The structure and robustness of an epiphyte - phorophyte commensalistic network in a neotropical inselberg

Abstract

Ecological networks describe the interactions between species, the underlying structure of communities, the function and stability of ecosystems. To date, network analyses have been extensively applied to understand mutualistic and antagonistic interactions, but few have examined commensal interactions, particularly in neotropical regions. The inselbergs of southeastern Brazil are considered one of the three most important regions in the world in terms of terrestrial species diversity and endemism but are poorly studied. In this study, we constructed the first epiphyte-phorophyte commensalistic network in a Brazilian inselberg and examined its structure and robustness to simulated species loss. A total of 138 phorophyte individuals belonging to eight species were observed in 20 2 m × 50 m transects, interacting with 5,039 individuals of vascular epiphytes belonging to 85 species. The epiphyte-phorophyte network structure exhibited a low degree of specilization (H_2'), low connectance and robustness; when the most connected phorophyte species were sequentially removed the number of secondary extinctions was high, based on robustness metrics. One generalist phorophyte, *Pseudobombax* sp. nov., was particularly important, hosting a high number of epiphyte species. A single phorophyte individual of *Pseudobombax* supported 46% of the total richness of the epiphyte community studied. Our results demonstrate that the richness and abundance of epiphytes were correlated with phorophyte size (as measured by the DBH, diameter at breast height), probably due to increased habitat area and the time available for colonization. We conclude that phorophyte size and species identity are important factors for predicting the structure of epiphyte-phorophyte interaction networks.

We discuss the conservation implications of phorophyte loss and secondary extinctions of epiphytes in Atlantic Forest inselbergs.

Key words: Atlantic Forest, biodiversity hotspot, conservation, facilitation, host tree

INTRODUCTION

In the Brazilian Atlantic Forest, there are granitoids rock outcrops ecosystems, named inselbergs (Porembski *et al.* 1998). They are very old, isolated landscapes that formed between 625 and 490 Ma ago (Gradim *et al.* 2014). These residual landforms are characteristic mainly of tropical and subtropical regions, although they occur across all continents (Porembski 2007; Hopper 2009; Couto *et al.* 2016; De Paula *et al.* 2016). In Brazil, they are considered one of the three global hot spots in terms of diversity and endemism of terrestrial plant species (Porembski 2007, De Paula *et al.* 2016). Due to their insular nature and unique combination abiotic factors, the inselbergs are ecologically characterized by a range of harsh conditions, such as high temperatures and radiation, and low water and nutrient contents in the soil (Barthlott *et al.* 1993). These characteristics promote the occurrence of high numbers of geographically restricted, specialized, and threatened species (Porembski & Barthlott 2000; Porembski 2007; De Paula *et al.* 2016; Couto *et al.* 2017), and their conservation is of global importance (Porembski *et al.* 2016). However, these ecosystems are threatened, mainly by quarrying, invasive grasses, tourism and extraction of ornamental plants, resulting in biodiversity loss and degradation of their ecosystem services (Galindo-Leal *et al.* 2003; De Paula *et al.* 2016; Porembski *et al.* 2016; Hopper 2009).

Although the flora of theses inselbergs is characterized mainly by herbs and shrubs (Porembski 2007; De Paula *et al.* 2016; Couto *et al.* 2017), rupicolous trees, even though

rarer in these environments, are important for the promotion of the diversity of these ecosystems and have received little attention (Yarranton & Morrison 1974; Couto *et al.* 2016). Increasing this knowledge would be a source of basic information for both conservation and restoration of these unique environments, because the removal of tree species are highly damaging to the epiphytic communities they support.

Vascular epiphytes are plants that germinate and live on other plants (phorophytes) during some stage of their life cycle (Benzing 1990). They are structurally dependent on phorophytes that provide substrate and a variety of environments with different microhabitats in a single tree (Sanger & Kirkpatrick 2016). Epiphytes use phorophytes (trees) only as structural support and establish a commensal relationship. Thus, epiphyte-phorophyte interactions represent a type of commensalistic network (Burns 2007). To date, network analyses have mostly focused on mutualistic interactions (e.g., plants and their pollinators and seed dispersers) (Bascompte *et al.* 2003; Evans *et al.* 2013; Mello *et al.* 2015) or antagonistic interactions (Thébault & Fontaine 2010; Bellay *et al.* 2015). By comparison, there are few studies of commensal interactions (Cockle & Martin 2015; Ceballos *et al.* 2016), particularly among epiphytes-phorophytes. This is possibly due to the logistical difficulties associated with the sampling of this group of plants in the forest canopy. This also makes species identification difficult and hampers complete inventories of the epiphytic flora. Few studies of epiphyte-phorophyte interactions have been conducted, all of them in tropical and subtropical (Silva *et al.* 2010; Zhao *et al.* 2015) and temperate forests (Burns 2007; Taylor *et al.* 2016). Further, some studies comprised low species richness communities (Burns 2007; Blick & Burns 2009; Ceballos *et al.* 2016) or considered only a subset of the existing epiphytic species, such as orchids (Silva *et al.* 2010) or bromeliads (Sáyago *et al.* 2013).

Ecological networks describe the interactions between species, the underlying structure of communities, the function and stability of ecosystems (Thébault & Fontaine 2010; Memmott *et al.* 2004). Network analyses of epiphyte-phorophyte interactions have found nested structures for different forests (Burns 2007; Sáyago *et al.* 2013; Ceballos *et al.* 2016). In a nested network, species with fewer interactions (specialists) are connected with species that have many interactions (generalists) (Bascompte *et al.* 2003). Epiphyte-phorophyte networks also exhibit low levels of specialization (Sáyago *et al.* 2013; Zhao *et al.* 2015; Ceballos *et al.* 2016; Taylor *et al.* 2016). This may result from the selection of epiphytes by specific phorophytes traits (Sáyago *et al.* 2013; Zhao *et al.* 2015; Ceballos *et al.* 2016) and several tree species may be appropriate phorophytes, reducing the vulnerability of epiphytes to perturbations. Thus, the complexity and structure of epiphytes-phorophytes networks have been in described few studies. However, to our knowledge, no study to date examined the tolerance of the network to species extinctions (Dunne *et al.* 2002; Memmott *et al.* 2004). The ‘robustness’ of a network is related to the tolerance of the network to species extinctions (Dunne *et al.* 2002; Memmott *et al.* 2004). In a commensalistic network, the robustness can be assessed by sequentially removing primary phorophyte species from the network and calculating the number of epiphyte secondary extinctions that occur as a result (Dunne *et al.* 2002; Memmott *et al.* 2004; Ings *et al.* 2008). Such an approach is useful in evaluating whether a network is particularly fragile to disturbance and can be used in ecosystem restoration (Pocock *et al.* 2012). Studies in different environments comparing epiphyte species richness show that phorophyte size is an important factor determining the diversity and abundance of vascular epiphytes (Flores-Palacios & García-Franco, 2006; Sáyago *et al.* 2013; Zhao *et al.* 2015; Wagner *et al.* 2015; Wang *et al.* 2016). Tree size is related with other tree characteristics such as increase in habitat area, greater microhabitat heterogeneity, tree architecture and bark structure (Zhao *et al.* 2015; Woods *et al.* 2015; Wang *et al.* 2016). The diameter at breast height

(DBH) has been used as proxy for age and size of phorophytes (Flores-Palacios & Garcia-Franco, 2006; Taylor *et al.* 2015; Zhao *et al.* 2015; Wang *et al.* 2016).

