INTRODUCTION

Many researchers now argue that the future of biodiversity may depend on the availability and appropriate management of human-modified forests—HMFs (Banks-Leite et al., 2014; Chazdon, 2014; Wright & Muller-Landau, 2006). These arguments are supported by evidence from well-studied taxa, such as vertebrates and trees, which consistently shows some level of species’ resilience to habitat modification (Banks-Leite et al., 2012; Gibson et al., 2013; Mascarenhas & Mariano-Neto, 2014). However, not all taxa are...
affected by disturbance in the same way. Epiphytic plants, plants that live on other plants, are likely more sensitive to disturbance because of their structural dependence on large trees, lack of seed banks, dispersal limitation, and sensitivity to microhabitat quality and availability (Petter et al., 2016; Zotz, 2016). Currently, the responses of epiphytes to large-scale habitat disturbance are poorly known, and given the importance of these species to ecosystem functioning (Gotsch et al., 2016; Mendieta-Leiva et al., 2020; Zotz, 2016), it is imperative that the value of human-modified forests to protect and maintain this speciose community is fully understood.

HMFs comprise a suite of different types of forests, which include secondary-growth forests following clear-cut, forests degraded by fire, logging, or cattle, as well as small pockets of fragmented old-growth forests product of human pressure (Putz & Redford, 2010). Under this conceptual umbrella, HMFs already comprise 60% of the world’s forests (Grantham et al., 2020), and their prevalence is only likely to increase given the ongoing deforestation and reforestation dynamics (Chazdon, 2014). HMFs also rarely occur in large continuous areas and, for this reason, are subjected to the additional effects of habitat loss and fragmentation, which further impacts plant communities (Farah et al., 2017; Ibáñez et al., 2014).

The effects of habitat loss, fragmentation, and disturbance on fauna and flora have been intensively studied in recent decades (Brooks et al., 2002, 2017; Haddad et al., 2015; Newbold et al., 2015). Global-scale models have estimated a loss of 76.5% of species richness and 39.5% of total abundance due to human pressure (Newbold et al., 2015), while fragmentation experiments demonstrate a decrease of 13–75% of species richness of terrestrial plants, arthropods, and birds (Haddad et al., 2015). There is also evidence to show that habitat cover improves landscape connectivity and positively influences tree richness and abundance (Mascarenhas & Mariano-Neto, 2014; Püttker et al., 2020). However, how vascular epiphytes, or their different ontogenetic stages, are affected by local- and landscape-scale variables changes in HMFs is poorly understood.

Human modification of forests negatively affects vascular epiphytes assemblages. The decrease of forest area drives a reduction of species richness through multiple pathways (Pinheiro-Ulbrich et al., 2018). For example, open habitats such as pasturelands are a potential dispersal barrier for animal-dispersed taxa (Acevedo et al., 2020; Mondragón, Valverde, & Hernández-Apilinar, 2015; Reid et al., 2016; Werner & Gradstein, 2008). Large trees, which positively drive vascular epiphytes richness and colonization over time (Ruiz-Cordova et al., 2014; Woods et al., 2015), are rare in HMFs and usually disappear within the first three decades after disturbance (Laurance et al., 2000). HMFs also have strong edge effects, that is, hotter and drier conditions near the forest edge (Ewers & Banks-Leite, 2013), impacting epiphytes communities (Parra-Sánchez & Banks-Leite, 2020) as drought-intolerant species are filtered out (Einzmann et al., 2016; Rapp & Silman, 2014; Werner & Gradstein, 2008).

Alterations of the landscape affects epiphytes differently across their life stage due to, for instance, the differential dependence on atmospheric water. Juvenile individuals lose water more intensely than conspecific adults because of their smaller surface-to-volume area (Mondragón, Valverde, & Hernández-Apilinar, 2015; Schmidt & Zotz, 2002; Winkler et al., 2005) and may experience higher mortality than adults after human modification of forests. Seedling recruitment also decreases on isolated trees, driving changes in community composition to more drought-tolerant species, in part due to the alteration in abiotic seedling requirements (Mondragón, Valverde, Hernández-Apilinar, et al., 2015; Werner & Gradstein, 2008). Because of this higher mortality, low abundance of juveniles could threaten the regeneration of the epiphyte community (Mondragón, Valverde, Hernández-Apilinar, et al., 2015; Winkler et al., 2005; Zotz, 2016).

