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Host tree traits in pasture areas affect forest and pasture specialist epiphyte species differently

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PREMISE: Epiphytes have commensal relationships with their host trees. Besides the influence of tree traits, little has been discussed concerning the ecology of epiphytes in disturbed habitats (e.g., pasture). We herein tested whether the occurrences of pasture and forest specialist epiphytes in pastures are affected differently by tree traits. We hypothesized that (H1) the richness and abundance of generalist epiphytes would be positively associated with area availability; (H2) the richness and abundance of forest epiphyte species would be associated both with (H2.a) area availability and (H2.b) tree traits related to higher seed adherence, and/or (H2.c) less severe habitat (e.g., high humidity and more shade).

METHODS: We sampled 9567 epiphyte individuals from 16 species on 759 scattered remnant trees. The epiphyte species were divided into two ecological groups: forest specialists and pasture specialists. We evaluated four host tree traits: two related to tree size (crown area and trunk diameter) and two related to habitat type (crown leaf density and bark rugosity).

RESULTS: The richness and abundance of both pasture and forest specialists were positively related with tree size. However, the abundance of pasture specialists was negatively related with crown leaf density, whereas richness of forest epiphytes was positively related with bark rugosity.

CONCLUSIONS: Large scattered trees tend to present higher richness and abundance of both pasture and forest specialist epiphytes compared to the smaller trees. However, high crown leaf density limits abundance of pasture specialist epiphytes, whereas rugose bark increases the richness of forest epiphytes.

KEY WORDS agricultural landscapes; commensalism; conservation; habitat enrichment; holoepiphytes; isolated trees; scattered trees.

Epiphytes represent approximately 9% of the vascular flora worldwide (Zotz, 2013), and provide vital resources for a wide range of invertebrate and vertebrate species (Barrancos et al., 2017; Duarte and Gandolfi, 2017). Epiphytes have high diversity and endemism in tropical forests (Forzza et al., 2012; Freitas et al., 2016), but they are being reduced as a result of habitat loss (Barthlott et al., 2001; Köster et al., 2009; Del Castillo et al., 2013; Armenta-Montero et al., 2015). One of the major global causes of deforestation is the conversion of forests into pasture, which represents approximately 70% of all land use in the tropics (Holl, 1999; Woods et al., 2015). Besides the direct loss of arboreal strata (i.e., potential epiphyte hosts), the conversion of forest areas into pastures affects microclimates and microhabitats available to epiphyte species (Holl, 1999; Larrea and Werner, 2010).

The maintenance of some scattered trees in pastures appears to be a valuable landscape-scale conservation strategy (Manning et al., 2009; Harvey et al., 2011; Einzmann et al., 2016; Karvatte et al., 2016; Siqueira et al., 2017) because these trees may act as “stepping stones,” facilitating epiphyte dispersal among forest fragments of the pasture matrix (Manning et al., 2009; Athayde and Morellato, 2014). Besides conservation at a landscape scale, the presence of scattered trees increases the epiphytes’ local species pool, acting as a biodiversity reservoir (e.g., Hietz-Seifert et al., 1996). If host traits are indeed important for the diversity of epiphytes, local diversity of epiphytes could be increased by protecting and growing trees with different habitat types (e.g., rugose barks vs. smooth barks; crown with dense leaf cover vs. crown with sparse leaf cover), sheltering a wide range of epiphyte species (Hietz-Seifert et al., 1996; Boelter et al., 2014).

A range of tree traits may define habitat quality for epiphyte colonization and accumulation. For example, trunk diameter (e.g., Sáyago et al., 2013) and crown size (e.g., Ventre-Lespiaucq et al., 2017) may positively influence the number and abundance of epiphyte species. Large trees, which tend to be older (O'Brien et al., 1995; Zotz and Vollrath, 2003) and have received epiphyte seed rain for longer periods than young trees. Therefore, tree age is one of the main reasons that larger trees have more diverse epiphyte communities (Zotz and Vollrath, 2003) than smaller ones. Moreover, traits that facilitate epiphyte seed adherence (e.g., bark types) and allow species to inhabit harsh environments in disturbed habitats must also be considered. For example, Vergara-Torres et al. (2010) found different epiphyte species compositions among tree height classes, as well as among habitats with different bark characteristics (barks with different rugosities and peeling degrees). Crown size (e.g., Hayward et al., 2017), crown leaf density (e.g., Duarte and Gandolfi, 2017), and canopy density (e.g., Sáyago et al., 2013) may also influence epiphyte occurrence in forest trees.