In this study, we investigated the network structure and robustness of an epiphyte-phorophyte commensalistic network in an inselberg in Southeastern Brazil, a tropical system of high ecological importance (Porembski 2007). We also evaluated how different weights of the links in the network can influence the structure of the system. Our expectation was that the network structure is nested, with a low degree of specialization, as found for the majority of the interaction networks involving vascular epiphytes. We used phorophyte diameter (represented by DBH) as a surrogate for phorophyte size and hypothesized that the size of the phorophyte is the best predictor of interaction frequencies and metrics of the vascular epiphyte-phorophytes network. Phorophyte size represents a number of aspects that affect vascular epiphyte richness and abundance, including mainly age (the time available for establishment of epiphytes) and surface area and microhabitats available for colonization of epiphytes (Zhao *et al.* 2015; Wang *et al.* 2016). Thus, we also investigated whether phorophyte size correlates with the richness and abundance of epiphyte species in the inselberg.

METHODS

Study site

The study was conducted in a montane granite-gneiss inselberg in the State of Espírito Santo, southeastern Brazil (20°56'19.94"S and 41°32'39.77"W), situated at 782 m of altitude (Fig. 1) in September 2015. This inselberg has an area of about 2.5 ha covered with rupestral vegetation growing on very shallow soils (litholic humic neosol) (Embrapa 2009), which at some points, shows a small layer of leaf litter, above a thicker layer of soil. The inselberg is well preserved and is inserted in a transition matrix between semi-deciduous

mountain forest, dense ombrophilous forest and anthropogenic areas, namely coffee plantations (*Coffea arabica* L.), grasslands and eucalyptus forests (Couto *et al.* 2016). Climate is Cwb (Köppen 1948) moderate humid subtropical, mesothermal humid, with rainy summers and dry winters.

Data collection and specimen vouchering

We sampled holoepiphytes (complete life cycle on host tree) and hemiepiphytes (with a life stage as terrestrial plants) and phorophytes in 20 linear transects of 50 m x 2 m distributed systematically at parallel intervals of 10 m and vertically at 5 m (Gentry 1982). This arrangement allowed us to maximize environmental variation in the sampling. All phorophytes (shrubs/trees) present in the transects with DBH (diameter at breast height) ≥ 5 cm were sampled.

For each phorophyte we recorded the presence and abundance of vascular epiphyte species. We counted all epiphyte stands to obtain abundance (Sanford 1968). Following Sanford (1968), we considered as a ‘stand’ a group of rosettes (Bromeliaceae), leaves (ferns, Gesneriaceae), or stems (Orchidaceae, Araceae, Cactaceae) of a single epiphyte species spatially separated from another group of the same species by a space in the tree devoid of epiphytes or occupied by another species.

The identification of vascular epiphytes occurring in the inselberg was based on Couto *et al.* (2016) with reference materials deposited in the herbarium of the Biology Museum Prof. Mello Leitão (Museu de Biologia Professor Mello Leitão - MBML) and in the herbarium of the Federal University of Espírito Santo (VIES). The nomenclature of the angiosperms (magnoliids, monocotyledons and eudicots) followed the suggestions of APG IV (The Angiosperm Phylogeny Group 2016) and ferns (monilophytes) following PPG I (The Pteridophyte Phylogeny Group 2016).

Estimation of sampling completeness of interactions

We plotted the number (richness) of accumulated interactions as sampling effort increased for each phorophyte species to estimate network sampling completeness. We adapted the methodology of Traveset *et al.* (2015) for each of the eight phorophyte species from which more than five individuals were sampled. We calculated the asymptotic estimated epiphyte richness (S_E) using the non-parametric diversity estimation Chao 2 (Chao 2005; Gotelli & Colwell 2011). Posteriorly, we calculated the percentage of estimated asymptotic richness detected (% S_{OBS}):

$$\% S_{OBS} = 100 * S_{OBS} / S_E$$

where S_{OBS} is the observed epiphytes richness in the samples (phorophytes linkage level) and S_E is the epiphyte richness estimated with Chao 2. The Chao 2 estimator is based on species presence / absence of data that quantifies rarity or the number of singletons (species that appear in only one sample) and duplicates (species that occur in two samples). Chao 2 was applied because it is the more robust estimator for small sample sizes (Chao *et al.* 2009). Chao 2 was estimated using the R statistical software (R Development Core Team 2016) with the ‘vegan’ package (Oksanen *et al.* 2016).

Network analysis

We examined the structure and complexity of the networks using standard metrics. Connectance (C) consists of the actual number of observed interactions in relation to the number of theoretically possible interactions in the network. It varies from 0 (without interaction) to 1 (all species linked to each other) (Jordano 1987). We used the specialization index (H_2'), to evaluate the network specialization (Blüthgen *et al.* 2006), by selectivity in the use of resources of the whole network, which varies between 0 (full generalization) and 1 (full specialization). The significance of H_2' was estimated by randomization (1000

interactions), using the Patefield null model (Blüthgen *et al.* 2006). Generality and vulnerability (Tylianakis *et al.* 2007) were also calculated to examine epiphyte-phorophyte interaction asymmetries. Generality is the weighted average number of phorophytes connected to epiphytes, and vulnerability estimates the epiphytes connected to phorophytes (Sáyago *et al.* 2013; Zhao *et al.* 2015).

We examined network nestedness by *NODF* (nested metric based on overlap and decreasing fill) (Almeida-Neto *et al.* 2008). For epiphyte-phorophyte networks, nestedness represents phorophyte species with low interactions forming a subset of species that maintains large numbers of interactions. It varies from 0 (non-nested) to 100 (fully nested) (Almeida-Neto & Ulrich 2011). We assessed nestedness significance using empirical values from the null distribution. For this, we calculated 1000 random matrices using the null model 2 (CE) proposed by Bascompte *et al.* (2003), producing a matrix of the same size and the same number of interactions as the one produced, and we tested the probability of an interaction occurring considering the number of occurrences in the rows and columns.

Robustness (*R*) was used to measure the tolerance of the network to species extinctions (Dunne *et al.* 2002; Memmott *et al.* 2004). Although sampling biases are likely to affect network-level analyses such as this, our aim was to provide the first measure of the ‘fragility’ of the networks for the region. Robustness was calculated by considering the secondary extinction of epiphytic species resulting from the extinction of primary species of phorophytes. $R \rightarrow 0$ corresponds to a very rapid reduction in the slope of the curve, reflecting a disturbed system after the first species is removed; whereas $R \rightarrow 1$ represents a very robust system, where decrease in the curve corresponds is very slow, and thus represents a system in which most epiphytes remain after the removal of most phorophytes. The community robustness was measured through the area below the extinction curve (Memmott *et al.* 2004; Burgos *et al.* 2007), by sequentially deleting the most connected (generalist) to less

connected (specialists) phorophytes. Using this method, it is also possible to verify if the generalist species of phorophytes that are removed leads to the removal of the species of epiphytes that interact only with these hosts. It was generated from extinction curves through the function *second.extinct* (1000 randomizations).

All analyses were carried out using the function ‘network level’ from the ‘bipartite’ package (Dormann *et al.* 2008) in R statistical software (R Development Core Team 2016)., except for nestedness that was carried out using ANINHADO version 3.0.2 (Guimarães-Jr & Guimarães 2006).

Organization of interactions

The species’ degree (k_i) is defined by the number of interactions that each species has. In general, species with few interactions (i.e. species with low degree value) are usually referred to as specialists, whereas those that establish many interactions (high degree value) are regarded as generalists. The push/pull (PP) was calculated to characterize the direction of asymmetric interactions based on the dependencies of the species (Vázquez *et al.* 2007). This metric ranges from -1 to 1 and the closer to 1 the greater the dependence. Species strength (SS), suggested by Bascompte *et al.* (2006), has a high correlation with the degree of the species and is understood as the sum of the dependencies of the epiphyte species for a phorophyte species. The higher the value, the more generalized the phorophyte because more epiphyte species depend on it. Analyses were carried out using the function ‘species level’ from the ‘bipartite’ package (Dormann *et al.* 2008) in R statistical software (R Development Core Team 2016).

