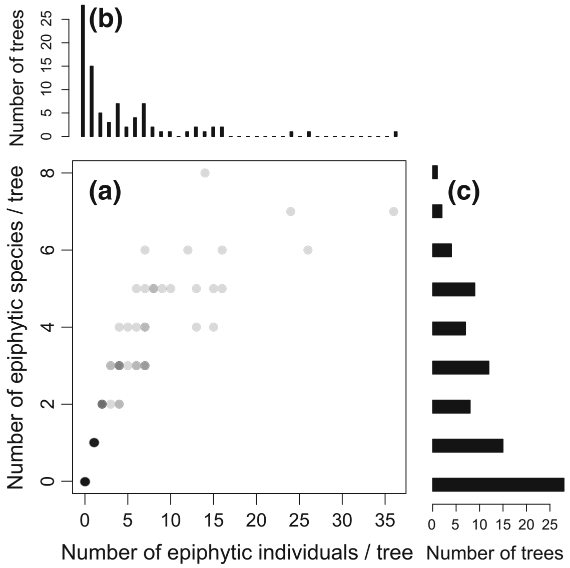

Fig. 1 **a** Relationship between number of epiphytic species per tree (richness) and number of epiphytic individuals per tree (abundance). *Darker dots* indicate higher number of observations. **b** Frequency distribution of number of epiphytic individuals per tree. **c** Frequency distribution of number of epiphytic species per tree

Table 1 Results for the negative binomial GLM (best model) explaining abundance (number of epiphytic individuals per tree)

	Estimate	SE	z	p
(Intercept)	−1.6095	0.7880	−2.04	0.04110
dbh	0.0359	0.0204	1.76	0.07818
Height	0.1462	0.0615	2.38	0.01747
C. floribundus	−0.1868	0.4029	−0.46	0.64289
P. gonoacantha	−2.8676	0.6532	−4.39	0.00001
Early	−0.7848	0.4229	−1.86	0.06348
Late	−0.1836	0.3462	−0.53	0.59589
y	0.0995	0.0498	2.00	0.04555
y^2	−0.0038	0.0014	−2.75	0.00592
V8	−0.0771	0.0251	−3.07	0.00214
V11	−0.0680	0.0347	−1.96	0.05041

Values of tree species/groups are in comparison to *Alchornea sidifolia*

SE standard error, *early* other early-successional tree species, *late* late-successional tree species

Piptadenia gonoacantha showed a significantly lower number of individuals per tree than any of the other species/groups. These (*A. sidifolia*, *C. floribundus*, other early-successional species, and late-successional species) showed no significant differences among each other (Fig. 2).

Abundance showed a significant, non-monotonic spatial trend along y (Fig. 2), corresponding to a distance-to-stream trend, showing a specially sharp decline at larger distances to the stream.

Keeping all other variables constant, the model predicts abundance to increase 15.7 % for every one meter increase in tree height ($e^{\beta_{\mathrm{height}}} = 1.1574$, Table 1, Fig. 2).

The variation partitioning between environmental and spatial variables (Fig. 3) showed a larger proportion of variation being explained by environmental variables than by pure spatial variables. Pure space (fraction [c]) explained 6.7 % of total variation, and environment ([a] + [b]) explained 26 %.

Species richness on individual trees

The mean number of epiphytic species per tree (richness) was 2.16 (SD = 2.16). The maximum number of species on one tree was eight (Fig. 1c). Trees with higher number of individuals also showed, in general, higher number of species (Fig. 1a).