The relationship between epiphytes and tree traits has been studied for forest habitats, but not for nonforest habitats such as pastures. Previous studies on pastures have established that traits such as crown complexity and size (Flores-Palacios and García-Franco, 2006; Poltz and Zotz, 2011; Izuddin and Webb, 2015), tree size (Sillett and Bailey, 2003; Testo and Watkins Jr., 2012), and bark rugosity (Poltz and Zotz, 2011) are positively related with epiphyte richness and abundance. Other studies have shown negative relationships between epiphyte diversity and traits such as crown size (Poltz and Zotz, 2011) and deciduousness (Rosa-Manzano et al., 2014). However, it remains unclear whether these positive and negative effects are biased by the overdominance of epiphyte generalist species in pastures. In anthropogenic land use situations, such as pastures, generalist epiphyte species commonly dominate the community (Holl, 1999; Poltz and Zotz, 2011; Estavillo et al., 2013; Izuddin and Webb, 2015) because they are largely xeromorphic (Rundel and Dillon, 1998; Einzmann and Zotz, 2017), atmospheric (Chaves et al., 2016), reproductively self-compatible (Orozco-Ibarrola et al., 2015), and perform clonal growth (Lu et al., 2020).

Many studies have linked tree traits with general epiphyte occurrence, but there has been little discussion about how tree traits affect separate species groups (e.g., atmospherics; Chaves et al., 2016) and even fewer studies consider these questions in anthropogenic matrices and degraded sites (Guevara and Laborde, 1993; Hietz-Seifert et al., 1996; Izuddin and Webb, 2015; Kiebacher et al., 2017). Investigating how different epiphyte species respond to host tree traits in nonnatural ecosystems is therefore a necessary approach. Werner and Gadstein (2008) found that xerotolerant genera (e.g., *Tillandsia*) are significantly more abundant on scattered trees in pastures than in intact forests of moist montane forests from Ecuador; the opposite pattern was reported for mesophytic genera. Many studies performed in Mexico have shown that some species of xerotolerant epiphytes may be more abundant in anthropogenic disturbed areas, such as secondary forests, lumbered pine-oak forest sites, isolated trees in pastures, and shaded coffee plantations, than in natural forests (Flores-Palacios and García-Franco, 2004; Wolf, 2005; Toledo-Aceves et al., 2012; Carvajal-Hernández et al., 2014). Thus, it is reasonable to expect a dominance of generalist epiphytes in disturbed sites, such as pastures.

Here we investigated whether tree traits differentially influence the diversity of pastures and forest specialist epiphytes in pastures. We hypothesized that (H1) the richness and abundance of generalist epiphytes would be positively associated only with area availability (i.e., trunk diameter and crown volume); (H2) richness and abundance of forest epiphyte species would be associated with both (H2.a) area availability (i.e., trunk diameter and crown volume) and (H2.b) tree traits related to higher seed adherence (i.e., rugose bark) and/or (H2.c) less severe habitats with high humidity and more shade (i.e., high crown leaf density). Generalist species are widely distributed on open and nonnatural habitats, indicating that the area availability should be the only filter to their occurrence. On the other hand, forest specialist species seem to require habitat-smoother features to increase the non-natural habitat occurrence, which could improve mainly the seed and seedling survival (e.g., rugose bark providing root support and humid source, and/or shaded habitat provided by the high crown leaf density).

MATERIALS AND METHODS

Study site

Our study was carried out in 15 areas of pasture located in the municipality of Alfenas, in southern Minas Gerais State, Brazil

TABLE 1. Geographic coordinates and environmental characteristics of the 15 pasture areas studied.