Other data analysis

Spearman's rank correlations were calculated to examine the relationships between the epiphyte richness and abundance and tree DBH. The data of DBH of phorophytes were compared using Kruskal-Wallis test, followed by multiple comparisons with *a posteriori* Dunn test (Zar, 2010). Differences were considered significant at $p < 0.05$. Analyses were performed in R statistical software (R Development Core Team 2016).

RESULTS

Richness and diversity

138 phorophytes from eight species and eight families, hosted 5,039 individuals of vascular epiphytes from 85 species, 44 genera and 11 families (refer to Appendix S1 for the complete list of epiphyte species). The epiphytic families most represented were Orchidaceae (34 species, 40%), Bromeliaceae (22 species, 26%) and Polypodiaceae (8 species, 10%) (Fig. 2, Appendix S2).

The richness and abundance of epiphytes showed high correlation with the size of phorophytes. The richness of epiphytes increased significantly with DBH (Spearman's correlation; $r^2 = 0.64$, $p < 0.001$), as did the abundance of epiphytes increased significantly with DBH (Spearman's correlation; $r^2 = 0.55$, $p < 0.001$).

Network structure

Estimation of sampling completeness showed that the sampling effort was adequate. We detected a large proportion of all interactions for the whole epiphyte-phorophyte network (~ 80%) (Appendix S3). Variation in network structure across transects was low (Table 1). We found low specialization ($H_2' = 0.30$; $p < 0.01$) between epiphytes and phorophytes, and low connectance ($C = 0.23$). Theoretically, 680 interactions between species of epiphytes and

phorophytes are possible, but only 156 interactions (23%) were recorded (Fig. 3, Appendix S4). The species of epiphytes interacted on average with two species (2.05 species) of phorophytes (generality), while the eight species of phorophytes interacted on average with eighteen (18.01) species of epiphytes (vulnerability). The phorophyte-epiphyte network was nested ($NODF = 57.50$; $p < 0.01$), showing asymmetry in the interactions (Appendix S4). The network exhibited low robustness ($R = 0.21$) (Fig. 4), meaning phorophyte-epiphyte interactions are little tolerant and sensitive to perturbations, with potential implications for extinction risk. For this commensalistic network, the loss of the most generalist phorophyte, *Pseudobombax* sp. nov., promoted a very rapid reduction in the slope of the curve, reflecting a disturbed system, leading to a local secondary extinction of approximately 45% of the species of epiphytes (Fig. 4, Appendix S4). The removal of the second most generalist phorophyte (*Guapira opposita*), although it is the most abundant phorophyte, caused little impact on the network, since this phorophyte had few unique (occurring only in this phorophyte) interactions.

Organization of interactions

The number of interactions (degree) for phorophyte species varied from 1 to 71 (Tables 2, Appendix S1). The phorophyte *Pseudobombax* sp. nov. showed the greatest number of interactions in the network (71 species of epiphytes – 46% of 156 interactions) (Fig. 3; Appendix S1). Of these, 38 (45%) were exclusive species for this phorophyte, being 16 (42%) species of Orchidaceae, eight (21%) species of Bromeliaceae, four (10%) species of Araceae, four (10%) species of Polypodiaceae, two (5%) species of Aspleniaceae and one (3%) species for Araliaceae, Begoniaceae, Cactaceae and Piperaceae. In addition, *Pseudobombax* sp. nov. interacted with several endangered species (Appendix S2). *Oreopanax capitatus* (ORCAP) interacted with one species of vascular epiphyte, *Billbergia*

272 *horrida* Regel, that was also present on *Pseudobombax* sp. nov. (PSSPN); *Guapira opposita*
273 (GUOPP) and *Eugenia* cf. *longipedunculata* (EULON) (Fig. 3, Appendix S1). Five species of
274 phorophytes, *Bactris* sp. (BASP), *Clusia arrudea* (CLARR), *Eremanthus crotonoides*
275 (ERCRO), *Handroanthus* sp. (HASP) and *Oreopanax capitatus* interacted with one to nine
276 species of epiphytes (Tables 2, Appendix S1).

277 Two species of phorophytes, *Pseudobombax* sp. nov. and *G. opposita*, interacted
278 together, with almost 100% of the epiphytes recorded in this study (Fig. 3, Appendix S4).
279 *Guapira opposita* was the most abundant phorophyte (88 individuals, 62%) (Appendix S5),
280 followed by *Pseudobombax* sp. nov with 23 individuals (16%). *G. opoosita* interacted with
281 46 vascular epiphytes (Fig. 3, Appendix S4, S6), with nine exclusive species: *Billbergia*
282 *tweedieana*, *Campylocentrum brachycarpum*, *Epidendrum campaccii*, *Gomesa recurva*,
283 *Monstera adansonii*, *Pleopeltis squalida*, *Stelis argentata*, *Vriesea gigantea* and *Xylobium*
284 *variegatum*, and two endangered species for the Espírito Santo state flora (*Acianthera*
285 *saurocephala* and *Bulbophyllum cantagallense*) (Appendix S1, S2).

286 We observed that epiphytic richness per individual phorophyte varies from one (on
287 *Oreopanax capitatus*) to 39 species (46%) recorded on a single individual *Pseudobombax* sp.
288 nov. (Fig. 5). *Pseudobombax* sp nov. was the most generalist phorophyte species (degree =
289 71). When compared with all other phorophyte species, the dependence of epiphyte species in
290 this phorophyte is evident (species strength = 58.7) and (push/pull = 0.8), strongly affecting
291 the epiphytes in the interaction (Table 2). It was also the largest sized phorophyte with 117
292 cm of diameter. We found significant differences among the DBH species of phorophytes
293 (Kruskal-Wallis: $H = 50.376$, $df = 7$, $p < 0.05$), and *Pseudobombax* sp. nov. differed from all
294 other species (Appendix S5).

295 The most important phorophytes for the epiphytic flora in the inselberg were
296 *Pseudobombax* sp nov. and *Guapira opposita* which together interact with almost 100% of

epiphytes and exclusively interacted with 14 (16%) epiphytic species (Fig. 3, Appendix S4). These phorophytes share 33 (39%) species of vascular epiphytes (Fig. S1). The other phorophytes interacted largely with an epiphytic flora that were present in these two phorophytes species (Fig. 3, Appendix S4).

The most abundant vascular epiphytes were *Tillandsia usneoides* (1,167 individuals, 23%) followed by *Tillandsia recurvata* (699 individuals, 14%), *T. tenuifolia* (543 individuals, 11%) and *Vriesea lubbersii* (392 individuals, 8%) (Appendix S2). All belong to the family Bromeliaceae, subfamily Tillandsioideae. The epiphyte *T. usneoides* was the most generalist (high vertex degree value; $k = 7$) species and occurred on seven of the eight species of phorophytes (Fig. 3, Appendix S1).

DISCUSSION

The present study is, to our knowledge, the first to use ecological network analysis to investigate the structure and complexity of epiphyte-phorophyte commensalistic interactions in a Neotropical inselberg. We found a diverse epiphytic community, an unexpected feature for this type of environment (see Porembski *et al.* 1998). Our results support the hypothesis that phorophytes with larger dimensions would have greater diversity of epiphytes and are the ones that most interact with them. In addition, we showed that phorophyte size, based on DBH, is an important factor for predicting the structure of the epiphyte-phorophyte interaction network. We found a nested pattern and low degree of specialization for the network, as has been found for other epiphyte-phorophyte networks in forest ecosystems (Burns 2007; Sáyago *et al.* 2013; Zhao *et al.* 2015). Generalist phorophytes that preserve unique interactions with the epiphytes are those that maintain the robustness of the network.

