



Forest and connectivity loss simplify tropical pollination networks

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Abstract

Mutualistic interactions between plants and pollinators play an essential role in the organization and persistence of biodiversity. The structure of interaction networks mediates the resilience of local communities and ecosystem functioning to environmental changes. Hence, network structure conservation may be more critical for maintaining biodiversity and ecological services than the preservation of isolated species in changing landscapes. Here, we intensively surveyed seven 36 km² landscapes to empirically investigate the effects of forest loss and landscape configuration on the structure of plant–pollinator networks in understory vegetation of Brazilian Atlantic Forest. Our results indicate that forest loss and isolation affect the structure of the plant–pollinator networks, which were smaller in deforested landscapes, and less specialized as patch isolation increased. Lower nestedness and degree of specialization (H'_2) indicated that the remaining plant and bee species tend to be generalists, and many of the expected specialized interactions in the network were already lost. Because generalist species generate a cohesive interaction core in these networks, these simplified networks might be resistant to loss of peripheral species, but may be susceptible to the extinction of the most generalist species. We suggest that such a network pattern is an outcome of landscapes with a few remaining isolated patches of natural habitat. Our results add a new perspective to studies of plant–pollinator networks in fragmented landscapes, showing that those interaction networks might also be used to indicate how changes in natural habitat affect biodiversity and biotic interactions.

Keywords Bees · Interaction networks · Mutualistic web · Fragmented landscapes · Brazilian Atlantic Forest

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Introduction

Biodiversity is more than a collection of species. Biotic interactions involve many partners, are complex, dynamic, and play an essential role in the organization and persistence of biodiversity (Fortuna and Bascompte 2006; Bascompte 2009a). Ecological networks of biotic interactions provide an efficient approach to understand the complex set of connections among several species when simultaneously influenced by many different factors (Bascompte et al. 2003). The study of mutualistic interaction networks, such as plant–pollinators, may improve the ecological knowledge beyond species diversity studies to assess the impacts of habitat change on biodiversity and ecological processes functioning (Forum and Memmott 2005; Sabatino et al. 2010; Ferreira et al. 2013; Moreira et al. 2015, 2017). Those studies can provide more complete guidance for conservation of biodiversity, ecological processes, and natural environments.

Plant–pollinator interaction networks tend to be highly nested with generalist species interacting with each other

and with specialist species, but not other specialists making a dense core of interactions (Tylianakis et al. 2010). Theoretical models suggest that the structures of mutualistic networks are in general resilient to random extinctions, but the extinction of well-connected generalists can result in quick network collapse due to extinction cascades and species loss (Bascompte 2009a; Kaiser-Bunbury et al. 2010). Harsh structural changes are more probable when key generalists are lost. Despite the robustness of some aspects of this structure, these networks are expected to change with habitat loss, with local extinction of species being preceded by subtler changes in the role of species in the network with cascading effects and secondary loss of species (Memmott et al. 2004; Ashworth et al. 2004; Sabatino et al. 2010).

Biodiversity is currently threatened by ongoing species overexploitation and agriculture expansion (Maxwell et al. 2016). Landscape changes due to the loss of native vegetation may alter the abundance and richness of pollinators, by altering the availability of floral and nesting resources (Brosi et al. 2008; Viana et al. 2012; Ferreira et al. 2013). Likewise, spatial isolation of habitat patches may negatively affect plant–pollinator interactions by limiting movement and abundance of available pollinators at a given site (Garibaldi et al. 2011). The consequent lower pollination may reduce cross-pollination, increase inbreeding depression, and cause genetic erosion of plant populations, consequently reducing plant reproductive success and yield (Osborne et al. 1999; Steffan-Dewenter and Tscharntke 1999; Biesmeijer et al. 2005; Klein et al. 2007; Sabatino et al. 2010).

Interactions among specialist species could then be more sensitive to landscape changes than those with generalists (e.g., Aizen et al. 2012; Ferreira et al. 2015). These shifts in network characteristics may directly affect their robustness and lead to secondary extinctions, loss of interactions, and, consequently, ecosystem function disruption (Sabatino et al. 2010; Blüthgen and Klein 2011). However, there are still theoretical controversy and few empirical data regarding the effects of the loss of natural environments on network characteristics such as nestedness (the extent to which interactions with specialist species are a subset of interactions with generalist species) and complementary specialization— H'_2 (the extent to which specialist species interact with other specialists) (Blüthgen and Klein 2011; Weiner et al. 2014). Few empirical studies have actually investigated the effects of deforestation on the structure of plant–pollinator networks, with even fewer information available in tropical regions (Hagen and Kraemer 2010; Gómez et al. 2011; Ferreira et al. 2013; Dáttilo et al. 2015; Moreira et al. 2015, 2017). The existing network studies show a positive influence of increasing cover of natural vegetation, particularly when the landscape heterogeneity is high (Moreira et al. 2015; Boscolo et al. 2017; Moreira et al. 2017). Such positive effects on network structure are likely associated with

the maintenance of pollinator populations and reproductive success of plants (Nery et al. 2018).