Pasture	Code	Latitude	Longitude	Trees	Density (trees/ha)	Elevation (m a.s.l.)
1	H47	21°41′S	45°31′W	31	16	874.5
2	P21	21°26′S	45°45′W	9	5	810
3	P9	21°12′S	45°46′W	22	11	897.7
4	PMT	21°30′S	45°52′W	157	80	884.5
5	P7	21°28′S	45°55′W	49	25	833.5
6	PZV	21°09′S	45°56′W	203	104	800.5
7	P4	21°13′S	46°05′W	14	7	790
8	P2	21°03′S	46°06′W	56	29	983
9	P23	21°18′S	46°07′W	34	17	1003
10	PD	21°26′S	46°08′W	20	10	861
11	P19	21°24′S	46°09′W	53	27	881.5
12	P27	21°20′S	46°10′W	21	11	924.5
13	P13	21°25′S	46°13′W	31	16	962.3
14	T3	21°13′S	46°20′W	45	23	876.7
15	T4	21°17′S	46°22′W	14	7	832.8

(45°56′49.28″W, 21°25′33.69″S) (Table 1). Only 9% of the original seasonal semideciduous forest cover remains in this area, and it is highly fragmented. The most common land use types are pastures (51%), coffee plantations (17%), and annual crops (specially sugarcane and corn, 7%) (Olivetti et al., 2015). We selected 15 pasture areas (Fig. 1) adjacent to forest fragments to contain the highest possible density of scattered trees. We delimited a single plot of 1.96 ha in each pasture (100 × 196 m). The plots were installed near (3 m) the forest fragment edge, and their length was limited to 100 m because of the smallest sampled pasture (Fig. 2). Mean annual rainfall in the region was 1500 mm, with mean monthly temperatures of 17–24°C, and two well-defined seasons (warm and wet; cold and dry). Study area elevations were between 790–1000 m a.s.l. (Alvares et al., 2013).

Tree surveys

We sampled all trees within the plots with a minimum diameter at breast height (DBH) of 5 cm, comprising a total of 759 trees from 92 species and 32 families (Appendix S1). We measured DBH, crown volume (using the ellipsoid volume formula: crown volume = 4/3 × π × crown vertical radi × crown horizontal radi), bark rugosity of the trunk and main connected branches (0) smooth bark, without grooves and cracks; and (1) rugose bark, with superficial grooves and superficial or deep cracks (Fig. 3), and crown leaf density (1 = sparse foliage, 2 = dense foliage, Fig. 4). We found no correlation (Pearson) between the tree traits.

Epiphyte survey

We surveyed all of the angiosperm holoepiphytes in each sampled tree using binoculars, recording epiphyte richness (number of species) and abundance (number of epiphyte stands). We considered an individual stand when the stand was spatially independent, that is, without roots and leaves overlap. We classified the epiphyte species into generalists and forest specialists according to a multinomial model based on estimated species relative abundance in two habitats, based on a method described by Chazdon et al. (2011), using the CLAM software (Chao and Lin, 2011). We used pasture plot data from the present study and data from forest fragments