Richness and diversity

The richness of vascular epiphytes in this study corroborates the data obtained by Couto *et al.* (2016) and showed relatively high richness recorded in studies that quantify the epiphytic flora in Brazilian rocky environments (Werneck & Espírito-Santo 2002; Conceição *et al.* 2007; Alves *et al.* 2008). This result certainly is related to the presence of large trees in the studied inselberg, such as some individuals of *Pseudobombax* sp. nov., that has crown branches with larger diameters and less inclination than the other phorophyte species. Moreover, the presence of exposed roots of considerable thickness on the rocky surface provides an important site for colonization by epiphytes (Couto *et al.* 2016).

As expected, we found a positive and significant correlation between richness and abundance of the epiphytic community with the size of phorophytes. The phorophyte size produces a complexity of ecological factors that are intimately related with the distribution of the epiphyte community. Large trees are usually older (Sáyago *et al.* 2013; Wang *et al.* 2016) and therefore they are exposed for a longer time to diaspore settlement events through seeds or plant parts (e.g., *Tillandsia usneoides*) (Callaway *et al.* 2002; Flores-Palacios & García-Franco 2006). This is due to the greater surface area exposed to receive the seed rain and for seedling establishment, the greater heterogeneity of microhabitat available, and the improvement in bark quality and larger exposition to air moisture and light (Woods *et al.* 2015; Zhao *et al.* 2015). These specific features of older phorophytes, in conjunction, are directly responsible for the greatest diversity and composition of epiphytic species in specific phorophytes (Krömer *et al.* 2007; Zhao *et al.* 2015; Woods *et al.* 2015; Ding *et al.* 2016). In contrast, small trees are generally young and have a small area available for colonization, with little variation in the environmental conditions (Woods *et al.* 2015; Wang *et al.* 2016). Exceptions can be observed for trees and shrubs from *campos rupestres*, where phorophyte size seems less important (Alves *et al.* 2008), as observed for arborescent genus *Vellozia*

(Velloziaceae). The phorophytes of this genus are small but known to live for several centuries (Alves 1994). They hosted epiphytic species considered restricted to the caudices of their species (see Porembski 2003; Alves *et al.* 2008; Menini Neto *et al.* 2013).

The vascular epiphyte families with highest richness in this study (Orchidaceae, Bromeliaceae and Polypodiaceae) are also the richest worldwide (Zotz 2013) and especially in neotropical regions (Gentry & Dodson 1987; Boelter *et al.* 2014; Freitas *et al.* 2016). These families have a wide distribution in ecosystems associated with the Brazilian Atlantic Forest (Couto *et al.* 2016; Freitas *et al.* 2016).

Network structure

The epiphyte-phorophyte network exhibited low connectance, degree of specialization and nested structure. High connectance can promote the persistence and resilience of mutualistic networks (Thébault & Fontaine 2010) and antagonistic networks (Dunne *et al.* 2002), but we found low connectance similar to many other antagonistic parasite-host networks (Bellay *et al.* 2015), mutualistic plant-pollinators networks (Blüthgen *et al.* 2006) and commensal networks (Ceballos *et al.* 2016). In this study, the low interaction recorded may be related to the rocky environment which does not favor the establishment of diverse and structured arboreal and shrubby strata, restricting the number of species with large phorophytic individuals (Porembski *et al.* 1998; Porembski & Barthlott 2000). Normally, these large individuals which are more appropriate to the establishment of epiphytic flora (Zhao *et al.* 2015; Wang *et al.* 2016).

There was a low degree of specialization in the use of phorophytes by the epiphytes. This is an expected pattern for structurally dependent plants, such as the epiphytes (Wagner *et al.* 2015; Ceballos *et al.* 2016). Ecological theory does not predict strong interactions between commensal species, which are generally established between epiphytic and phorophyte species (Burns 2007; Sáyago *et al.* 2013, Zotz 2016). In general, low specialization

demonstrates that the representativeness of the phorophytes occurs similarly among the species of epiphytes. Two species of generalist phorophytes, *Pseudobombax* sp. nov. and *G. opposita*, interacted with almost 100% of the epiphyte species recorded in this study. The degree of specialization in commensal networks of epiphytes and phorophytes may be a result of the preference of epiphytes for specific phorophytes traits (Sáyago *et al.* 2013; Taylor *et al.* 2016). Although phorophyte specificity, the exclusive presence of one epiphyte species on one phorophyte species, is uncommon (Alves *et al.* 2008; Porembski 2003; Menini Neto *et al.* 2013), often some trees are better phorophytes for epiphytes than others (Laube & Zotz 2006; Wyse & Burns 2011; Sanger & Kirkpatrick 2016) due to their structural properties (e.g., as phorophyte size, inclination of the branches and bark type) (Wagner *et al.* 2015) or a combination of these factors (Sáyago *et al.* 2013; Boelter *et al.* 2014) which may vary among individual trees according to age (Burns & Zotz 2010; Taylor & Burns 2015). However, Callaway *et al.* (2002) and Wagner *et al.* (2015) suggested that epiphyte species should show more evident phorophyte specificity in habitats where climatic conditions are suboptimal for their performance, like rocky outcrops. These habitats have low diversity of potential phorophytes and low abundance of non-vascular epiphytes (such as mosses) and phorophyte specificity is more evident (see Wagner *et al.* 2015).

The specific environmental characteristics present in the study area, (see Porembski 2007; Hopper 2009), may favor the existing asymmetry between the interactions of epiphyte and phorophyte species. Here, we found that many epiphytic species were connected to few phorophyte species (generality = 2.05). Nevertheless, the phorophytes were associated with a lot more epiphytes species (vulnerability = 18.01) on average. The low value of generality (2.05) differs from that found in other studies of epiphyte-phorophyte networks in tropical forests (8.8 in Sáyago *et al.* 2013; 7.2 in Zhao *et al.* 2015; 8.47 in Ceballos *et al.* 2016). Tropical forests are highly homogenous at regional scales, favoring the presence of more

phorophytes, and providing a greater variety of habitats for epiphytes from the trunk base (including the understory trees and shrubs) to the upper crown (Krömer *et al.* 2007; Zhao *et al.* 2015). Consequently, the epiphytes interact with a greater number of phorophytes (Zhao *et al.* 2015; Ceballos *et al.* 2016).

The epiphyte-phorophyte network showed a nested structure. This pattern is commonly associated with mutualistic interaction networks (Jordano 1987; Bascompte *et al.* 2003; Campbell *et al.* 2015). The same was recently found in commensalistic networks of cavity-vertebrate nesters (Cockle & Martin 2015) and for phorophytes-epiphyte in forest environments (Burns 2007; Silva *et al.* 2010; Sáyago *et al.* 2013; Ceballos *et al.* 2016). These findings suggest that network size, vascular epiphyte succession, species abundance and phorophytes traits are important. We found that the phorophyte species with low interactions were also the phorophytes that had smaller diameters and hosted epiphyte communities that are subsets of the communities found in larger phorophytes, which showed higher interactions. Zhao *et al.* (2015) for montane tropical forests in southeastern China reported a similar result. Specialist epiphytes can only occur in older larger host trees (Burns 2007), contributing then to the nested pattern. *Pseudobombax* sp. nov. has a high diversity of specialist epiphytes, and other phorophytes have an epiphytic flora that derive from this phorophyte, leading the epiphyte-phorophyte interaction to a nested pattern. However, another factor that can contribute to the nestedness is a sequential colonization by epiphytes; so that pioneer species are beneficial to the specialist epiphytes species (see Burns 2007; Silva *et al.* 2010; Ceballos *et al.* 2016). Nevertheless, in our study it was not possible to observe this event.