In the present study, we investigated the effects of forest loss and changes in landscape connectivity on the structure of plant–pollinator networks in the understory of the Brazilian Atlantic Forest. The Brazilian Atlantic Forest was historically degraded and is profoundly threatened and diverse but still poorly studied (Myers et al. 2000; Ribeiro et al. 2009). We focused on bees, the main group of pollinators for angiosperms (Bawa 2007) and the most abundant group of flower-visiting insects in our study region (70% of all sampled flower visitors). There is evidence for the negative effects of forest loss on bee abundance (Ferreira et al. 2015). Mostly for social bees, the effects of landscape changes on a local scale seem to depend on regional forest cover, with negative effects detected when landscapes had less than 35% of forest cover (Ferreira et al. 2015). Information on the impacts of forest loss over pollination interactions in tropical environments is fundamental to develop better strategies for their conservation and maintenance (Ashworth et al. 2004; Pigozzo and Viana 2010). The rarest and more specialized interactions are strongly affected by forest loss (Ashworth et al. 2004; Aizen et al. 2012; Ferreira et al. 2015). In this scenario, we asked the following questions: Will forest loss affect the numbers of species and their role as specialist or generalist species in the interaction networks? And, will forest loss affect the patterns of species interactions in these networks? Our hypothesis was that forest loss and lower landscape connectivity would lead to smaller networks with fewer species both of plants and bees, and also that in these networks, there would be less specialists and more generalized interactions. We expected that loss and fragmentation of native forest would not only reduce network size and number of interactions in the networks, but also imply in changes on visitation patterns that may be reflected on the values of nestedness and complementary specialization. We thus expected that forest loss would reflect higher values of nestedness and lower values of complementary specialization, due to specialists lost.

Materials and methods

Study area

This study was conducted in a region that encompasses some of the largest remnants of Tropical Atlantic Forest in northeastern Brazil in the state of Bahia. The Atlantic Forest is considered a priority area for biodiversity conservation, classified as a “Biodiversity Hotspot” (Myers et al. 2000). Mainly due to anthropogenic activities, such as agricultural expansion and urban growth, there is only about 12% of its original extent left (Ribeiro et al. 2009). The fragmentation

process that has taken place over the years resulted in the presence of non-forested areas (consisting mostly of pasture, crops and urban areas) and areas of forested environments in various levels of degradation (Zaú 1998). The climate is humid tropical (Af–Köppen–Geiger) with an average temperature varying between 24 and 27 °C and total yearly rainfall higher than 2000 mm (Peel et al. 2007). Altitude varied from 23 to 416 m a.s.l. (Table 1). Because we intended to compare whole landscapes, seven square areas (landscapes) of 6 × 6 km (36 km²) were randomly selected covering a gradient of 15, 25, 30, 35, 40, 45, and 55% of forest cover (Fig. 1a), based on the Atlas of Forest Remnants of the Atlantic Forest (<http://www.sosma.org.br> and <http://www.inpe.br>). The size of the landscapes was considered broad enough to encompass important ecological processes at population level affecting plant–pollinator networks, such as possible local extinctions of pollinators.

To standardize sampling conditions and minimize the effects of varying environmental conditions which could bias our results, we established three criteria for site selection. (1) Each study landscape was located in the center of a larger square 18 × 18 km landscape (324 km²), both with similar forest cover proportion. (2) The selected study areas did not have higher Largest Patch Index (LPI) (McGarigal 2002) than the surrounding 324 km² landscapes. The LPI reports the percentage of the landscape occupied by the largest forest patch. Since these landscapes were nested within each other, by applying these criteria, we avoided the existence of large source areas surrounding the 36 km² landscape which could bias our results (Fig. 1a). (3) At least 80% of the environments between forest patches consisted of deforested areas composed mostly of open low height vegetation

physiognomies, such as pasture and/or herbaceous/shrub plantations and non-urban areas.

Data sampling

Within forest patches in each landscape, we installed eight hexagonal plots of 25 m side (0.16 ha each) distant at least 50 m from any forest edge (Fig. 1b). These plots were located at least 600 m apart from each other to avoid spatial autocorrelation and ensure data independence (Taki and Kevan 2007). We sampled 55 plots instead of 56 (eight sites in seven landscapes), since one plot could not be sampled due to logistic constraints. Data were sampled in 2011 in two periods (January–April and August–November) to avoid the most intense rainy season (from May to July). We surveyed each hexagonal sampling plot for flower-visiting bees, during warm, dry days (20–31 °C), between 6:00 and 17:00 h. We started each sampling day by searching for plants with open flowers where we could observe visiting insects. We did a sampling circuit, pausing for 15 min in front of an individual from each plant species with open flower in the hexagon. We then sampled an individual from another plant species, and then an individual from another plant, and so on. We sequentially repeated the 15 min periods in each flowering plant species within the hexagon throughout the day. We finished one circuit and started to sample again the first plant sampled during the beginning of day, and all the other plants in the same sequence. We did this circuit during all day to try to sample all the plants in various times and to avoid sampling one species only in the morning and another species only in the afternoon. We also took care to sample all plant species in the hexagon, irrespectively of their abundance, and not only the most abundant species.

We used entomological or sweep nets to sample bees that visited the flowers in the strata up to two meters above the ground. We also collected samples of the flowering branches of all plant species found in the plot for identification. All sampled bee and plant species were identified by experts to the most specific taxonomic level possible, according to the classification proposed by Michener (Michener 2007) and APG III (Bremer et al. 2009), respectively. Bees were deposited in the Zoological Museum at the Federal University of Bahia (UFBA). Plants were deposited at the Herbarium Alexandre Leal Costa (ALCB) at UFBA.