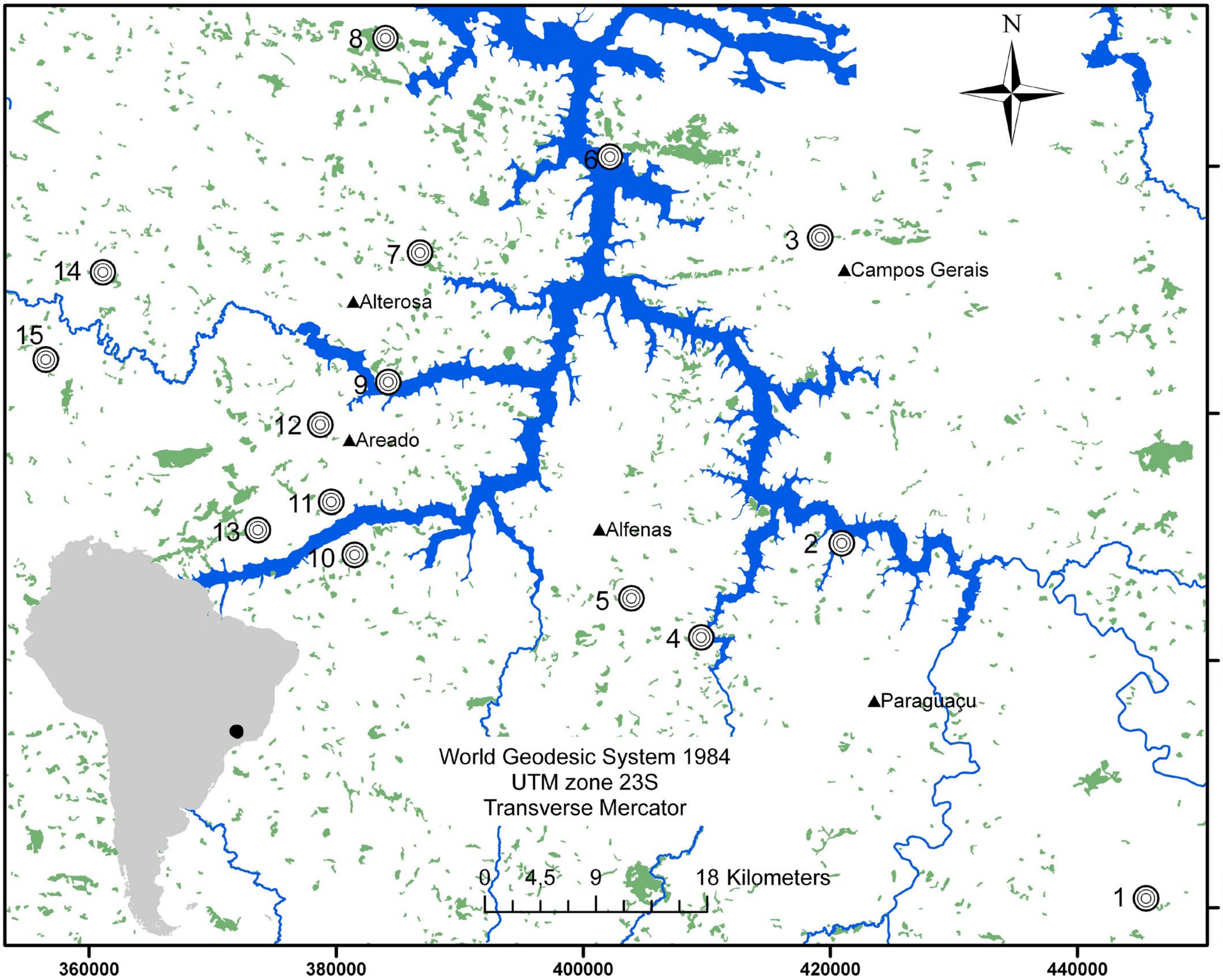

FIGURE 1. Map showing the 15 studied pastures, located in the southeast of Brazil. Additional information on the pastures is summarized in Table 1.

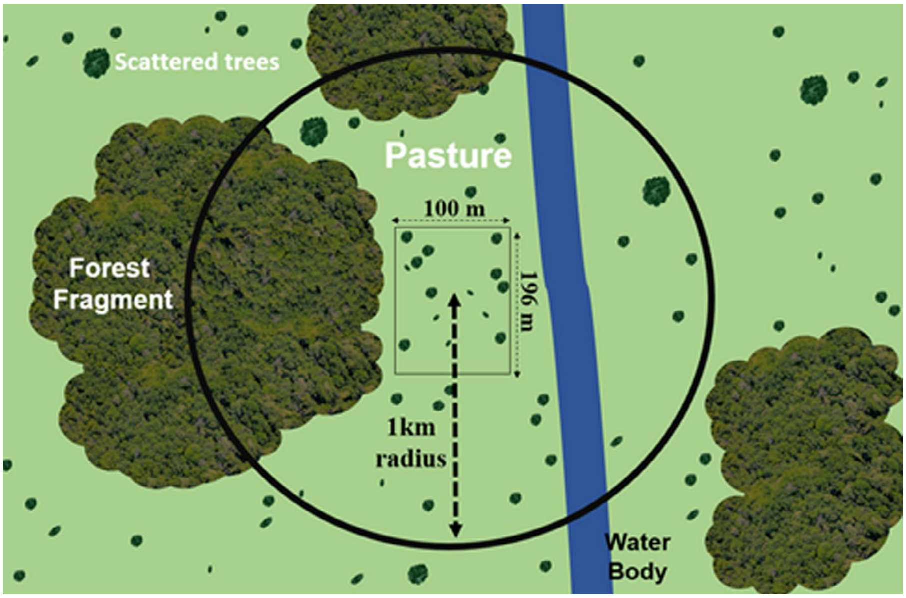

FIGURE 2. Example of pasture sampling strategy. All plots were 100 × 196 m (1.96 ha) and placed at a maximum distance of 3 m from the forest fragment edge. The plot format was based on the smallest pasture included in the study, which was limited by a water body. Each pasture was selected following the criterium of having 10–50% of plot area covered by forest (i.e., forest fragments and stepping stones) inside a buffer with 1 km of radius, centralized in the plot.