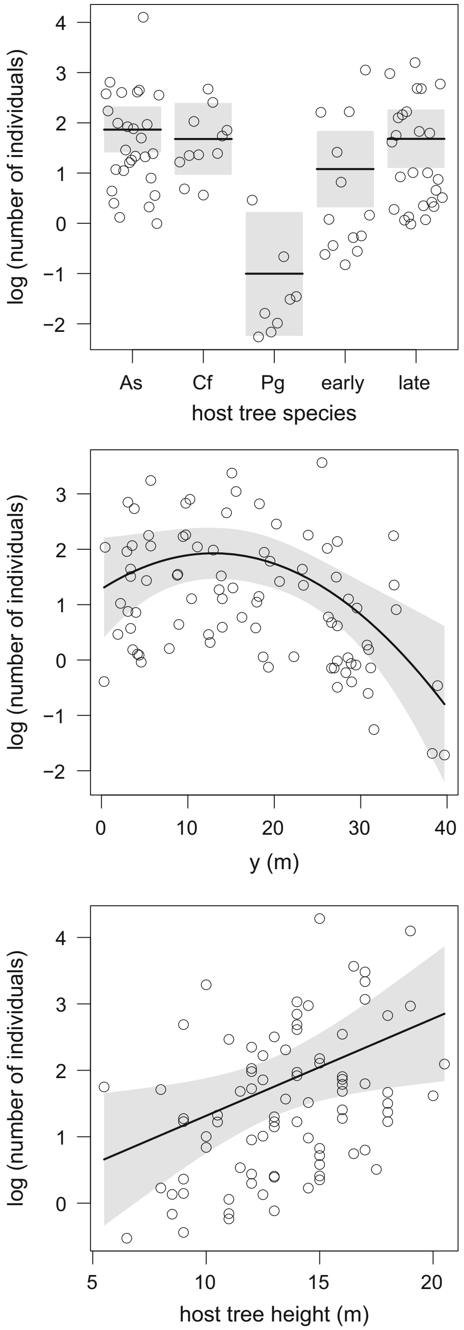

Fig. 2 Conditional plots and partial residuals showing the effects of each significant environmental explanatory variable on abundance (number of epiphytic individuals per tree) as the other explanatory variables are held constant, according to the best GLM. Grey areas: 95 % confidence bands. As, *Alchornea sidifolia*; Cf, *Croton floribundus*; Pg, *Piptadenia gonoacantha*; early, other early-successional species; late, late-successional species. Conditions used in construction of plots: dbh = 24.91; height = 13.75; V8 = −0.1785; V11 = 0.4101; $y = 17.06$; tree species = As

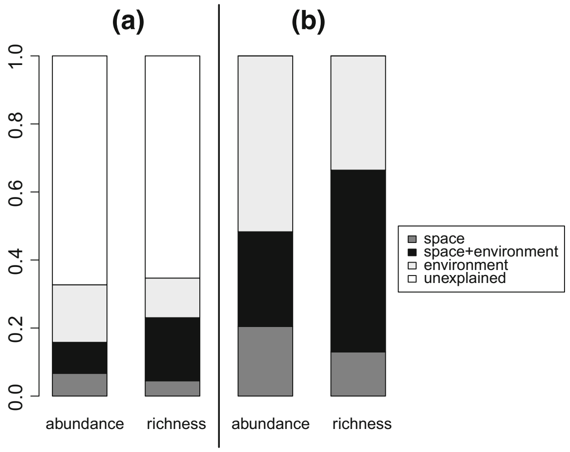

Fig. 3 Relative contributions of pure environment, PCNM variables ("space"), and spatially structured environment ("space + environment") in explaining epiphyte abundance and richness among host trees. **a** Proportion of total variation (adjusted McFadden pseudo R^2). **b** Proportion of explained variation only

The best general model explaining richness, after variable selection on both environmental and PCNM variables, retained tree height, tree species/group, y and y^2, and five PCNMs (V1, V3, V11, V13, and V17). However, y and y^2, V11 and V13 were not significant (Table 2). Presence of lianas, dbh, and all other PCNMs were excluded in the variable selection process. We also found no significant two-way interactions among the environmental variables. The best model explained 35 % of the variation in richness ($\overline{R}^2_{\text{MFd}} = 0.3524$).