Data analyses

Plant and bee communities can widely vary among landscapes. We used interaction network metrics to quantitatively analyze how forest spatial distribution affected the structure of these networks. Atlantic forest understory presented less floral resources than we expected, resulting in relatively small networks. It is important to notice that the networks

Table 1 Location of the seven study areas of 36 km² (3600 ha) of tropical lowland rainforests sampled along a gradient of forest cover from 15 to 55% of the Atlantic Forest in Bahia, Brazil

Cities	Forest cover (%)	Altitude	Geographic coordinates
Presidente Tancredo Neves	15	181	13°23'28" S 39°19'06" W
Valença	25	144	13°20'32" S 39°11'43" W
Ubaíra	30	416	13°07'19" S 39°39'34" W
Nilo Peçanha	35	31	13°38'58" S 39°12'37" W
Wenceslau Guimarães	40	249	13°33'14" S 39°42'07" W
Camamu	45	23	14°00'51" S 39°10'56" W
Jaguaripe	55	47	13°11'44" S 39°01'26" W

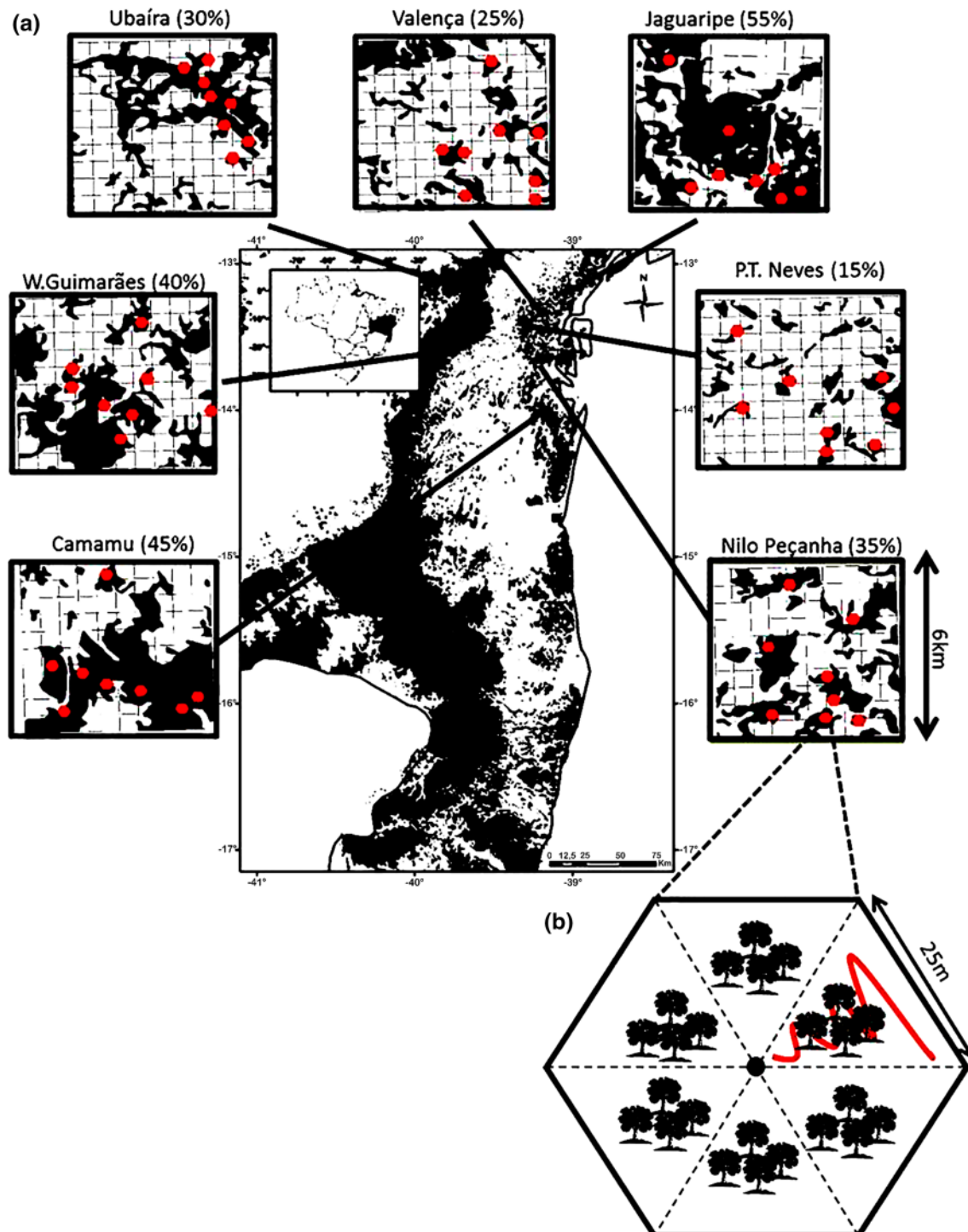


Fig. 1 **a** Seven sampled 36 km² (3600 ha) study areas in Atlantic Forest of Bahia Brazil, forest cover from 15 to 55%, in black forest patches and white non-forest matrix. **b** Hexagonal plots as red dots in each landscape representation, with 25 m sides (0.16 ha area). The

inner line (red) represents the standardized path to sample flower-visiting bees from the center to the edges of the hexagons. Color version of this figure is available online

did not represent the entire plant–pollinator communities and interactions, but samples comparable in the context of the questions addressed in this study. For each 36 km²

landscape, we calculated three response variables describing the structure of networks: (1) network size—the sum of the total number of bees and plant species per network; (2)

network nestedness—the extent to which interactions with specialist species are a subset of interactions with generalist species. Network nestedness was calculated as the “Nestedness metric based on overlap and decreasing fill” (NODF2) (Almeida-Neto et al. 2008). To verify if our networks were nested or merely organized by chance, we generated 100 null randomizations of each network using “shuffle.web” of the package Bipartite in R (R Development Core Team 2019). With that information, we calculated the mean difference in nestedness between the randomized and each observed network, where positive values indicate higher nestedness than randomly expected; and finally, (3) index of complementary specialization H'_2 —the extent of reciprocal specialist interactions. The H'_2 is mathematically independent of the total observation frequency and specifies the degree of complementary specialization in the entire network. It varies between 0 and 1, lower values corresponding to networks with less specialized interactions (Blüthgen and Klein 2011; Weiner et al. 2014). Those metrics are considered sensitive to landscape changes (Tylianakis et al. 2007; Bascompte and Jordano 2007; Bascompte 2009b; Weiner et al. 2014). All metrics were calculated using the bipartite package in software R (R Development Core Team 2019). In this work, we employed the terms generalist and specialist in relation to the number of interactions that each species presented in the networks. A species performing interactions with only one species in a landscape will be considered specialist, but it may be able to interact with several other visitors in other landscapes. Species that interact with few partners across all its range are denominated “true specialist”.