adjacent to our pasture plots (Gonçalves et al., unpublished data) to classify the epiphyte species. The CLAM method classified the species into four groups: 1–generalists; 2–habitat A specialists (pasture); 3–habitat B specialists (forest fragment); and 4–too rare to classify. We used $P < 0.05$ and $K > 0.5$ (i.e., liberal classification rules; Chazdon et al., 2011) as a threshold to classify our species into these four groups. None of our sampled epiphyte species were classified into 1–generalists. Additionally, we excluded all species classified as 4–too rare to classify because these do not fit into our group approach, which is essential to answer our hypotheses. Therefore, we used only the epiphyte species classified as 2–pasture specialists (hereafter "pasture epiphyte group") and 3–forest specialists (hereafter "forest epiphyte group") in the analyses.

Analysis

We built generalized linear mixed models (GLMMs) to assess the effects of the independent variable (i.e., host trait) on dependent variables (i.e., epiphyte richness [number of species] and abundance [number of epiphyte stands]). We considered pasture as a random effect because host trees were aggregated in 15 different pastures. We used "stepwise forward" for model selection (Derksen and Keselman, 1992). We started the stepwise analysis using the tree trait that was most correlated with the epiphyte variable (from the Pearson correlation) and included the other variables in decreasing order of correlation. We stopped the stepwise analysis when the inclusion of a variable resulted in a value higher than the corrected Akaike Information Criterion (AICc) value from the model (Derksen and Keselman, 1992). We used AICc because of the low relation between sample size (15 pasture) and independent variables (sample size/independent variables < 40; Burnham and Anderson 2002). Within each model, we only considered variables with a significant coefficient ($P < 0.05$). We modeled epiphyte richness per host tree as Poisson variables, and total epiphyte abundance per host tree as negative binomials because of the high dispersion in the epiphyte abundance. All statistical analyses were carried out using the R software version 3.4.1 (R Core Team, 2019), and the 'lme4' (GLMM; Bates et al., 2015) and 'bbmle' (AKAIKE; Bolker et al., 2017) packages.

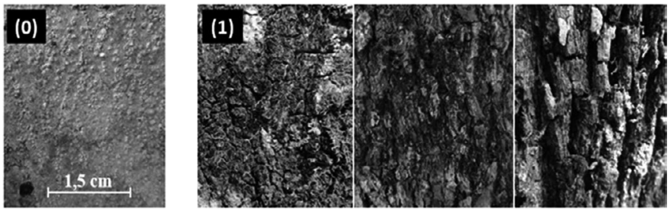

FIGURE 3. Bark rugosity was categorized as (0) smooth bark, without grooves and cracks; and (1) rugose bark, with superficial grooves and superficial or deep cracks.

RESULTS

We recorded 9567 holoepiphyte individuals from 16 species and four families (Table 2). These included three pasture specialist species (N = 8823; 92.2%), six forest species (N = 533; 5.6%), and seven species too rare to classify (N = 211; 2.2%). The three most abundant pasture specialist species were *Tillandsia recurvata* (Bromeliaceae, 6731 individuals; 70.36%), *T. pohliana* (1530; 15.99%), and *T. tricholepsis* (562; 5.87%). The three most abundant forest species were *Brassavola tuberculata* (Orchidaceae, 270 individuals; 2.82%), *Polystachya concreta* (Orchidaceae, 100; 1.05%), and *Trichocentrum pumilum* (Orchidaceae, 79; 0.83%). The most abundant families were: Bromeliaceae (8934 individuals; 93.38%), Orchidaceae (510; 5.33%), Cactaceae (62; 0.65%), and Piperaceae (61; 0.64%). Cactaceae and Piperaceae were each represented by only one species.

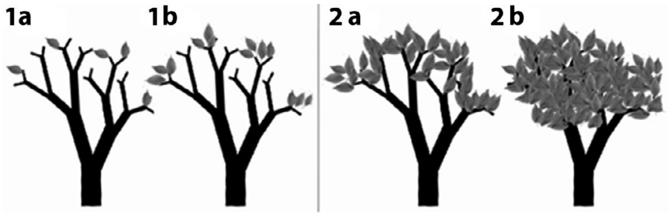

FIGURE 4. Crown foliage density was categorized as (1) sparse foliage in the crown, with a predominance of scattered leaves (1a) or with the formation of small leaf groups (1b); (2) dense crown foliage, with continuous leaf coverage on the outer branches (2a) or crown fully covered by leaves (2b).