The local extinction of vascular epiphytes has a cascading effect on other taxa and potentially impacting local ecosystem functioning. Experimental studies of removal of epiphytes from trees show a reduction of bird visiting species (Cruz-Angón & Greenberg, 2005), invertebrates (Cruz-Angón et al., 2009) and herpetofauna (McCracken & Forstner, 2014). Ecosystem functions might also be reduced, such as CO₂ sequestration via biomass production, interception and storage of atmospheric water, and reduction in light along the tree strata gradient (Gotsch et al., 2016; Zotz, 2016). For these reasons, it is crucial that we better understand how epiphyte communities are structured in HMF.

We examined epiphyte richness, community composition and abundance across life stages in different forest habitats in the highly endangered Atlantic Forest of Brazil. We expect that old-growth forest would have the highest species richness, followed by human-modified forests and pasture with predicted lowest species richness. We then assessed how local-scale (tree structure) and landscape-scale (forest cover, fragment area, and proximity) variables impact the epiphyte community in HMFs.

2 | MATERIAL AND METHODS

2.1 | Study area

The study area is located in the Brazilian Atlantic Forest in São Paulo state, within the municipalities of Taubaté, São Luiz do Paraitinga, and Lagoinha (Figure 1). The study area has 28% forest cover in various successional stages, and the matrix is dominated by pastures and plantations of *Eucalyptus* and *Pinus*. Elevation ranges from 860 to 1470 m.a.s.l. The predominant types of soil are Latosol and Cambisol (Radambrasil, 1983). The tree composition is predominantly Montane Ombrophilous Dense Forest species (Veloso et al., 1991). The study area also covers part of the last continuous tract of Atlantic Forest, with over 1 million hectares within a cluster of several National Parks.

2.2 | Sampled sites

Surveyed sites were part of the “Biodiversity and Ecosystem Functioning in Degraded and Recovering Amazonian and Atlantic...
Forests” (ECOFOR) project (site selection in the Online Resource). Fieldwork was conducted from May 2015 to August 2016 in three habitat types: i) three sites in an old-growth continuous forest in the Santa Virginia Nucleus of Serra do Mar State Park, hereafter “control forest”; ii) 12 sites within human-modified forests surrounded by pastures with isolated trees with discrete boundaries, hereafter “HMFs”; and iii) three sites in open matrix as sites dominated by species of Poaceae with sparse trees, hereafter “pastures.” Our design includes the extremes of habitat quality for epiphytes, from highly suitable (old-growth forests—with high humidity, low sun exposure, and high host structural heterogeneity) to less suitable habitat (pastures—with low humidity, high sun exposure, and low host structural heterogeneity).

Sampling plots of $10 \times 250$ m were randomly placed in the control forest, HMFs, and pasture selected by ECOFOR (Appendix S1). In control forest, we surveyed permanent plots from a previous study (Joly et al., 2012). Plots in the control forest were located at an average distance of 765 m (range: 381–1150 m) away from each other. Plots in HMFs were established ~$100$ m from forest edge, and plots in pasture were established ~$586$ m (range: 471–690 m) from forest fragments.

### 2.3 Epiphyte sampling

At each sampling plot, we surveyed the canopy of five trees that were safe for climbing based on our tree selection’s criteria (Appendix S1). Trees were separated between 10 and 50 m from each other. Epiphytes were sampled in the canopy, which we defined as the section of the tree higher than two meters from the main trunk, while outer branches were inspected by binoculars, and surveyed using a pole when possible.