To represent forest loss and landscape connectivity, we used two landscape class-level metrics as explanatory variables: (1) Forest Cover (FC—percentage of forest remaining in the landscape); and (2) Landscape connectance index (CONNECT), which represents, among all possible pairs of patches, the percentage of those less than 50 m apart (McGarigal 2002). This distance represents the mean foraging flight capabilities of bees (Greenleaf et al. 2007). Landscape structure data were obtained from a vector layer available from the Atlas of Forest Remnants of the Atlantic Forest (<http://www.sosma.org.br> and <http://www.inpe.br>). The classification was based on CBERS and Landsat five satellites images from 2005 to 2008. Despite the time lag between these images and study data sampling, field observations and comparisons with 2011 images indicated only a few negligible changes in the landscapes. The vector layer was rasterized to 20 m pixels using QGIS 2.0.1 (Team 2013), and landscape metrics were calculated in Fragstats 4.1 (McGarigal 2002).

Considering that the influence of landscape context on biological populations tends to be highly complex, with several factors acting together, we choose a model selection approach to analyze our data. We used as selection criterion

the maximum likelihood between models in search of the model that would better describe the data. For each response variable (Network size, Nestedness, and Index of complementary specialization— H'_2), we ordered models using the lowest values of the Akaike Information Criterion (AIC). We used the Akaike weight of evidence (w) to evaluate the probability of a model to be the one that best explains the data set. We also calculated the pseudo R^2 by squaring the coefficient of correlation between observed and predicted values of the response variable to assess how well the best competing models explained the variation in the data (Burnham and Anderson 2004). To assess how landscape affected plant–bee interaction network structure, we used Generalized Linear Models—GLM, with Poisson error distribution and log link function for count data (network size) and for network nestedness and H'_2 we used Gaussian error distribution. On network nestedness models, network size was included as a covariate to address its possible mathematical effect on the other variables (Blüthgen et al. 2008). However, no influence of networks size was detected. We applied Pearson’s correlation tests and verified correlation among response variables and also among explanatory variables. We also included a null model comprised by an intercept without considering the effect of any of the explanatory factors (Burnham and Anderson 2004; Zuur et al. 2009). All analyses were performed using the software R 3.6.0 (R Development Core Team 2019).

Results

We sampled 198 individuals of 59 plant species and 483 individuals of 60 bee species (Fig. 2; species lists are presented in Online Resource 1) establishing networks ranging from 18 to 37 links per landscape (Table 2). All networks had a similar number of plants, ranging from nine to 15 species. In this work, the most generalist plants were of the families Rubiaceae (genus *Psychotria* and *Palicourea*), Piperaceae (genus *Piper*), Melastomataceae, and the Bignoniaceae (*Adenocalyma coriaceum*). Among the plants, we observed a similar proportion on the number of generalist species and specialists within each network (see Online Resources 2 for species interactions descriptions). We defined specialist plant species as those interacting with only one bee species. Most networks had twice as many specialists than generalist plant species. An exception was network WG 40% with six generalists and four specialists (see Fig. 2).

Regarding the floral visiting bees, we saw that there were more bee species than plants in the networks ranging from 9 to 26 species. On this side of the networks we have seen that there were a higher proportion of specialists in relation to generalists. We found three times as many specialist