Piptadenia gonoacantha trees showed a significantly lower richness than any of the other tree species/groups, with the exception of other early-successional species (Fig. 4).

Keeping all other variables constant, the model predicts richness to increase 13 % for every one meter increase in tree height ($e^{\beta_{\text{height}}} = 1.1304$, Table 2, Fig. 4). If dbh is included in the model and height is excluded, dbh also shows a significant effect ($\beta_{\text{dbh}} = 0.0281$, SE = 0.0098, $z = 2.88$, $p = 0.004$). If height and dbh are both included in the model, dbh is not significant ($\beta_{\text{dbh}} = 0.0072$, SE = 0.0114, $z = 0.63$, $p = 0.5273$), but tree height is ($\beta_{\text{height}} = 0.1073$, SE = 0.0391, $z = 2.74$, $p = 0.0061$).

The variation partitioning analysis (Fig. 3) showed a larger proportion of variation being explained by environmental variables than by pure spatial variables.

Table 2 Results for the negative binomial GLM (best model) explaining epiphytic species richness

	Estimate	SE	*z*	*p*
(Intercept)	−0.6047	0.5333	−1.13	0.2568
Height	0.1226	0.0306	4.01	0.0001
C. floribundus	−0.2056	0.2202	−0.93	0.3505
P. gonoacantha	−2.0116	0.5397	−3.73	0.0002
Early	−1.1184	0.2958	−3.78	0.0002
Late	−0.3744	0.2284	−1.64	0.1011
y	−0.0041	0.0424	−0.10	0.9223
y^2	−0.0003	0.0012	−0.29	0.7748
V1	−0.0503	0.0234	−2.15	0.0316
V3	0.1094	0.0375	2.92	0.0035
V11	−0.0454	0.0245	−1.86	0.0631
V13	0.0328	0.0224	1.46	0.1433
V17	0.0863	0.0391	2.21	0.0274

Values of tree species/groups are in comparison to *Alchornea sidifolia*

SE standard error, *early* other early-successional tree species, *late* late-successional tree species

Pure space (fraction [c]) explained 4.5 % of total variation, and environment ([a] + [b]) explained 30.2 %.

Species composition on individual trees

The best general RDA model, after variable selection on both environmental and PCNM variables, retained tree height, tree species/groups, y and y^2, but none of the PCNMs (Table 3), explaining 14.5 % of the total variation in species composition ($R^2_{\text{adj}} = 0.145$).

The RDA triplot for this model (Fig. 5) shows *M. squamulosa* and *P. astrolepis* to be associated to lower y values (host trees nearer to the stream), while *Rhipsalis teres* (Vell.) Steud., *Philodendron imbe* hort. ex Engl. and *Ficus luschnathiana* (Miq.) Miq. are associated to larger distances to the stream. *P. astrolepis* and *M. squamulosa* were associated to taller trees, while *F. luschnathiana* and *A. bromeliifolia* showed an association to shorter trees.

According to the variation partitioning analysis, pure environment [a] explained 8.2 % of species composition variation, spatially structured environment [b] explained 6.3 %, and pure space [c] explained 0.7 %.