The number of species and individuals of vascular epiphytes were recorded from each tree. Following Sanford (1968), we defined an individual as a set of singular stems spatially separated from another set of stems of the same or another species, an empty space, or dwelling in independent twigs. Individuals were classified into three ontogenetic stages: seedlings, juveniles, and adults based on a combination of observed features. We classified seedlings as all small-sized individuals with radicle (embryonic root), hypocotyl (embryonic shoot), and cotyledons and/or initial leaves. We classified juveniles as all individuals with differentiated tissues, rhizomes, stem, and/or pseudobulbs, a developed root system, with absence of reproductive structures and few individuals per stand. Finally, adult plants were all large individuals, that is, large individuals within the observed variation in the local population, with evidence of developed floral or reproductive structures, large ramets, many stems per stand, and prominent root systems. Differentiation between ontogenetic stages is difficult in the field, and we recognized that potential errors might have occurred. Nonetheless, we aimed to reduce systematic errors by validating our observations with footage taken in the field (around 3000 photographs and six hours of video; for a similar approach, see Zuleta et al., 2016). All dubious individuals were discarded. Identification to species, or morphospecies, was conducted only on adult individuals, following specialized literature review and consultation with local experts. Nomenclatural standardization was based on “The Plant List” data base names (The Plant List, 2010) (Table 1).

### 2.4 Environmental variables

We used three sets of predictors to determine the role of local- and landscape-scale variables, and climate and topography on community structure.
TABLE 1  Description of the environmental variables and forest structure of each sampled site. Forest cover was extracted from radii of 500 m, 1000 m, 1500 m, 2000 m, and 3000 m (fc. 500, fc. 1000, fc. 1500 m, fc. 2000, and fc. 3000 m, respectively), proximity index (at 1000-m radius) and fragment area (ha). Tree structure was represented by mean values of tree DBH (cm), tree density (trees per plot), and tree height (m). Elevation (m.a.s.l.) and precipitation (mm)

| Habitat  | Fc.500 | Fc.1000 | Fc.1500 | Fc.2000 | Fc.3000 | Fragment area (ha) | Proximity | Trees DBH (cm) | Tree density | Tree high (m) | Elevation (m.a.s.l.) | Precipitation (mm) |
|----------|--------|---------|---------|---------|---------|--------------------|-----------|----------------|--------------|---------------|----------------------|-------------------|
| Control  | 100    | 100     | 100     | 100     | 100     | 17,500             | 4.51      | 97.3 (88.4–106.2)| 157          | 22 (15.3–18)  | 1031                 | 210               |
| Control  | 100    | 100     | 100     | 100     | 100     | 17,500             | 4.51      | 85.8 (80–91.6)  | 139          | 14.3 (13.5–15) | 1049                 | 225               |
| Control  | 100    | 100     | 100     | 100     | 100     | 17,500             | 4.51      | 64.53 (57.5–75.2)| 99           | 14.5 (13–16)  | 1029                 | 228               |
| Fragment | 51.35  | 39.92   | 33.74   | 27.63   | 24.49   | 85.3               | 2.41      | 54.19 (57.5–75.2)| 192          | 10.51 (9–12.1) | 838                  | 96.6              |
| Fragment | 32.13  | 25.29   | 17.01   | 11.98   | 8.89    | 98.15              | 1.27      | 30.15 (28.6–36.2)| 160          | 10.91 (8.9–12.9) | 705                  | 178.54            |
| Fragment | 24.32  | 10.68   | 14.27   | 11.53   | 8.57    | 15.56              | 1.26      | 34.99 (24.29–45.69)| 150          | 12.36 (11.8–13) | 681                  | 153.34            |
| Fragment | 42.99  | 33.51   | 31.92   | 34.07   | 29.78   | 169.88             | 1.51      | 69.70 (58.2–81.2)| 365          | 9.78 (9.1–10.3) | 937                  | 82.55             |
| Fragment | 81.64  | 48.82   | 39.42   | 38.11   | 39.08   | 20.52              | 2.61      | 59.05 (37.85–80.25)| 179          | 11.36 (10.12–72)| 1049                 | 99.24             |
| Fragment | 43.7   | 20.78   | 16.61   | 14.02   | 12.79   | 60.24              | 1.75      | 71.98 (58.08–85.68)| 512          | 8.93 (8.9–83)   | 915                  | 114.44            |
| Fragment | 66.85  | 70.44   | 57.37   | 41.71   | 26.59   | 247.66             | 3.06      | 48.45 (37.9–59)  | 143          | 11.76 (11.1–12.3)| 758                  | 177.62            |
| Fragment | 31.21  | 26.79   | 29.44   | 30.31   | 37.56   | 58.47              | 3.4       | 62.89 (53.73–72.05)| 213          | 11.38 (11.1–16.8)| 982                  | 80.49             |
| Fragment | 34.27  | 14.51   | 10.84   | 9.61    | 10.54   | 32.22              | 1.08      | 67.51 (51.7–83.32)| 142          | 12.8 (11.5–14.1)| 735                  | 143.17            |
| Fragment | 54     | 47.23   | 42.49   | 39.85   | 28.27   | 10.67              | 3.25      | 59.67 (45.77–73.57)| 120          | 9.78 (9.1–10.46)| 760                  | 181.91            |
| Fragment | 39.11  | 38.59   | 38.06   | 38.1    | 37.84   | 30.36              | 5.35      | 83.35 (45.55–81.15)| 221          | 12.21 (11.7–12.7)| 1172                 | 93.98             |
| Pasture  | 0      | 5.22    | 4.78    | 4.67    | 4.33    | 0                 | 0.66      | 12.1 (7.1–17.1)  | 8            | 4.3 (3.5–5)    | 1090                 | 106.1             |
| Pasture  | 0      | 3.06    | 2.87    | 2.79    | 2.64    | 0                 | 0.14      | 32.7 (28.1–37.3) | 16           | 7.8 (6.3–9.2)  | 830                  | 104.57            |
| Pasture  | 0      | 7.86    | 6.55    | 6.44    | 6.39    | 0                 | 0.52      | 18.1 (8.8–27.4)  | 5            | 6.4 (5.8–7)    | 706                  | 163.25            |
Local-scale variables—We measured diameter at breast height (DBH in cm²) and height (m) of all trees that we sampled for canopy epiphytes using a clinometer, and tree density per plot for all trees with DBH ≥ 10 cm.