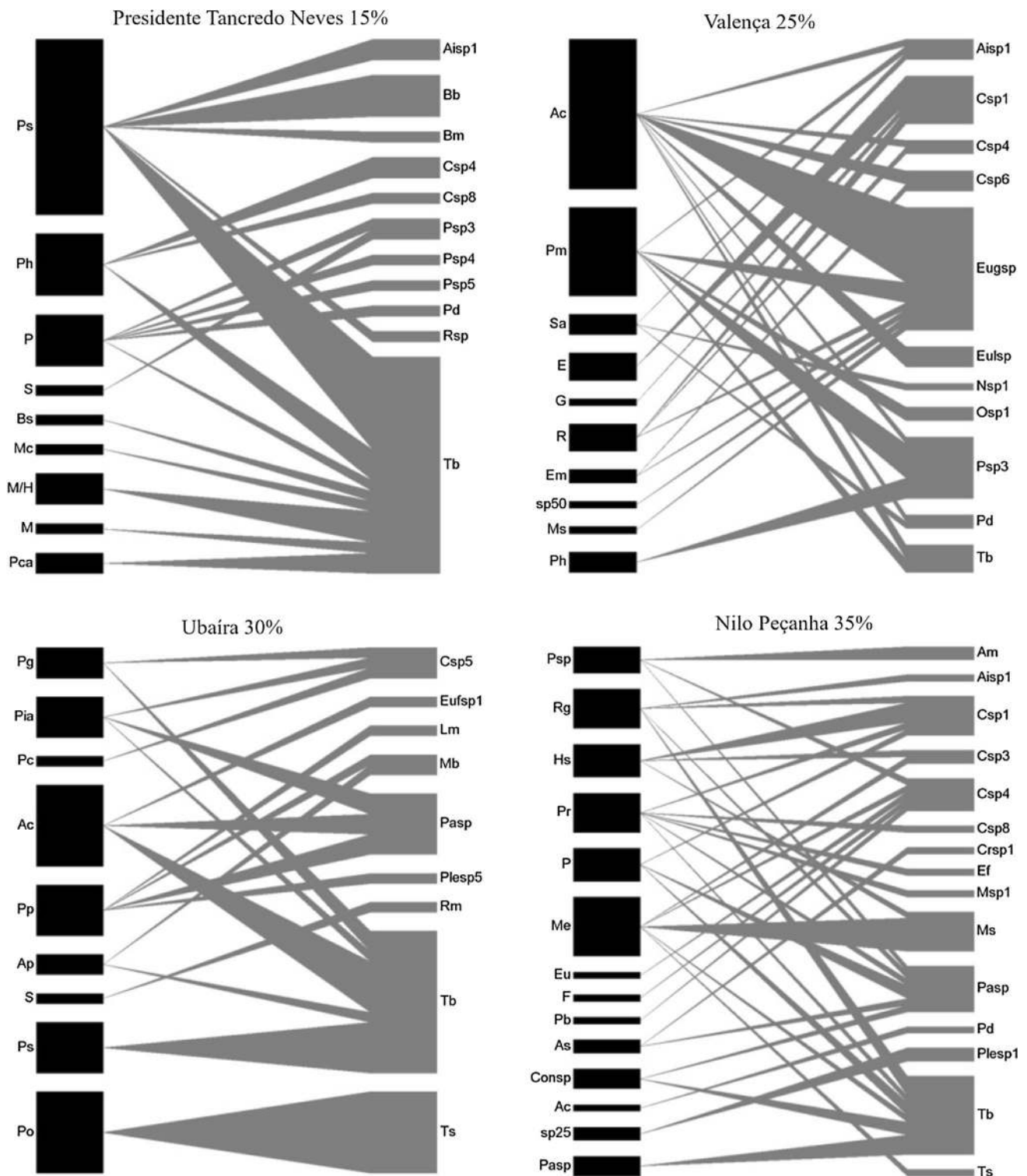


Fig. 2 Plant–bee networks for seven sampled landscapes on the Atlantic Forest in Bahia Northeastern Brazil, presented in order of the amount of forest (%) in each landscape. Rectangles represent plant (left) and bees (right). The widths of the rectangles are propor-

tional to the species abundance at the landscape, and the size of the triangles connecting the rectangles represents the frequency of interactions (see Online Resources 4, for plants and bees species names and codes). Color version of this figure is available online

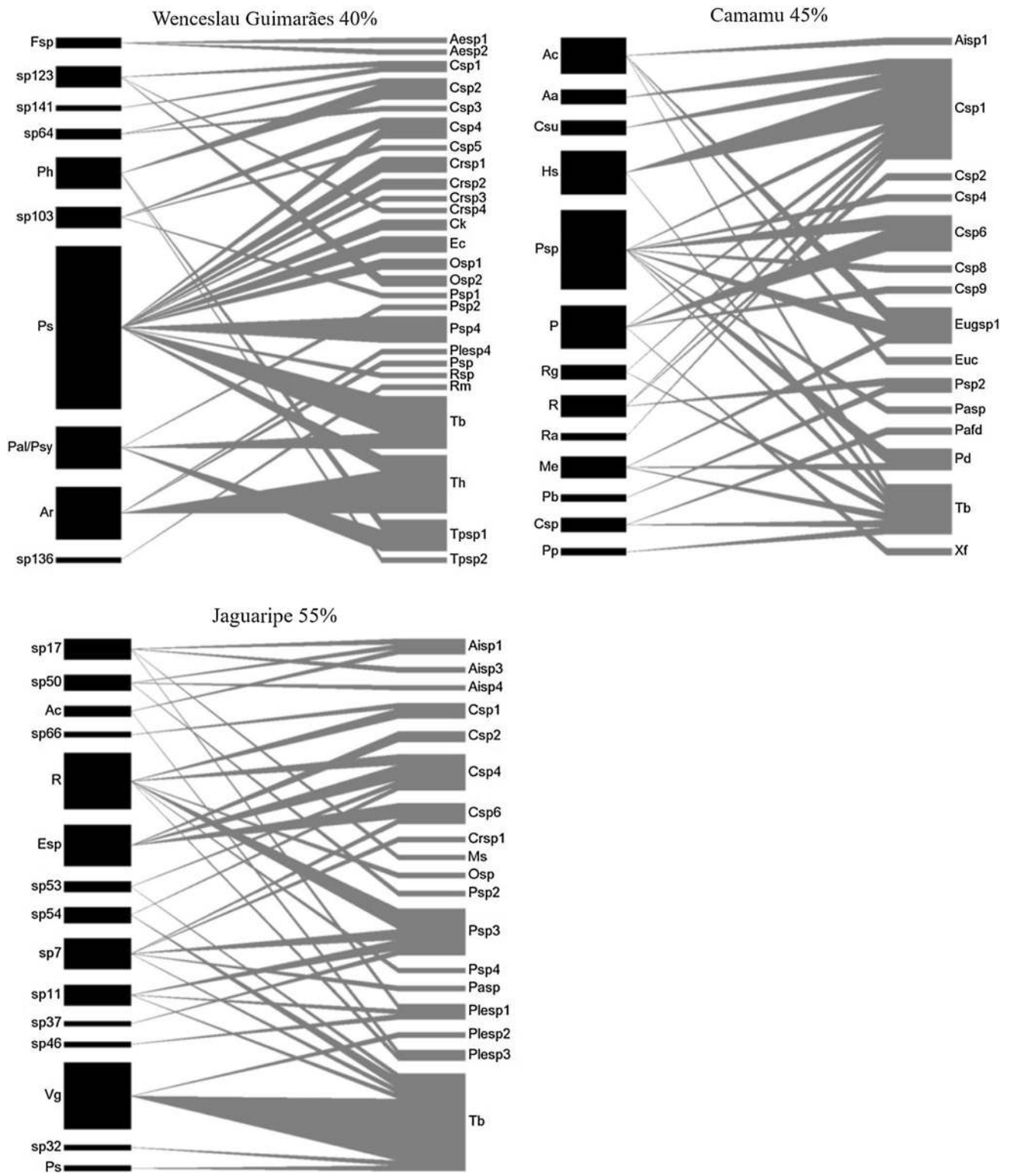


Fig. 2 (continued)