The studied community appeared to be a fragile, sensitive to disturbance system. The removal of the more generalist phorophyte specie, *Pseudobombax* sp. nov, can rapidly lead to a collapse in the system, lowering diversity due to the secondary extinctions of many

epiphytes. *Pseudobombax* sp. nov. had many unique interactions in the network, as 45% of species of the epiphytes species occurred exclusively on this phorophyte. Many of such epiphytes are listed as threatened with some risk of extinction (e.g., *Barbosella spiritusanctensis* - Orchidaceae and *Oreopanix capitatus* - Araliaceae). This pattern was also found with antagonist networks, predator-prey (Dunne *et al.* 2002), host-parasite (Solé & Montoya 2001), and mutualistic plant–ant networks (Barriga *et al.* 2015). In the same way as to food webs (Dunne *et al.* 2002) the loss of highly connected species has serious consequences for the persistence of the network. Nevertheless, removal of specialist species (with few interactions) usually has little effect on the network structure (Dunne *et al.* 2002). Here, the extinction of specialist species as *Oreopanix capitatus*, *Bactris* sp., *Eremanthus crotonoides* and *Clusia arrudea* caused little impact on the secondary extinction of epiphytes. This was because these phorophytes do not have unique interactions and host an epiphytic flora that was present mainly in *Pseudobombax* and *Guapira opposita*. Therefore, the way species are removed from the network may affect communities in different ways, and this is related to the nature of the interaction among the removed species (Solé & Montoya 2001). . These results show the importance of the identification and protection of highly connected species. They play an important role in maintaining the richness and robustness of the network and should receive special attention in the conservation of the ecological processes that maintain diversity (Solé & Montoya 2001; Memmott *et al.* 2004).

The inselberg flora is naturally fragile (Martinelli 2007, Hopper 2009; Porembski *et al.* 2016). The resilience of this type of environment is very low compared to the surrounding ecosystems (Hopper *et al.* 2009), mainly due to its very restrictive environmental filters that select a very specific and endemic flora in each rock outcrop or specific region. In forest ecosystems, removal of important phorophytes leads to the significant loss of local epiphytic diversity (see Obermülle *et al.* 2012). The turnover of these large phorophytes by others

would probably take many years, even with highly diverse tree communities. The *Pseudobombax* species is, to our knowledge, the main phorophyte kind of rocky areas of the Atlantic Forest and replace it does not seem to be that simple. The inselbergs in the Brazilian Atlantic Forest are exposed to a number of threats, ranging from the loss and fragmentation of marginal habitats (Galindo-Leal *et al.* 2003), by quarrying (Martinelli 2007; Couto *et al.* 2016), by the invasion by exotic species (Martinelli 2007, De Paula *et al.* 2016; Couto *et al.* 2017) and indiscriminate collection of species for horticultural purposes (e.g. attractive giant bromeliads, such the genus *Alcantarea* (Versieux & Wanderley 2015; some orchids as *Aspasia lunata* and *Encyclia patens*; ferns and araceaes).

Organization of the species

As already presented by other authors who studied rocky ecosystems (Werneck & Espírito-Santo 2002; Alves *et al.* 2008), phorophytes with low longevity (e.g. *Eremanthus erythropappus* (DC.) MacLeish, *Hyptinodendron asperimum* (Spreng.) Harley and *Myrsine monticola* Mart.) supported the lowest richness of epiphytes. We observed that individuals of *Eremanthus crotonoides*, a phorophyte with low longevity, hosted few epiphytes. These were usually two species of wide geographic distribution: *Tillandsia usneioides* and *T. gardneri* (Zotz 2013). Longer-lived trees, *Guapira opposita* and *Pseudobombax* sp. nov., hosted many others epiphytes species, such as Orchids, Bromeliads and Aroids.

In this study, an individual of *Pseudobombax* sp. nov. (9 m in height and 117 cm of the DBH), hosted the highest species richness (39 species). Thus, the richness for epiphytes on individuals of phorophytes was intermediate, considering the absolute values of richness, as compared with other studies in tropical forest environments (21 species in Kersten &

Silva 2001; 30 in Kersten *et al.* 2009; 83 in Krömer *et al.* 2005; 126 in Schuettpelz & Trapnell 2006; 50 in Zotz & Schultz 2008).

In conclusion, we observed that generalist phorophytes, such as *Pseudobombax* play an important role in maintaining the richness and robustness of the network. This species needs to receive protection in conservation and restoration activities to prevent secondary extinctions, especially in these fragile inselbergs ecosystems., We propose that future research should address changes in inselberg network structure in space and time and even include other types of interactions, such as herbivory.

REFERENCES

- Almeida-Neto M. & Ulrich W. (2011) A straightforward computational approach for measuring nestedness using quantitative matrices. *Environ. Model. Softw.* **26**, 173-178.
- Almeida-Neto M., Guimarães P., Guimarães P. R., Loyola, R. D. & Ulrich, W. (2008) A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. *Oikos* **117**, 1227–1239.
- Alves R. J. V., Kolbek, J., & Becker J. (2008) Vascular epiphyte vegetation in rocky savannas of southeastern Brazil. *Nordic J. Bot.* **26**, 101–117.
- Alves R. J. V. (1994) Morphological age determination and longevity in some *Vellozia* populations in Brazil. *Folia Geobot. Phytotax.* **29**, 55-59.
- Barriga P. O., Dormann C. F., Gbur E. E. & Sagers C. R. (2015). Community structure and ecological specialization in plant- ant interactions. *J Trop Ecol* **31**, 325–334.
- Barthlott, W., Gröger A., & Porembski S. (1993). Some remarks on the vegetation of tropical inselbergs: diversity and ecological differentiation. *Biogéographica* **69**, 105–124.
- Bascompte J., Jordano P. & Olesen J. M. (2006). Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science* **312**, 431-433.

495 Bascompte J., Jordano P., Melián C. & Olesen J. M. (2003). The nested assembly of plant-
 496 animal mutualistic networks. *Proc. Natl. Acad. Sci.* **100**, 9383–9387.

497 Bellay S., Oliveira E. F., Almeida-Neto M., Abdallah V. D., Azevedo R. K., Takemoto, R.
 498 M. & Luque J. L. (2015). The patterns of organization and structure of interactions in a
 499 fish-parasite network of a neotropical river. *Int. J. Parasitol.* **45**, 549–557.

500 Benzing D. H. (1990). *Vascular epiphytes*. Cambridge University Press, Cambridge. 354p.

501 Blick R. & Burns K. C. 2009. Network properties of arboreal plants: Are epiphytes,
 502 mistletoes and lianas structured similarly? *Perspect. Plant Ecol. Evol.* **11**, 41–52.

503 Blüthgen N., Menzel F. & Blüthgen N. (2006). Measuring specialization in species
 504 interaction networks. *BMC Ecology* **6**, doi:10.1186/1472-6785-6-9.

505 Boelter C. R., Dambros C. S., Nascimento H. E. M. & Zartman C. E. (2014). A tangled web
 506 in tropical tree-tops: effects of edaphic variation, neighbourhood phorophyte composition
 507 and bark characteristics on epiphytes in a central Amazonian forest. *J. Veg. Sci.* **25**, 1090-
 508 1099.

509 Burgos E., Ceva H., Perazzo R. P. J., Devoto M. & Medan, D. (2007) Why nestedness in
 510 mutualistic networks? *J. Theor. Biol.* **249**, 307– 13.