Landscape-scale variables—We quantified forest cover (Fahrig, 2003), fragment area, and proximity index (Gustafson & Parker, 1994). We combined maps provided by “Instituto Florestal” (Instituto Florestal do Estado de São Paulo, 2010) and “SOS Mata Atlântica” (SOS Mata Atlantica & INPE, 2014), to calculate the proportion of forest cover for each site, fragment size, and connectivity. Fragment size and percent of forest cover were calculated in ArcGIS 10.2 (ESRI, 2011). Forest cover is a proxy of how habitat loss influences species richness in a fixed plot responds in its neighbor buffer area (Supplementary material; Fahrig, 2013). We measured forest cover at five local landscapes of 500 m, 1000 m, 1500 m, 2000 m, and 3000 m from the centroid of the studied plots (hereafter, FC. 500, FC. 1000, FC. 1500 m, FC. 2000, and FC. 3000 m) to find the most informative spatial scale or “scale of effect” (Supporting material; Jackson & Fahrig, 2015). Thus, the scale of effect reflects the spatial extent that yields the strongest biodiversity–landscape relationship (Jackson & Fahrig, 2015). Connectivity was calculated using the proximity index, which accounts for area of surrounding fragments and weights this by distance (Gustafson & Parker, 1994) within 1000-m and 1500-m radii in FRAGSTATS 4.2 (McGarigal et al., 2012).

Climate and topography—We obtained data from the “Departamento de Aguas e Energia Elétrica” (http://www.hidrologia.daee.sp.gov.br) on the mean monthly rainfall from the past 15 years for seven stations located in the study area. The mean multiannual rainfall for each site was interpolated using the Spline interpolation method and extracted in ArcGIS 10.2. Elevation was measured directly in the field using the Garmin device GPSMAP 62s.