bees compared to generalists in NP 35%, CAM 45%, and JG 55% and twice more specialists compared to generalists in VAL 25% and UBA 30%. In PTN 15%, there was

a single generalist bee among ten specialist species, while in WG 40%, there was no bee with a generalist pattern of interaction. Most of bees were small, had short tongue, and

Table 2 Plant–bee network metrics sampled in seven landscapes of 36 km² (3600 ha) in a gradient of forest cover from 15 to 55% (see Table 1), in the Atlantic Forest of Bahia, Northeastern Brazil

Cities	Network size	<i>N</i> of interactions	<i>N</i> of bee species	<i>N</i> of plant species	H'_2	Nestedness
Presidente Tancredo Neves	20	19	11	9	0.27	16.69
Valença	21	26	11	10	0.41	20.34
Ubaira	18	18	9	9	0.65	28.13
Nilo Peçanha	29	34	15	14	0.37	16.16
Wenceslau Guimarães	36	32	26	10	0.71	23.19
Camamu	28	33	15	13	0.28	13.05
Jaguaripe	33	37	18	15	0.47	17.22
Mean	26.43	28.4	15	11.43	0.45	19.25

Metrics include forest cover, network size, number of interactions, bee species and plant species, complementary specialization (H'_2), and nestedness

were from the families Apidae and Halictidae, e.g., *Trigona braueri* and *Ceratina (Ceratinula) sp.*, respectively.

The difference in nestedness between the randomized and observed networks were all positive, indicating consistent higher nestedness than what was expected by chance (see Online Resources 3 for nestedness and forest cover relation). We observed a negative correlation between network nestedness (NODF2) and Network Index of complementary specialization H'_2 (Pearson $r = -0.85$, $t = -3.6$, $df = 5$, $p = 0.015$), indicating that in more nested networks, the interactions were less specialized. Therefore, there was

an inverse correlation between nestedness and network specialization. Landscapes with less forest had smaller regular shaped patches than landscapes with more forest, which presented fewer and larger patches with a tendency of greater patch shape irregularities. Model coefficients of determination (R^2) were high (above 0.5 for the best models) and showed that the best models explained an important proportion of variation in the response variables (Table 3). In addition, AIC weight of evidence (w) showed that for each response variable, the selected model (lowest AIC) was at least twice as likely in the set to be considered as the best

Table 3 Results of Plant–Bee Network models, three best models for each response variable (network size, nestedness and complementary specialization), from generalized linear models, network size (Poisson), nestedness, and complementary specialization (Gaussian) ordered by AIC

Models	ΔAIC_c	W	r^2
Network size			
Network size ~ forest cover	0	0.796	0.58
Network size ~ landscape connectance	4	0.108	0.21
Null model	4	0.096	–
Number of interactions			
Number of interactions ~ forest cover	0	0.548	0.64
Number of interactions ~ forest cover + landscape connectance	1.4	0.274	0.70
Number of interactions ~ forest cover * landscape connectance	2.9	0.126	0.75
Network nestedness			
Nestedness ~ landscape connectance + network size	0	0.956	0.85
Nestedness ~ landscape connectance	7.3	0.025	0.43
Null model	9.2	0.009	–
Nestedness ~ network size	10.7	0.005	0.08
Nestedness ~ forest cover	10.9	0.004	0.04
Nestedness ~ forest cover + network size	12.7	0.002	0.08
Complementary specialization (H'_2)			
H_2 ~ landscape connectance	0	0.990	0.82
Null model	10	0.007	–
H_2 ~ forest cover	11.6	0.003	0.05

Explanatory variables, Forest Cover, Landscape Connectance Index for a 50 m distance. AIC weighted (w) values, and proportion of the variability of the response variables explained by the explanatory variables in the models (r^2) are presented. We included only non-correlated variables in models. On network nestedness models, network size was included as a covariate to address its mathematical effect

one (Table 3). Model selection results showed that network size (number of all plants and bee species altogether) and the number of interactions in the networks were positively influenced by forest cover. With more forest, networks tended to get larger and more diverse, with an average of 31.5 species in landscapes above 30% of remaining forest. Below this value, the mean number of species was 19.6, suggesting a possible threshold effect on network size (Fig. 2). Our results also showed more interactions performed within networks in landscapes with more forest cover. Network size was more related to the number of floral visitors (Pearson $r=0.94$; $p=0.002$) than to the number of plants (Pearson $r=0.60$; $p=0.15$). Network nestedness was lower in landscapes with more connected forest patches. The maximum nestedness happened in areas with lower landscape connectivity.

The models also showed that network specialization (H'_2) was positively related with forest cover and the landscape connectance index. In landscapes with more forest and higher landscape connectance there were more specialized interactions in the networks (greater H'_2) (Fig. 3). Specialization also varied with the relative frequency of partner interactions (i.e. bees with higher visitation frequency were observed visiting plants which had fewer connections).