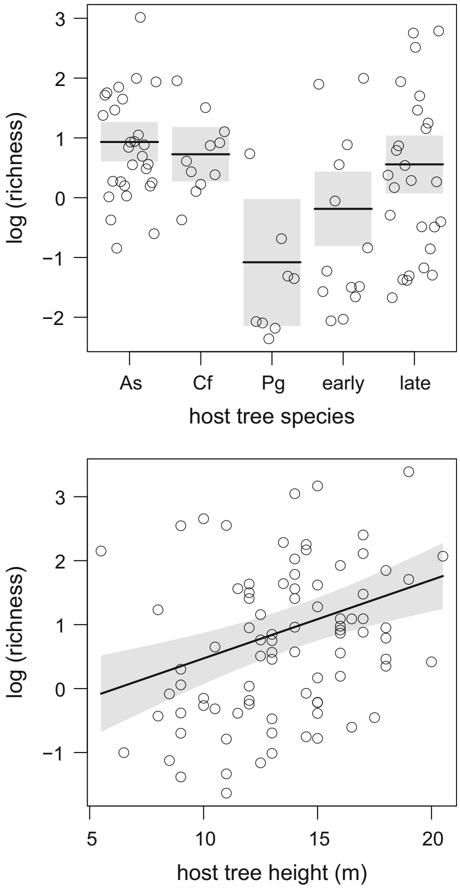

Fig. 4 Conditional plots and partial residuals showing the effects of each environmental explanatory variable on richness as the other explanatory variables are held constant, according to the best GLM. *Grey areas* 95 % confidence bands. As, *Alchornea sidifolia*; Cf, *Croton floribundus*; Pg, *Piptadenia gonoacantha*; early, other early-successional species; late, late-successional species. Conditions used in construction of plots: height = 13.75; $y = 17.06$; V1 = 2.283; V3 = 1.282; V11 = 0.4101; V13 = − 0.1131; V17 = 0.2012; tree species = As

Discussion

The 22 epiphytic species found inside the plot correspond to ca. 60 % of the 37 epiphytic species found in the Reserve as a whole (Dislich and Mantovani 1998). Of the 15 epiphytic species not found in the plot, nine are rare, not having been observed on more than two trees in the whole Reserve by Dislich and Mantovani (1998). Other two species are restricted to specific areas inside the Reserve, not covered by the plot. Excluding rare species and those

Table 3 Significance tests for the explanatory variables of the global model for the redundancy analysis (RDA) with environmental variables, performed on Hellinger-transformed epiphyte abundances

	DF	Var	*F*	*p*
Species/group	4	0.05926	2.8697	0.00001
Height	1	0.02832	5.4858	0.00001
y^2	1	0.01279	2.4766	0.01245
y	1	0.01034	2.0026	0.03931
Residual	78	0.40270		

Terms added sequentially (first to last)

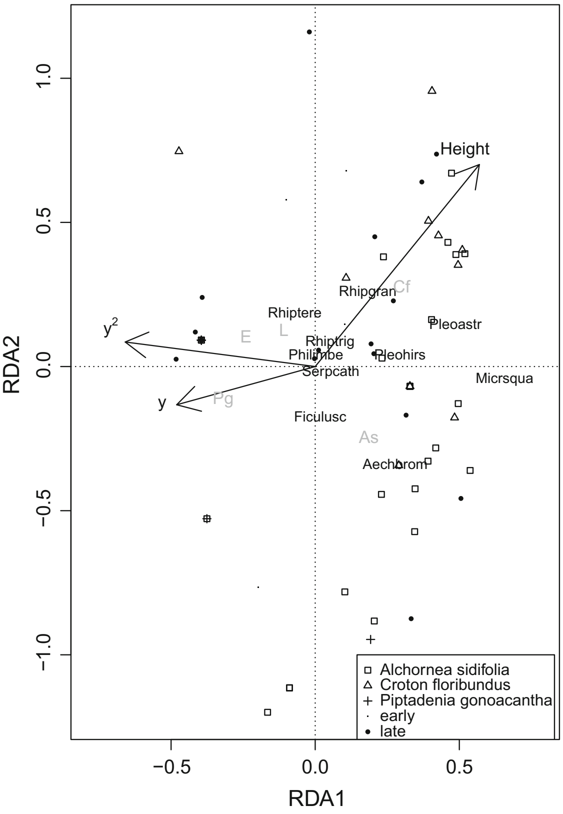

Fig. 5 Redundancy analysis correlation triplot (scaling 2) of the Hellinger-transformed epiphyte abundances on individual trees, constrained on host tree species/group, *y*, y^2 and height. Only species that do not overlap with others are labeled, with higher priority for most abundant species. *Letters* in *grey* represent the centroids of tree species/groups: As, *Alchornea sidifolia*; Cf, *Croton floribundus*; Pg, *Piptadenia gonoacantha*; E, other early-successional species; L, late-successional species. Abbreviations for epiphytic species are given in Online Resource 2

with restricted distribution, the present survey recorded 84.6 % of the vascular epiphytic species in the Reserve.