2.5 | Statistical analysis

Response variables—We excluded all adult individuals that we could not identify to species or morphospecies; then, we calculated for adult individuals—total observed species richness, total abundance, and community composition per plot. All analyses were done at plot rather than tree level because not all sampled trees hosted epiphytes. Species richness and abundance were log-transformed to improve normality (log10 + 1). We used principal coordinates analysis (PCoA) based on Sørensen dissimilarity index calculated on a presence/absence matrix to determine community composition. PCoA was used to generate independent vectors as response variables to regress against our predictors. We used the PCoA axis two (21.8% explained variance) as a measure of changes in community composition, as preliminary results showed that the first axis (28.2%) did not correlate to any of our environmental variables (Figure S2—axis 1 clusters pastures and control forest next to each other). Total abundance was analyzed independently for the three ontogenetic stages. We additionally estimated species richness at each habitat type using rarefaction- and extrapolation-based sampling curves of Hill numbers (extended explanation in Appendix S1; Hsieh et al., 2016).

2.6 | Testing for the influence of local-, landscape-scale variables, climate, and topography

First, we ran a Mantel test to assess whether community composition was spatially autocorrelated across sites. We used Sørensen distance matrix and the Euclidean distance among plots, and our preliminary results indicate that community composition was spatially autocorrelated when all sites (control forest, HMFs, and pastures) were analyzed together (Mantel, r = 0.38, p = .002). This is because all control sites were in the far east part of the study region, and their community composition was significantly different to the human-modified landscapes. This pattern is linked to the process of habitat loss and fragmentation, in which pristine sites are usually clustered together. However, this spatial autocorrelation disappeared when HMFs were analyzed separately, removing controls and pastures (Mantel, r = 0.67, p = .35). For this reason, we ran two analyses. First, we fitted a generalized least squared models (gls) using data from pastures, HMFs and controls, which accounted for the spatial distance between sites by including an exponential spatial correlation structure class (latitude and longitude at each plot) and Maximum log-likelihood method (“ML”). Second, we fitted linear regression models (lm) on the HMFs only. Both types of models were fitted with one response variable (species richness, total abundance, or community composition) and one predictor at a time (due to high correlation among predictors, Table S1). All models tested the following predictors: i) habitat type, tree density, and average tree height representing the local conditions of each plot; ii) forest cover (percentage), proximity index (log10), and fragment area (ha) representing the landscape configuration and composition at each site; and iii) climate and topography, precipitation (multiannual average), and elevation (m.a.s.l.). We further complemented the community composition analysis by fitting a regression model with segmented relationships due to the inferred nonlinear pattern (Figure S3). The segmented model was fitted with the best predictor found in our gls models and community composition using the sequential hypothesis testing method for the breakpoint estimates, and Gaussian distribution family (Muggeo, 2003, 2016).

In all models, we used average DBH per plot as an offset term to account for the effect of tree size on epiphytes structure (Flores-Palacios & García-Franco, 2001). The best predictors were selected based upon Akaike information criterion (hereafter AIC), pseudo-R-squared, adjusted R-squared, and visual inspection of diagnostic plots. All statistical analyses were conducted with R (Development, 2011), with the packages “vegan” (version 2.2-1; Oksanen et al., 2017), jtools (Long, 2019), and “nlme” (Pinheiro, Bates, DebRoy, 2020). Maps were generated using ArcGIS (version 10), and plots depicting statistical analyses were done in base R (Development, 2011). All explanatory variables were standardized...
to have means equal to zero and two standard deviations to adjust the differences in scales.

3 RESULTS

In total, we surveyed 90 trees and documented 1943 individuals representing 181 epiphyte species, belonging to 19 families (Table S2), including 56 species of Orchidaceae and 37 species of the Bromeliaceae family, as the richest families. We identified 89% (160 species) of individuals to species level and the remaining to morphospecies (21 morphospecies). The two most abundant species were Octomeria gracilis (Orchidaceae, 579 individuals; only found in the control forest) and Pleopeltis hirsutissima (Polypodiaceae, 408 individuals; dominant in HMFs).

The control forest had the highest observed and rarefied species richness and total observed abundance among all habitats (gls p-value < .001; Figure 2, Figure S2, and Table S3), with 1308 adult individuals from 172 species belonging to 19 families, whereas HMFs only hosted 471 adult individuals (24.5% of total number of adult individuals) from 28 species (15.5% of total number of species), and pastures hosted 54 individuals (2.8% of total number) from 2 species (1% from total number).