TABLE 2. Epiphyte species and groups. Group classification (based on CLAM methods): (2) pasture specialists ('pasture specialist group'), (3) forest specialists ('forest specialist group'), and (4) too rare to classify. No species was classified as (1) generalist. Dispersion modes are: Zoo, zoochoric; and Anem, anemochorous. The 'Ref.' column shows the reference for the dispersion classification.

Family	Species	Group	Dispersal	Ref.
Bromeliaceae	*Aechmea bromeliifolia* (Rudge) Baker	3	Zoo	1
	Billbergia porteana Brong. Ex Beer	3	Zoo	1,2
	Tillandsia pohliana Mez	2	Anem	2
	Tillandsia recurvata (L.) L.	2	Anem	2
	Tillandsia tricholepis Baker	2	Anem	2
	Tillandsia loliacea Mart. Ex Schult. & Schult.f.	4	Anem	3
	Tillandsia streptocarpa Baker	4	Anem	2
	Tillandsia sp.	4	Anem	*sensus*
Cactaceae	*Epiphyllum phyllanthus* (L.) Haw.	3	Zoo	4
Orchidaceae	*Brassavola tuberculata* Hook	3	Anem	2
	Trichocentrum pumilum (Lindl.) M.W. Chase & N.H. Williams	3	Anem	2
	Polystachya concreta (Jacq.) Garay & Sweet	3	Anem	2
	Epidendrum pseudodifforme Hoehne & Schltr.	4	Anem	2
	Gomesa flexuosa (Lodd.) M.W. Chase & N.H. Williams	4	Anem	2
	Oncidium sp1.	4	Anem	2
Piperaceae	*Peperomia tetraphylla* (G. Forst.) Hook. & Arn.	4	Zoo	2

Ref. 1. Gonçalves and Waechter (2003), 2. Citadini-Zanette et al. (2013), 3. Marcusso and Monteiro (2016), 4. Tomazi and Figueiredo (2002).

The richness and abundance of pasture specialist epiphyte species were positively correlated with tree size (DBH and crown volume); however, their abundance was negatively correlated with crown leaf density (Table 3; Pasture). Trees with sparse foliage (66.6%) or dense foliage (33.4%) in the crown hosted all three pasture specialist epiphytes. However, trees with sparse foliage hosted 7128 individuals (80.8%) of pasture specialist epiphytes, whereas trees with dense foliage hosted only 1695 individuals (19.2%).

The richness and abundance of forest epiphyte species were positively correlated with tree size (abundance only with DBH), and richness was also positively correlated with bark rugosity (Table 3; Forest). Trees with a smooth bark (45.5%) hosted only three epiphyte species and 15 individuals (3.4%) from the forest specialist group, whereas trees with rugose bark (54.5%) hosted all six epiphyte species from the forest group, totaling 518 individuals (96.6%).

TABLE 3. Best model from the richness and abundance of pasture and forest specialist epiphytes.

	Epiphyte	Tree traits	Coefficients	Std. Error	Hypothesis confirmed
Pasture	Richness	DBH | crown volume	4.42e-03 | 2.41e-04	1.92e-03 | 8.25e-05	H1
	Abundance	Crown leaf density | DBH | crown volume	–0.51 | 0.03 | <0.001	0.21 | 0.004 | <0.001	Partially H1
Forest	Richness	Bark rugosity | DBH | crown volume	1.13 | 0.014 | <0.001	0.44 | 0.004 | <0.001	H2.a and b
	Abundance	DBH | crown volume	0.05 | <0.001	0.007 | <0.001	H2.a

DISCUSSION

Our results only partially support H1 and H2. Tree size was not the only trait that influenced the diversity of pasture specialist epiphyte species (H1); crowns leaf density also negatively influenced their abundance. Additionally, tree size influenced the diversity of forest specialist epiphyte species (H2.a). Moreover, chance of seed adherence (i.e., rugose bark) influenced forest specialist epiphyte richness (H2.b), but less severe habitat (i.e., dense crown leaf coverage) (H2.c) did not. Therefore, our results indicate that bigger trees tend to have more species and individuals of both pasture and forest specialist epiphytes than smaller trees. However, while crown with dense leaf cover decreased the abundance of pasture specialist epiphytes, trees with highly rugose bark tended to have more forest epiphyte species.