Three of the five most abundant species (*M. squamulosa*, *P. astrolepis* and *A. bromeliifolia*) have wide geographic distribution ranges, reaching the whole latitudinal extension of the Neotropics (Dislich and Mantovani 1998). It is possible that the plasticity that allows these species to survive in a wide range of environmental conditions has also allowed them to reach high abundances in this secondary vegetation patch. *M. squamulosa* is considered to be a "generalist" or "pioneer" species in forests in Curitiba, Paraná (Southern Brazil) (Borgo and Silva 2003), being able to withstand highly variable microclimatic conditions and being found also in open areas and near the edges of fragments.

Epiphyte richness on a local scale is considered to be influenced by total rainfall, higher rainfall favouring a greater richness (Gentry and Dodson 1987). The successional stage of the forest is also thought to have an influence on epiphyte abundance and diversity. Forests in initial successional stages usually show fewer epiphyte species and individuals than forests in later succession (Barthlott et al. 2001; Woods and DeWalt 2013). Epiphytes (in particular Orchidaceae) seem to be especially sensitive to habitat disturbance (Turner et al. 1994) and isolation (Turner et al. 1996), being prone to local extinction. Being in a secondary, disturbed, and isolated forest patch, the USP plot is therefore expected to show a less developed epiphytic synusia in comparison to other primary or relatively undisturbed forests.

The overall vascular epiphyte richness found in our plot (22 species on 86 trees) is within the range of other studies in the Atlantic Forest under similar conditions of precipitation, disturbance, fragmentation, and successional status. Bataghin et al. (2010) found 13 species on 90 trees with dbh >20 cm. Kersten and Silva (2002) recorded 34 species on 110 trees (dbh >9.55 cm). Dettke et al. (2008) found 22 species on 90 trees with dbh >15 cm. Dias-Terceiro et al. (2015) recorded 12 species on 1277 trees and shrubs with dbh >3.2 cm (only 65 actually carrying epiphytes). Barbosa et al. (2015) recorded 25 species on 40 trees with dbh >10 cm. Laurenti-Santos (2008) sampled trees with dbh >10 cm in two nearby sites and found 30 species on 102 trees in one of them and 29 species on 98 trees in the other.

Abundance and richness on individual trees

Our data show some significant effects of environmental variables on the abundance and species richness of epiphytes found on individual host trees.

First of all, host tree species do have an effect, especially in that *P. gonoacantha* trees carry less epiphytes than trees of other species, keeping other variables constant. *P. gonoacantha* conspicuously features shedding bark—older trees of the species in the USP Reserve show a noticeable accumulation of bark-originated litter on the ground around their trunk bases. Shedding bark is known to negatively affect recruitment and survival of epiphytes (López-Villalobos et al. 2008; Wyse and Burns 2011). Apart from that, there seems to be no notable differences in abundance and richness among tree species/groups, with the exception of a lower richness on other early-successional trees as compared to *A. sidifolia* trees in the plot. This may be explained by a tendency of early-successional trees to grow fast and die early, thus not allowing the full establishment of epiphytic species.

Distance to the stream (y) was found to have a negative effect on epiphyte abundance. Although we made no direct measurements, we expect this variable to be correlated to a gradient of increasing temperature and decreasing air humidity with increasing distance to the stream, both eventually related to water availability for the epiphytes. An analogous environmental gradient, at least in terms of water availability, is also thought to be the fundamental gradient controlling the vertical stratification of epiphytes in tropical forests (Krömer et al. 2007; Wagner et al. 2013).