511 Burns K. C (2007) Network properties of an epiphyte metacommunity. *J. Ecol.* **95**, 1142-
 512 1151.

513 Burns, K. C & Zotz , G. (2010) A hierarchical framework for investigating epiphyte
 514 assemblages: networks, meta-communities, and scale. *Ecology* **91**, 377–385.

515 Callaway R. M., Reinhart K. O., Moore G. W., Moore D. J. & Pennings S. C. (2002).
 516 Epiphyte host preferences and host traits: mechanisms for species-specific interactions.
 517 *Oecologia* **132**, 221–230.

518 Campbell C., Yang S., Albert R & Shea K. (2015) Plant–pollinator community network
 519 response to species invasion depends on both invader and community characteristics.
 520 *Oikos* **124**, 406–413.

521 Ceballos S. J, Chacoff N. P. & Malizia A. (2016) Interaction network of vascular epiphytes
 522 and trees in a subtropical forest. *Acta Oecol.* **77**, 152-159

523 Chao A. (2005) *Encyclopedia of Statistical Sciences*. Wiley, New York. p. 7909–7916.

524 Chao A., Colwell R. K., Lin C. W. & Gotelli N. J. (2009) Sufficient sampling for asymptotic
 525 minimum species richness estimators. *Ecology* **90**, 1125–1133.

526 Cockle K. & Martin K. (2015) Temporal dynamics of a commensal network of cavity-nesting
 527 vertebrates: increased diversity during an insect outbreak. *Ecology* **96**, 1093–1104.

528 Conceição A. A., Giulietti A. M. & Meirelles S. T. (2007). Ilhas de vegetação em
 529 afloramentos de quartzito-arenito no Morro do Pai Inácio, Chapada Diamantina, Bahia,
 530 Brasil. *Acta Bot. Bras.* **21**, 335-347.

531 Couto D. R., Dias H. M., Pereira M. C. A., Fraga C. N. & Pezzopane J. E. M. (2016).
 532 Vascular epiphytes on *Pseudobombax* (Malvaceae) in rocky outcrops (inselbergs) in
 533 Brazilian Atlantic Rainforest: basis for conservation of a threatened ecosystem.
 534 *Rodriguésia* **67**, 583-601.

535 Couto D. R., Francisco T. M., Manhães V. C., Dias H. M. & Pereira M. C. A. (2017) Floristic
 536 composition of a Neotropical inselberg from the state of Espírito Santo, Brazil: a relevant
 537 area for conservation. *Check List*. **13**, 2043

538 De Paula L. F. A., Forzza R. C., Neri A. V., Bueno, M. & Porembski S. (2016) Sugar Loaf
 539 Land in south-eastern Brazil: a centre of diversity for mat-forming bromeliads on
 540 inselbergs. *Bot. J. Linn. Soc.* **181**, 459-476.

541 Ding Y., Liu G., Zang R., Zhang J., Lu, X. & Jihong Huang, J. (2016) Distribution of
 542 vascular epiphytes along a tropical elevational gradient: disentangling abiotic and biotic
 543 determinants. *Sci. Rep.* **6** (19706) doi: 10.1038/srep19706.
 544 Dormann C. F., Gruber B. & Frund J. (2008) Introducing the bipartite package: analyzing
 545 ecological networks. *R News* **8**, 8–11.
 546 Dunne J. A., Williams R. J. & Martinez N. D. (2002) Network structure and biodiversity loss
 547 in food webs: robustness increases with connectance. *Ecol. Lett.* **5**, 558–567.
 548 Embrapa (2009) *Sistema brasileiro de Classificação de solos*. Centro nacional de pesquisas
 549 de Solos, Rio de Janeiro. 412p.
 550 Evans D. M., Pocock M. J. O. & Memmott J. (2013) The robustness of a network of
 551 ecological networks to habitat loss. *Ecol Lett.* **16**, 844–852.
 552 Flores-Palacios A. & García-Franco J. G. (2006) The relationship between tree size and
 553 epiphyte species richness: testing four different hypotheses. *J. Biogeogr.* **33**, 323–
 554 330
 555 Freitas L., Salino A., Neto L. M., Almeida T. E., Mortara S. R., Stehmann J. R.,
 556 Amorim A. M., Guimaraes E. F. *et al.* (2016) A comprehensive checklist of vascular
 557 epiphytes of the Atlantic Forest reveals outstanding endemic rates. *Phytokeys* **58**, 65-79.
 558 Galindo-Leal C., Jacobsen T. R., Langhammer P. F. & Olivieri S. (2003) State of the
 559 hotspots: the dynamics of biodiversity loss. *In*: Galindo-Leal C. & De Câmara, I. G. (eds).
 560 The Atlantic Forest of South America: biodiversity status, threats, and outlook. Center for
 561 Applied Biodiversity Science and Island Press, Washington, pp. 12–23.
 562 Gentry A. H. & Dodson C. H. (1987) Contribution of non trees to species richness of a
 563 tropical rain forest. *Biotropica* **19**, 149-156.
 564 Gentry A. H. (1982) Patterns of Neotropical plant species diversity. *Evol. Biol.* **15**, 1-84.

564 Gotelli N. J. & Colwell R. K. (2011) Estimating species richness. *In*: Magurran A. E. &
565 McGill, B. J. (eds). Biological diversity: frontiers in measurement and assessment. Oxford
566 University Press, Oxford. p. 39-54.

567 Gradim C., Roncato J., Pedrosa-Soares A. C., Cordani U., Dussin I., Alkmim F. F. &
568 Babinski M. (2014) The hot back-arczone of the Araçuaí orogen, Eastern Brazil: From
569 sedimentation to granite generation. *Braz. J. Geol.* **44**, 155-180.

570 Guimarães Jr P. R. & Guimarães P. R. (2006) Improving the analyses of nestedness for large
571 sets of matrices. *Environ. Modell. Softw.* **21**, 1512–1513.

572 Hopper S. D. (2009) OCBIL theory: towards an integrated understanding of the evolution,
573 ecology and conservation of biodiversity on old, climatically buffered, infertile
574 landscapes. *Plant Soil* **322**, 49-86.

575 Ings T. C., Montoya J. M., Bascompte J. *et al.* (2008) Ecological networks – beyond food
576 webs. *J. Anim. Ecol.* **78**, 253-269.

577 Jordano P. (1987) Patterns of mutualistic interactions in pollination and seed dispersal:
578 connectance, dependence asymmetries, and coevolution. *American Naturalist*. **129**, 657–
579 677.

580 Kersten R. A. & Silva S.M. (2001) Composição florística e estrutura do componente epifítico
581 vascular em floresta da planície litorânea na Ilha do Mel, Paraná, Brasil. *Rev. Bras. Bot.*
582 **24**, 213-226.

583 Kersten R. A., Borgo M. & Silva S. M. (2009) Diversity and distribution of vascular
584 epiphytes in an insular Brazilian coastal forest. . *Int. J. Trop. Biol.* **57**, 749-759.

585 Köppen W. (1948) *Climatologia: con un estudio de los climas de la tierra*. Mexico, Fondo de
586 Cultura Econômica. 438p.

587 Krömer T., Kessler M. & Gradstein R. S. (2007) Vertical stratification of vascular epiphytes
 588 in submontane and montane forest of the Bolivian Andes: the importance of the
 589 understory. *Plant Ecol.* **189**, 261-278.

590 Krömer T., Kessler M., Gradstein S. R. & Acebey A. (2005) Diversity pat- terns of vascular
 591 epiphytes along an elevational gradient in the Andes. *J. Biogeogr.* **32**, 1799-1809.

592 Laube S. & Zotz G. (2006) Neither host-specific nor random: vascular epiphytes on three tree
 593 species in a Panamanian lowland forest. *Ann. Bot.* **97**, 1103-1114.