We found that forest cover was the most important predictor across local and landscape metrics (gls p-value < .001; Figure 4 and Table S2, S4, and S6). Forest cover (measured at 3000-m radius—identified as the scale of effect) significantly increased species richness and total abundance of adults (gls, slope_richness = 1.26, slope_abundance = 1.22, p-value < .001; Figure 4 and Table S2). Elevation was also positively correlated to abundance of adults (gls, slope = 0.833, p-value = .038; Table S2). Likewise, habitat type significantly influenced community composition with communities in the control forest significantly different to those in HMF and pastures (gls p-value < .001; Figure 2c; Table S6). Although we found a

![FIGURE 2](image-url)  
Box-and-whisker plots of a) average of species richness, b) average abundance of adult plants, and c) community composition (PCoA axis 2) in plots located at each land use type. Boxes show the median, 25th, and 75th percentiles, and error bars show 10th and 90th percentiles.
threshold in community composition at around 30% forest cover using the entire dataset (segmented lm for forest cover at 1000 m, estimate = 0.2187, t-value = 2.492, breakpoint = 0.361, p-value = .028, adjusted-R^2 = 0.582; Figure 4), there is no evidence that increasing forest cover in the landscapes across HMFs makes any difference to epiphytes community composition (lm; slope = 0.894, p-value > .06, Table S6).

Habitat types and forest cover (measured at 1500-m radius) significantly affected the abundance of juveniles and seedlings (gls, slope_{juveniles} = 2.01, slope_{seedlings} = 1.73, p-value < .007; Figures 2 and 3; Table S4, S6). However, no juveniles or seedlings were found in pastures. Noteworthy, seedlings and juveniles were twice more abundant than adults in the control forests (total adults: 1308, juveniles: 2253, seedlings: 2188), in contrast to the lower abundance of adults, juveniles, and seedlings in HMFs (total adults: 471, juveniles: 259, seedlings: 275). The patterns became negligible after removal of controls in our linear models (Table S3, S6, and S7). Neither local nor landscape-scale predictors seem to exert any effect on species richness, total abundance, community composition, or on the abundance of any ontogenetic stage across HMFs.

4 | DISCUSSION

Our results show that old-growth continuous forests provide a unique habitat for epiphytes that simply cannot be replaced by fragments of human-modified forests. We found that human-modified forests host only 12% of the species found in continuous old-growth
forest and 24% of the total adult individuals. The low number of seedlings and juveniles in HMFs will only exacerbate these differences in the future. These dramatic impacts of habitat disturbance on forest species reinforce the unparallel role that pristine or old-growth forests have in sustaining biodiversity in the tropics (Gibson et al., 2013).

We have found one of the most detrimental effects of habitat modification on species richness and total abundance in human-modified forests, as we observed nearly 83% of epiphyte species to be restricted to old-growth forest. The number of species and individuals in our HMFs are statistically similar to pastures (Figure 2), which is the most hostile habitat for epiphytes species (Figure 3), highlighting the dramatic decline in epiphyte communities. Several meta-analyses have shown the adverse impacts of human modification of the landscape on different taxa. Newbold et al. (2015) found a loss of 76.5% in species richness and 39.5% total abundance under human pressures, whilst Haddad et al. (2015) found a decrease of 13–75% in species richness of terrestrial plants, arthropods, and birds in fragmentation experiments at global scale. Barlow et al. (2007), on the other hand, found that just 5–57% of the species pool was unique to the primary forests in the Amazon. The magnitude of species loss in our study is also comparatively higher to previous studies on epiphyte (Nöske et al., 2008; Köster et al., 2009; Köster et al., 2013).