This is the first study to separately address the effects of host tree traits for forest and pasture specialist epiphyte species in pasture areas. Overall, studies on epiphytes and tree traits approached the epiphyte assemblage together (e.g., Zotz and Schultz, 2007) or in separate taxonomic groups (e.g., botanical groups; Callaway et al., 2002; families; Einzmann et al., 2015). Few studies have analyzed data on epiphytes according to functional or ecological traits (e.g., atmospherics; Chaves et al., 2016). In studies on the epiphyte community in pastures, the epiphyte variables have been considered for the entire epiphyte assemblage (Hietz-Seifert et al., 1996; Flores-Palacios and García-Franco, 2004, 2006; Izzudin and Webb, 2015) or for separate botanical groups (Sánchez et al., 2016; Kiebacher et al., 2017; Ventre-Lespiauqc et al., 2017).

Generalist epiphyte species tend to be favored in disturbed habitats (e.g., pasture specialist epiphytes), because they typically tolerate warm and sunny microclimates. Therefore, they can be dominant in disturbed habitats, with area availability (i.e., presence and size of trees) being the only limiting factor (Acunã-Tarazona et al., 2015; Engemann et al., 2016). We found that richness and abundance of pasture specialist epiphytes were positively associated with larger crown volumes and trunk diameters, as we had hypothesized. Some studies have shown a positive relationship between richness of the entire epiphyte assemblage and the DBH (Hietz-Seifert et al., 1996; Flores-Palacios and García-Franco, 2006; Izzudin and Webb, 2015) or height of remnant trees in pasture (Hietz-Seifert et al., 1996). Additionally, studies performed in nonnatural habitats such as pastures have shown that the area available to epiphyte communities seem to be unsaturated, even for generalist species with high abundances (Flores-Palacios and García-Franco, 2006; Einzmann and Zotz, 2017). In our study for example, only approximately 30% of the trees in the sampled pastures hosted epiphytes. Einzmann and Zotz (2017) showed that scattered trees in pastures in Panama were not saturated with epiphytes; this indicates that other factors (e.g., dispersion and/or germination) may be limiting epiphyte species' occurrence in pasture trees. In Mexican pasture trees, Flores-Palacios and García-Franco (2006) also found that habitat area is widely available to epiphyte colonization.

Our results also draw attention to the negative effect of habitats with more shade (higher crown leaf density) on the abundance of pasture specialist epiphytes, partially rejecting our H1 because this shows that not only tree size is important for pasture specialist epiphytes. Although there is evidence showing that generalist epiphytes can live in many different habitats, we found that the abundance of pasture specialist species decreases in trees with crowns with dense leaf cover. Crown leaves act as irradiation filters by intercepting sunlight and shading crown habitats, thus influencing epiphyte occurrence (Cardelús and Chazdon, 2005). Generalist epiphyte species, which typically occur in environments under high solar irradiance (Engemann et al., 2016), may be disadvantaged in tree crowns with dense leaf coverage. For example, Winkler et al. (2005) found in Mexico that all of the four studied *Tillandsia* species presented higher seedling mortality on shaded rather than on sun-exposed branches planted on 11 different trees. We also partially confirmed H2. We found that forest epiphyte richness and abundance were associated with large crown volume and trunk diameter, as well as with high seed adherence (rugose bark), as we had hypothesized. However, the crown leaf density, which generates a microclimatically less severe habitat, was not associated with this epiphyte group (i.e., the variable was absent in the best model). Scattered trees in pastures can minimize the harsh environmental conditions (e.g., high irradiation and low humidity) in this habitat (Taylor and Burns, 2015; Einzmann and Zotz, 2017), especially for big trees (Manning et al. 2006), which create microhabitats favorable to the occurrence of many species (e.g., O'Brien et al., 2019; Peláez et al., 2019). The colonization and growth of specific epiphyte species (e.g., forest epiphytes) are facilitated on large trees (mainly on the trunks and main branches) in which the harsh pasture microclimate may be buffered by the large number or density of branches (Mehltreter et al., 2005). Hietz-Seifert et al. (1996) found similar numbers of epiphyte species when comparing shaded scattered trees in pastures and forest trees. Moreover, large, old trees may favor the establishment and survival of epiphyte species with specific humidity requirements because of the presence of dense bryophytic mats (Krömer et al., 2014). Large crowns, even those with low leaf density, may reduce harsh climatic conditions of pasture habitats for these forest epiphyte species. Additionally, large crowns may have a larger variety of microhabitats (Dunn, 2000), increasing epiphyte species' chances of recruitment and survival.