594 Martinelli G. 2007. Mountain biodiversity in Brazil. *Rev Bras Bot.* **30**, 587-597.

595 Mello M. A. R., Rodrigues F. A., Costa L. F., Kissling W. D., Şekercioğlu Ç. H. *et al.* (2015)
 596 Keystone species in seed dispersal networks are mainly determined by dietary
 597 specialization. *Oikos* **124**, 1031–1039.

598 Memmott J., Waser N. M. & Price M. V. (2004) Tolerance of pollination networks to species
 599 extinctions. *Proc. Roy. Soc. Lond. Ser. B-Biol. Sci.* **271**, 2605–2611.

600 Menini Neto L., Van Den Berg, C., Forzza R. C. (2013) Taxonomic revision of *Pseudolaelia*
 601 Porto & Brade (Laeliinae, Orchidaceae). *Acta Bot. Bras.* **27**, 418-435.

602 Obermüller F. A., Silveira M., Salimon, C. I. & Daly D. C. (2012) Epiphytic (including
 603 hemiepiphytes) diversity in three timber species in the southwestern Amazon, Brazil.
 604 *Biodivers. conserv.* **21**, 565-575.

605 Oksanen J., Blanchet F. G., Friendly M. *et al.* (2016) *vegan: Community Ecology Package*,
 606 Available from: <<https://cran.r-project.org/package=vegan>>

607 Pocock M. J. O., Evans, D. M. & Memmott J. (2012) The robustness and restoration of a
 608 network of ecological networks. *Science* **335**, 973–977.

609 Porembski S. & Barthlott W. (2000) Granitic and gneissic outcrops (inselbergs) as centers of
 610 diversity for desiccation-tolerant vascular plants. *P. Ecol.* **151**, 19-28.

611 Porembski S. (2003) Epiphytic orchids on arborescent Velloziaceae and Cyperaceae:
 612 Extremes of phorophyte specialisation. *Nord. J. Bot.* **23**, 505-512.

613 Porembski S. (2007) Tropical inselbergs: habitat types, adaptive strategies and diversity
 614 patterns. *Rev. Bras. Bot.* **20**, 579-586.

615 Porembski S., Martinelli G., Ohlemüller R. & Barthlott W. (1998) Diversity and ecology of
 616 saxicolous vegetation mats on inselbergs in the Brazilian Atlantic rainforest. *Diver.*
 617 *Distrib.* **4**, 107-119.

618 Porembski S., Silveira F. A. O., Fiedler P. L., Watve A., Rabarimanarivo M., Kouame F. &
 619 Hopper S.D. (2016) Worldwide destruction of inselbergs and related rock outcrops
 620 threatens a unique ecosystem. *Biodivers Conserv.* **25**, 2827-2830

621 R Development Core Team (2016) R: A Language and Environment for Statistical
 622 Computing Vienna, Austria. Available from: [http:// www.R-project.org/](http://www.R-project.org/)

623 Sanford W. W. (1968) Distribution of epiphytic orchids in semi-deciduous tropical forest in
 624 southern Nigeria. *J Ecol.* **56**, 697-705.

625 Sanger J. C. & Kirkpatrick J. B. (2016) Fine partitioning of epiphyte habitat within Johansson
 626 zones in tropical Australian rain forest trees. *Biotropica*, doi: 10.1111/btp.12351.

627 Sáyago R., Lopezaraiza-Mikel M., Quesada M., Álvarez-Anorve M. Y., Cascante-Marín A.
 628 & Bastida J. M. (2013) Evaluating factors that predict the structure of a commensalistic
 629 epiphyte-phorophyte network. *Proc. Biol. Sci.* **280**, (20122821) doi:
 630 10.1098/rspb.2012.2821.

631 Schuettepelz E. & Trapnell D. W. (2006) Exceptional epiphyte diversity on a single tree in
 632 Costa Rica. *Selbyana* **27**, 65-71.

633 Silva I. A., Ferreira A. W. C., Lima M. I. S., Soares J. J. (2010) Networks of epiphytic
 634 orchids and host trees in Brazilian gallery forests. *J. Trop. Ecol.* **26**, 127-137.

635 Solé R. V. & Montoya J. M. (2001) Complexity and fragility in ecological networks. *Proc.*
636 *Biol Sci.* **268**, 2039–2045.

637 Taylor A. & Burns K. (2015) Epiphyte community development throughout tree ontogeny: an
638 island ontogeny framework. *J. Veg. Sci.* **46**, 902-910.

639 Taylor A., Saldaña A., Zotz G. & Burns K. (2016) Composition patterns and network
640 structure of epiphyte–host interactions in Chilean and New Zealand temperate forests.
641 *New Zealand J. Bot.* **54**, 204-222.

642 ter Steege H. & Cornelissen J. H. C. (1989) Distribution and ecology of vascular epiphytes in
643 lowland rain forest of Guyana. *Biotropica* **21**, 331-339.

644 The Angiosperm Phylogeny Group (2016) An update of the Angiosperm Phylogeny Group
645 classification for the orders and families of flowering plants: APG III. *Bot. J. Linnean*
646 *Soc.* **181**, 1-20.

647 The Pteridophyte Phylogeny Group (2016) A community-derived classification for extant
648 lycophytes and ferns. PPG I. *J Syst Evol* **54**, 563-603.

649 Thébault E. & Fontaine C. (2010) Stability of ecological communities and the architecture of
650 mutualistic and trophic networks. *Science* **329**, 853-856.

651 Traveset A., Olesen J. M., Nogales M., Vargas P., Jaramillo P., Antolín E. *et al.* (2015) Bird-
652 flower networks in the Galápagos unveil a widespread interaction release. *Nature*
653 *Communications* **6**, 6376.

654 Tylianakis J. M., Tscharnkte T., Lewis O.T. (2007) Habitat modification alters the structure
655 of tropical host-parasitoid food webs. *Nature* **445**, 202–205

656 Vázquez D. P., Melian C. J., Williams N. M., Bluthgen, N., Krasnov B. R. & Poulin R.
657 (2007) Species abundance and asymmetric interaction strength in ecological networks.
658 *Oikos* **116**, 1120–1127.

659 Versieux L. M. & Wanderley M.G.L. (2015) *Bromélias-gigantes do Brasil*. Capim Macio &
660 Offset Gráfica e Editora Ltda. Natal. 200p.

661 Wagner K., Mendieta-Leiva G. & Zotz G. (2015) Host specificity in vascular epiphytes: a
662 review of methodology, empirical evidence and potential mechanisms. *AoB Plants* **7**,
663 plu092.

664 Wang X., Long W., Schamp B. S., Yang X., Kang Y., Xie Z. & Xiong M. (2016) Vascular
665 epiphyte diversity differs with host crown zone and diameter, but not orientation in a
666 tropical cloud forest. *PLoS ONE* **11**, e0158548.

667 Werneck M. S. & Espírito-Santo M. M. (2002) Species diversity and abundance of vascular
668 epiphytes on *Vellozia piresiana* in Brasil. *Biotropica* **34**, 51-57.

669 Woods C. L., Cardelús C. L. & Walt S. J. (2015) Microhabitat associations of vascular
670 epiphytes in a wet tropical forest canopy. *J. Ecol.* **103**, 421-430.

671 Wyse S. V. & Burns B. R. (2011). Do host bark traits influence trunk epiphyte communities?
672 *New Zealand J. Ecol.* **35**, 296-301.

673 Yarranton G. A. & Morrison R. G. (1974) Spatial dynamics of a primary succession:
674 nucleation. *J. Ecol.* **62**, 417-428.