Our analyses also found a positive effect of tree size on epiphyte abundance and richness. Other studies about the effect of host tree characteristics on species richness of vascular epiphytes show a significant effect of tree dbh (Flores-Palacios 2006; Zotz and Schultz 2008; Hirata et al. 2009), an effect that was shown to be even more important in secondary forests (Köster et al. 2011). In our study, however, we did test for effects of dbh controlling for tree height (and vice versa), showing a significant effect of tree height, but no effect of tree dbh. In other words, for a given dbh, higher trees have higher abundance and species richness of epiphytes, but for a given tree height, thicker (i.e., older) trees do not show higher abundance or richness. These results support the importance of vertical stratification, more pronounced in higher trees, in controlling epiphyte richness on trees (Krömer et al. 2007), and do not support the idea that increase in species richness with size is due solely to the age of the tree (Yeaton and Gladstone 1982).

Controlling for the effect of environmental variables, we also found some spatial structure in epiphytic richness and abundance, with trees with high richness and abundance being found near other trees with high richness and abundance (positive spatial autocorrelation). It should be noted, however, that this effect of "pure space" is rather small if compared to the effect of the measured environmental variables on abundance and richness. Such an effect could be explained by either the influence of an unmeasured, spatially structured environmental variable, or else by an effect of dispersal.

Species composition on individual trees

In dispersal-assembly theories like Hubbell's (2001) neutral theory, species composition of assemblages is predicted to be explained by "pure space" as a result of dispersal limitation. Because the neutral model assumes that all individuals are ecologically equivalent, the model also predicts that species composition will not change systematically along environmental gradients. Niche-assembly theory, in contrast, predicts that assemblages change deterministically along environmental gradients, but not with space, because under strict niche-assembly, species membership in local communities is determined solely by their niche requirements and local habitat conditions (Chase and Myers 2011).

In our study, pure spatial effects on species composition variation were virtually absent. Environmental variables, on the other hand, were found to have a significant effect, although explaining a relatively low proportion of total variation. These results support a higher importance of niche-based processes, rather than dispersal, in structuring epiphytic assemblages on host trees in the studied plot.

Three of the assessed environmental variables were shown to be related to species composition: tree height, tree species/group, and distance to the stream. These are the same variables found to have an effect on richness, and some of the same considerations apply: distance to the stream is expected to be correlated to a gradient of increasing temperature and decreasing air humidity, which in turn is analogous to the environmental gradient thought to control the vertical stratification of epiphytes in tropical forests (Krömer et al. 2007; Wagner et al. 2013). The effect of tree height could also be linked to the vertical stratification of epiphytes: higher trees would carry epiphytes adapted to the conditions in the upper canopy, which would be absent on shorter trees. These interpretations could be assessed in further studies, by testing for vertical and horizontal (with distance to the stream) differentiation among the epiphytic species in the plot (Zotz 2007).

The inclusion of other explanatory environmental variables in the analysis could increase the variation explained by the environment, shifting the indications about the mechanisms structuring the community even more toward niche-based processes (Chang et al. 2013). Potential candidates for such additional environmental variables could be tree architecture, tree phenology, leaf traits, and bark chemistry, as well as tree growth rate, animal activity, canopy soil accumulation, and abundance of non-vascular epiphytes (Wolf et al. 2009).

In summary, our study has shown that some of the tree characteristics we measured do have an effect on epiphyte abundance, richness, and composition. In particular, tree species/groups (with *P. gonacantha* carrying little epiphytes), tree height, and distance to the stream showed an effect. On the other hand, the presence of lianas and trunk diameter showed no effect. In general, these results suggest bark-shedding and microclimatic gradients as being the most important factors structuring the epiphytic community in our plot. Spatial relations among trees also showed an effect on abundance, richness, and composition. Variation partitioning analyses, however, showed little or no effect of "pure space," as compared to environmental effects. We may conclude that our findings generally support a higher importance of niche-based processes, as compared to dispersal-based processes, in structuring epiphytic assemblages on host trees in the plot.

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