Some studies have found a positive relationship between bark rugosity and epiphyte diversity (Wyse and Burns, 2011; Ceballos et al., 2016; Chaves et al., 2016), but only two previous studies described a neutral effect of bark type on epiphyte diversity in pastures (Poltz and Zotz, 2011; Einzmann and Zotz, 2017). However, these later studies may be biased by the inclusion of only *Tillandsia* species in the analyses (Einzmann and Zotz, 2017), or by the dominance of anemochorous *Tillandsia* (Bromeliaceae) in the epiphyte community (Poltz and Zotz, 2011). Different from *Tillandsia* species, which have winged seeds with feathery appendages, the species from our forest epiphyte group are either (1) Orchidaceae or (2) have seeds that are dispersed by animals. The seeds of Orchidaceae species are also anemochorous, but they use another dispersal strategy. They are small and thin (called "dust seed") because they do not have an endosperm, and they must be associated with mycorrhizae to germinate (Yeh et al., 2019). Therefore, the rugosity of the bark probably helps the adherence of the orchid seeds and fungal spores. Additionally, bark rugosity may also assist in the adherence of seeds dispersed by animals. Scattered trees in pastures are usually an important refuge for animals. In an abandoned agriculture field in Uganda, Duncan and Chapman (1999) found that seed rain from bats and birds was larger under taller trees than under smaller ones. Therefore, the animals may defecate directly on the bark or branches of scattered trees (Guevara and Laborde, 1993). Bark rugosity may enable seed and feces adherence, which in turn are important for the establishment of seedlings.

In general, our data confirmed the existence of species selection under harsh pasture conditions because pasture specialist epiphyte species represented almost 94% of all epiphyte individuals, with a clear dominance over forest species. Einzmann and Zotz (2017) found a similar over-dominance of drought-tolerant species in a human-modified landscape of Panama, representing 58% of all epiphyte individuals. Comparing only pasture specialist species, we found a very clear dominance of *Tillandsia*, mainly of *Tillandsia recurvata*. This supports the previously observed general dominance and wide distribution pattern of this genus in nonnatural habitats, mainly to key characteristics of drought-tolerance and CAM photosynthesis strategy (Crassulacean acid metabolism) (e.g., Flores-Palacios, 2016; Einzmann and Zotz, 2017). Diversity management and conservation efforts must focus on forest specialist species, once the generalist species appear to be well adapted to harsh conditions of nonnatural matrices (e.g., pasture and secondary forest: Flores-Palacios and García-Franco, 2004; coffee plantation: Toledo-Aceves et al., 2012). Unfortunately, most pasture habitats have very few or no trees, and most scattered trees are declining around the world (Gibbons et al., 2008). Based on our results, for pastures or other open nonnatural matrices (e.g., restoration sites), we recommend the maintenance or planting of tree species that reach large sizes and have rugose bark. All trees in pastures can maintain populations of pasture specialist epiphyte species; however, only large individuals with rugose bark were capable of supporting a high diversity of species, including forest specialist epiphytes.

CONCLUSIONS

Our main conclusions stress that large, scattered trees tend to have higher richness and abundance of pasture and forest specialist epiphytes than small trees. However, high crown leaf density hampers pasture specialist abundance, whereas rugose bark increases the richness of forest epiphytes. Our study is the first to report the importance of considering ecological groups (i.e., pasture and forest species) in the analysis. We strongly recommend studying these groups separately. Moreover, to promote the conservation of forest epiphytes in pastures, we recommend the maintenance of big trees (i.e., those that can reach large sizes) with rugose bark.

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AUTHOR CONTRIBUTIONS

F.N.R. and J.P.C.E. conceived the study and designed the methodology; J.P.C.E. collected the data; J.P.C.E., F.N.R., and S.M. analyzed the data, and interpreted the results, with the contributions of A.F.N.F. and E.B.; J.P.C.E. drafted the article. All authors contributed critically to reviewing the article and have given final approval for publication.

DATA AVAILABILITY

All data used in our analyses were available in the data paper "Atlantic Epiphytes: a data set of vascular and non-vascular epiphyte plants and lichens from the Atlantic Forest," (website: https://doi.org/10.1002/ecy.2541).

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

APPENDIX S1. Tree species list and the respective variables information.

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