Discussion

Plant–pollinator networks comprised fewer species and fewer interactions in intensely deforested landscapes, mostly due to lower bee richness and compositional changes in the plant communities with which they interact. In landscapes with less forest cover, bee communities were a subset of the

communities observed in the landscapes with more forest. On the other hand, for plant communities, we observed a pattern of species turnover. As the landscapes lost forest, plant communities within the interaction networks not only got smaller, but also had different species compositions, indicating important changes in the assemblage of species that persisted in those landscapes.

The negative effect of deforestation and loss of connectivity on plants, pollinators, and their interaction networks was predicted (Tylianakis et al. 2010; Hipólito et al. 2012; Ferreira et al. 2013); however, to our knowledge, this is the first study to relate neotropical forest loss and connectivity to plant–pollinator networks. A previous study in Mexico discussed how the fragmentation of tropical forests affects the floral visitors of a single plant species, *Astrocaryum mexicanum* (Dáttilo et al. 2015); however, that study did not include a more comprehensive evaluation of the plant communities side of the interaction networks. Nevertheless, it showed that in Mexican tropical forests, fragment size positively influenced visitation rates, but did not affect the structure of the network comprised by *A. mexicanum* and its floral visitors, as the core generalist pollinator species remained stable (Dáttilo et al. 2015).

Another study showed that in the Brazilian savanna, the number of interactions was directly proportional to local habitat quality along with landscape heterogeneity (Moreira et al. 2015). In such landscapes, agriculture intensification and the availability of herbaceous vegetation fringing crops played an important role in determining the plant–pollinator network properties at larger scales (Moreira et al. 2015). There is evidence that pastures and open field physiognomies, in landscapes with high agricultural intensification,

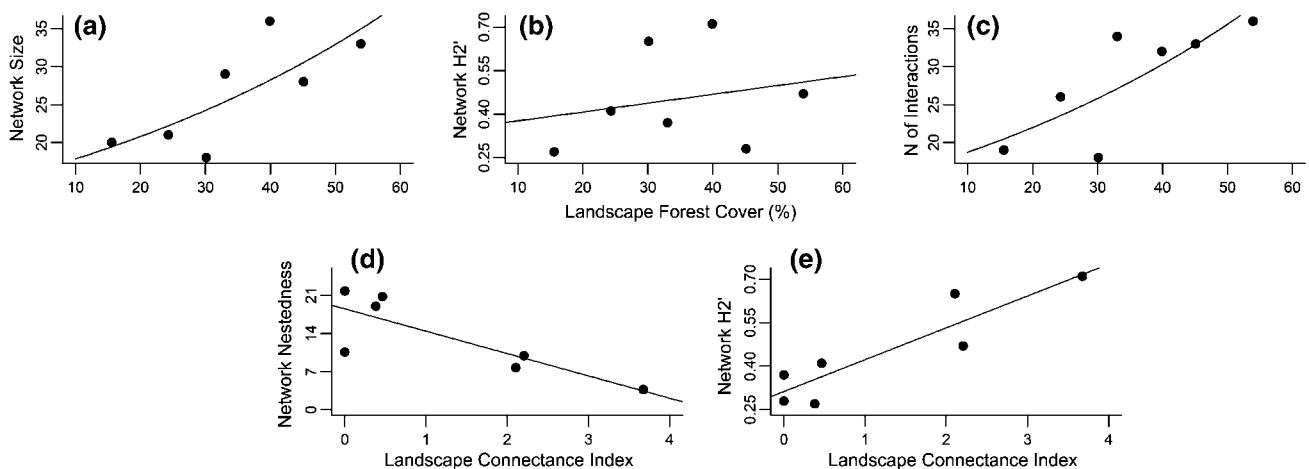


Fig. 3 Results of the best significant models of landscape explanatory variables effects on network structure, in seven fragmented landscapes on the Atlantic Forest in Bahia Northeastern Brazil. **a** Network size; **b** network complementary specialization H'_2 ; and **c** number of interactions in the networks were positively influenced by the per-

centage of forest in the landscapes. **d** Nestedness was negatively influenced by the landscape connectance index in a 50 m radius. **e** Network complementary specialization H'_2 was positively influenced by connectance index in a 50 m radius (CONNECT). Color version of this figure is available online

may also offer additional resources for bees and plants (e.g., Nery et al. 2018). In those landscapes, open environment areas offered a complementary source of resources for plants and bees and even in landscapes with low forest cover these areas may aid population-level landscape connectivity (Boscolo et al. 2017; Nery et al. 2018). When we consider that in the landscapes, we studied that the surrounding matrix was mainly composed of pastures with low flower availability, even along their edges, forest patches were probably the highest quality habitat available. Therefore, in the studied landscapes, forest cover is the most important factor to increase bee abundance, richness, and consequently plant–pollinator network size.

Studies on the effects of landscape changes on plant–pollinator interactions using approaches other than networks (e.g., Steffan-Dewenter and Tschardt 1999) have identified that the frequency of visits in small forest patches can increase in some plant species and decrease in others (Aizen and Feinsinger 1994a; Steffan-Dewenter and Tschardt 1999; Lopes and Buzato 2007). This occurs, because landscape changes create environmental filters by selecting plant species and associated pollinator functional groups able to persist in altered landscapes (Girão et al. 2007; Aizen et al. 2012). At the community level, both the number of interactions and pollination processes tend to be negatively affected by landscape changes (Aizen and Feinsinger 1994b), such as deforestation and connectivity loss.