Not only species richness was dramatically lower in HMFs when compared to old-growth forest, our findings also show that forest cover, area, or connectivity of HMFs did not exert any effect on species richness or abundance in vascular epiphytes. These results contrast with the trend usually reported for woody plants in HMFs. For instance, Mascarenhas and Mariano-neto (2014) and Rocha-Santos et al. (2017) found that forest cover has a positive effect on tree richness and abundance in the Brazilian Atlantic forest. Our findings also differed from the few available studies testing the effect of the landscape on epiphytes. For example, Reid et al. (2016) showed that trees embedded in landscapes with high forest cover hosted high numbers of vascular understory species in Costa Rica, and Pereira-Alvarenga & Pórto (2007) found a positive effect of area and connectivity in Amazonian non-vascular epiphytes species richness.

Although speculative, the lack of influence of forest cover, proximity, and fragment area on epiphyte communities in our study is probably due to the long history of habitat modification in the Atlantic forest and the sensitivity of epiphyte communities to abiotic changes. The Atlantic forest has been drastically altered over the last 500 years, where only 11% of the original forest remains and fragments are small (Ribeiro et al., 2009), and few have core areas suitable for epiphytes (Parra-Sánchez & Banks-Leite, 2020). Consequently, disturbance might lead to a simplification in microhabitats in the canopy strata and among tree crowns because host trees are young, thin and fast growing in HMFs (Acebey et al., 2003). This disturbance might have impacted propagule availability (Cascante-Marin et al., 2009), resource availability (Ruiz-Cordova et al., 2014), and provision of forest microhabitats for attachment, germination, and establishment (González del Pliego et al., 2016).

Interestingly, we found that communities in forests with more than 30% forest cover are more similar to epiphyte communities in the control forest. This threshold at 30% of forest cover mirrors other results reported for the Atlantic forest—40% for woody plants (Gonçalves Rigueira et al., 2013; Mascarenhas & Mariano-Neto, 2014), and 30% for mammals, birds, and amphibians (Banks-Leite et al., 2014). High levels of forest cover are related to better structural connectivity of the landscape (Fahrig, 2013; Martensen et al., 2012). However, these results should be interpreted with caution, given the spatial autocorrelation detected between HMFs and old-growth forests, the low number of species in HMFs, and the high abundance of species associated with disturbed areas. In fact, when analyzing only HMFs, we did not see any effect of forest cover in community composition. This adds to our findings suggesting that current conditions across HMFs are unsuitable for hosting a high diversity of specialized epiphytes.

Our results also show a bleak future for the epiphyte community. The observed pattern of absence of early ontogenetic stages in pastures and low abundance of seedlings and juveniles in HMFs (vs old-growth continuous forest) might indicate low dispersal of propagules to HMF and low provision of resources to sustain the early ontogenetic stages. This can create a further adverse scenario for population maintenance in the long term (Halpern et al., 2005), because of the high seedling mortality and lower tolerance to drought of early ontogenetic stages (Mondragón, Valverde, Hernández-Apolinar, et al., 2015; Winkler et al., 2005). Furthermore, the local extirpation of epiphytes might disrupt forest functions such as local water retention, CO₂ sequestration (Gotsch et al., 2016; Zotz, 2016), and a reduction of bird, invertebrates, and herpetofauna (Cruz-Angón et al., 2009; Cruz-Angón & Greenberg, 2005; McCracken & Forstner, 2014). After all, the presence of a species does not imply a viable population in the future, and current epiphyte communities in pastures and HMF likely resemble Janzen’s (2001) “living dead.”

Overall, our findings suggest that epiphytes are undergoing dramatic loss in HMFs of the Atlantic forest and preserving the continuous old-growth forests seems to be the only viable option at the moment to preserve such speciose taxa and the functions they perform in the ecosystem.

AUTHORS’ CONTRIBUTIONS
EPS and CBL conceived the idea and designed the methodology; EPS collected and analyzed the data; and EPS and CBL contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST
The authors have no relevant financial or non-financial interests to disclose.

DATA AVAILABILITY STATEMENT
The data that support the findings of this study are openly available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.w3r2280t8 (Parra-Sanchez & Banks-Leite, 2022).

ETHICAL APPROVAL
Fieldwork in the human-modified forests was carried out on private properties with each landowner’s permission. Sampling in the control forest was done under the permission COTEC: 260108–002.959/2016.

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