675 Zar, J. H. (2010) *Biostatistical Analysis*. Pearson Education Inc., Upper Saddle River, USA.
676 944p.

677 Zhao M., Geekiyanage N., Xu J., Khin M. M., Nurdiana D. R., Paudel E. & Harrison R. D.
678 (2015) Structure of the epiphyte community in a tropical montane forest in SW China.
679 *PLoS ONE* **10**, e0122210.

680 Zotz G. & Schultz S. (2008). The vascular epiphytes of a lowland forest in Panama- species
681 composition and spatial structure. *Plant Ecol.* **195**, 131-141.

682 Zotz G. (2013) The systematic distribution of vascular epiphytes-a critical update. *Bot. J.*
683 *Linn. Soc.* **171**, 453-481.

684 Zotz G. (2016) *Plants on Plants – The Biology of Vascular Epiphytes*. Springer International,
685 Germany. 282p.

686 **Tables**
687

688 **Table 1.** Mean and standard error (n = 20) of network metrics of interactions between vascular
689 epiphytes and phorophytes on a montane inselberg, Espírito Santo state, Brazil. H_2' :
690 characterizes the degree of specialization and *NODF* (nestedness metric based on overlap and
691 decreasing fill) see methods.
692

Metrics	Mean ($\pm$ standard error)
Connectance	0.53 $\pm$ 0.02
H_2'	0.47 $\pm$ 0.04
Generality	1.53 $\pm$ 0.08
Vulnerability	6.57 $\pm$ 1.03
<i>NODF</i>	41.41 $\pm$ 3.55

693
694 **Table 2.** Observed values of species strength (SS), push/pull and degree of the eight species
695 phorophytes in the network commensal phorophyte and epiphyte recorded on a montane
696 inselberg, Espírito Santo state, Brazil.
697

Phorophytes species	Code	Species strength	Push pull	Degree (k)
<i>Pseudobombax</i> sp. nov.	PSSPNOV	57.68	0.80	71
<i>Guapira opposita</i> (Vell.) Reitz	GUOPP	22.52	0.47	46
<i>Clusia arrudea</i> Planch. & Triana ex Engl.	CLARR	0.34	-0.07	9
<i>Eugenia</i> cf. <i>longipedunculata</i> Nied.	EULON	4.27	0.17	19
<i>Eremanthus crotonoides</i> (DC.) Sch. Bip.	ERCRO	0.06	-0.47	2
<i>Handroanthus</i> sp.	HASP	0.09	-0.15	6
<i>Bactris</i> sp.	BASP	0.01	-0.49	2
<i>Oreopanax capitatus</i> (Jacq.) Decne. & Planch	ORCAP	0.02	-0.98	1

699 Figure captions

700 **Fig. 1.** (A) Study area in Espírito Santo state, southeast Brazil. (B) Note the presence of litholic
 701 neosoil, shallow and a vegetation arboreal-shrub sparse, without the formation of a continuous
 702 canopy in much of the inselberg and predominance of typical elements of inselbergs south-
 703 american, as *Alcantarea* (Bromeliaceae). (C) *Pseudobombax* sp. nov.

704
 705 **Fig. 2.** Diversity of the main epiphytic families registered on a montane inselberg, Espírito
 706 Santo state, Brazil.

707
 708 **Fig. 3.** Network illustrating the interactions between epiphytes and phorophytes on a montane
 709 inselberg, Espírito Santo state, Brazil. Bars represent the species of epiphytes (on top) and
 710 phorophytes (bottom). The line width represent the observed interactions between the pairs
 711 (thicker line show greater interaction strength). (To identify the name of each species present
 712 in the network, see Table S1).

713 **Fig. 4.** Simulation of network robustness after removing of the most connected species of
 714 phorophytes to less connected in the network (by degree method) (Memmontt *et al.* 2004)
 715 phorophyte and epiphyte commensal interaction on a montane inselberg, Espírito Santo state,
 716 Brazil.

717
 718 **Fig. 5.** Richness of species (A) and abundance (B) of vascular epiphytes by phorophytes
 719 species on a montane inselberg, Espírito Santo state, Brazil. The black horizontal bar represents
 720 the median and the lines above and below represent the first and third quartile, in that order.

722 Appendix

723 **Appendix S1.** List of vascular epiphytes, their interaction with each phorophyte present in the
 724 studied network and total number of interactions (degree (k)) on a montane inselberg, Espírito
 725 Santo state, Brazil. The color in rows indicates the interaction. Code of species phorophytes:
 726 PSSPNOV (*Pseudobombax* sp. nov.); GUOPP (*Guapira opposita* (Vell.) Reitz); EULON
 727 (*Eugenia* cf. *longipedunculata* Nied.); CLARR (*Clusia arrudea* Planch. & Triana ex Engl.);
 728 HASP (*Handroanthus* sp.); BASP (*Bactris* sp.); ERCRO (*Eremanthus crotonoides* (DC.) Sch.
 729 Bip.); ORCAP (*Oreopanax capitatus* (Jacq.) Decne. & Planch.).

730
 731 **Appendix S2.** List of 85 vascular epiphytes, 44 genera distributed in 11 families showing the
 732 number of individuals and the number of colonized phorophytes on a montane inselberg,
 733 Espírito Santo state, Brazil. In front of the names of the families, the numbers of genera and
 734 species are shown in parenthesis.

735
 736 **Appendix S3.** Estimation of sampling completeness of interactions analyses for each
 737 phorophyte species from which more than five individuals were sampled. S_{obs} : number of
 738 interactions observed; Chao S (Chao2 estimator) (see methods); N: number of individuals

sampled of each species. Detection: the proportion of interactions observed out of all those that are expected. For the name of each phorophyte species see Table S1, this section.

Appendix S4. Phorophyte-epiphyte interaction matrix on a montane inselberg, Espírito Santo state, Brazil. Species are ordered, in rows (phorophytes) of larger size species for smaller species (DBH) and columns (epiphytes) from the most generalized to the most specializes. Black cells indicate presence of interactions. Identify the name of each phorophyte and epiphyte species see Table S1, this section.

Appendix S5. Tree species sampled on a montane inselberg, Espírito Santo state, Brazil, followed by No (number of phorophytes individuals); Trans (occurrence of species in transects), DA (absolute density); DR (relative density); FA (absolute frequency in transects); FR (relative frequency in transects). Data are means $\pm$ SD (standard deviation): Basal area; DBH (diameter at breast height); Total tree height; Height trunk (height until the first inversion for the primary branches) and Number of primary branches. For each species, different letters indicate significantly different in the DBH (Dunn test: $P < 0.05$).

Appendix S6. Species richness of epiphytes present in each phorophytes species on a montane inselberg, Espírito Santo state, Brazil. The bars represent the species richness (number of species for each phorophytes) and the numbers above each bar corresponds to the abundance of epiphytes. PSSPNOV: *Pseudobombax* sp. nov.; GUOPP: *Guapira opposita*; EULON: *Eugenia* cf. *longipedunculata*; CLARR: *Clusia arrudea*; HASP; *Handroanthus* sp.; BASP: *Bactris* sp.; ERCRO: *Eremanthus crotonoides*; ORCAP *Oreopanax capitatus*.

References Appendix

Kollmann L. J. C., Fontana A. P., Simonelli M. & Fraga C. N. (2007) As angiospermas ameaçadas de extinção no estado do Espírito Santo. In: Simonelli, M., Fraga, C.N. (Orgs.). Espécies da flora ameaçadas de extinção no estado Espírito Santo. IPEMA, Vitória, pp. 105-137.

MMA (Ministério do Meio Ambiente) (2014) Portaria Nº 443, 17/12/2014. Recognizes the official national list of endangered plant species. Available in: <http://www.mma.gov.br/biodiversidade/especies-ameacadas-de-extincao/atualizacao-das-listas-de-especies-ameacadas>. Access in: 15 de October de 2016.