Our results showed that in deforested landscapes, pollinator assemblages were composed mainly of few abundant bee species which performed most of the interactions in the network core, leading to lower nestedness and less specialization. These effects could be related to the loss of specialist plant and pollinator species and/or to changes in diet breadth of bees in response to resource availability (Burkle and Knight 2012; Weiner et al. 2014). We found that in deforested landscapes bee communities were a subset of the communities in landscapes with more forest. Moreover, specialist bee species were registered more frequently in landscapes with more forest cover (higher than 35%). For instance, the genera of bees *Ceratina* (*Crewella*), *Epicharis*, and *Osiris*, and the species *Chilicola kevani* became more abundant as forest cover increased. Although specialists seem to have been penalized by the loss of forest and no longer exist in those landscapes, generalist species may persist as forest cover decreased.

Differently from pollinators, plant assemblages replaced their species along the forest loss gradient, with not a single plant species occurring at all landscapes. Only two generalized plant species appeared in more than two landscapes, *Adenocalyma coriaceum* occurred in five landscapes and *Psychotria schlechtendaliana* in four landscapes. These changes in the plant assemblages also showed a trend of losing species with more specialized pollination requirements

as deforestation grows. Evidences of that trend were the losses of specialists such as *Ruellia affinis*, *Cordia superba*, and *Rauvolfia grandiflora* from the CAM 45% landscape, which were replaced by generalist plants in the networks in landscapes with less forest. Also, we observed a tendency of generalist plants to have a higher number of interactions in deforested landscapes, especially species from the Melastomataceae, Rubiaceae (*Psychotria hoffmannseggiana*, *Psychotria* sp.1, *P. martiana*), and Bignoniaceae (*A. coriaceum*) families.

Overall, there was a trend of both plant and bee species to take generalist roles with the reduction of the forest cover. For instance, the most generalist bees in networks were small and short-tongued, recognized as generalists in the use of their environments and floral resources (Michener 2007; Castro 2002; Mouga et al. 2015). In the studied landscapes, bee species tended to vary their behavior, playing a more specialist role and visiting one or two plant species in landscapes with more forest, but acting as a generalist visiting more plant species in landscapes with less forest (Fig. 2; Online Resources 2). For instance, bees such as *Partamona* sp. and *Euglossa* sp. increased the number of plants with which they interacted as the amount of forest in the landscape decreased. This result shows that generalist foraging behaviors seem to be increased by forest loss, possibly due to lower resource availability and diversity, as preferred plant species were no longer available. Similarly, species as *Chilicola kevanii*, unable to expand their diet breadth, seem to disappear as deforestation filter those specialists away. The core of remaining generalist bees included the nodes that may be holding all the interaction networks together, since, in less forested landscapes, generalist bee species may be able to keep visiting flowers and guarantee the reproduction of the plant species in these landscapes.

However, in all landscapes, we observed that plants with single links interacted with multi-linked generalist visitors, some of them expected to be inefficient pollinators (Fig. 2; Online Resources 2). In deforested landscapes, plants with more specific pollination requirements received more visits from generalized bees that may not be effective pollinators. This applies to plants with flowers that have long tubes, poricidal anthers, and heterostyly (for example *A. coriaceum*, *Solanum* sp., *Psychotria* sp., respectively). For instance, in the landscape with 15% of forest cover, *Solanum* sp. and the two *Miconia* species, which require strong bee vibration to release pollen from the anthers (Falcão et al. 2016; Brito et al. 2017) were visited mainly by generalist small and short-tongued bees that may not be efficient pollinators (Fig. 2; Online Resources 2). In the long run that may represent a problem for those plants' reproduction and for the reproduction of other plants that share pollinators. Additionally, lower pollinator diversity in less forested landscapes could decrease

network functional complementarity and pose negative effects on the reproductive success of plants, which in turn could affect the availability of resources for pollinators (Blüthgen and Klein 2011), resulting in negative cascading effects.

On the other hand, the specialist–specialist interactions registered, occurred with bee species known to be generalist in the use of resources elsewhere (Castro 2002; Wolowski and Freitas 2015), but that have performed a specialist behavior in these landscapes (*A. coriaceum* and *P. droryana* in NP 35%; a Poaceae plant species and *Trigona spinipes*; and *Solanum* sp. and *Rhectomia mourei* in UBA 30%). These interactions, however, do not represent truly specialized interactions nor are they beneficial to the plants. For instance, *A. coriaceum* need large bees to be efficiently pollinated (Alcantara and Lohmann 2010), Poaceae species are generally wind pollinated, and do not rely much on pollinators for reproduction (Wolowski and Freitas 2015), and *Solanum* sp. may not be efficiently pollinated by *Rhectomia mourei* (Falcão et al. 2016).

In the landscape with less remaining forest (15%), different pollinator populations may have been locally extinct in small fragments, leading to a critical situation for the reproduction of plant species that depend on pollinators that no longer occur there. As a consequence, there might still be floral resources for generalist visitors in these landscapes, but some plant species may no longer reproduce. Over time, this shall lead to negative ecological consequences for the maintenance of small forest fragments in the landscape. Conversely, higher amounts of forest may facilitate bee movements throughout the landscape, increasing overall pollen flow. In these better connected landscapes, more abundant and diverse floral resources would allow bees to select flowers in a more specialized way.

The general pattern of specialist species (plants and bees) interacting with generalist species also explains the observed nested plant–pollinator networks we found. The higher nestedness and lower specialization observed in more deforested regions may arise from more isolated smaller patches which support only generalist bees due to their better ability to access the remaining limited resources available. The nested structure might make networks more resilient to the loss of interactions and to the extinction of species with a few links (Memmott et al. 2004; Vázquez and Aizen 2004; Aizen et al. 2012). Nestedness is also expected to provide functional redundancy (but not necessarily functional diversity) and the possibility of alternative routes for system persistence if some of the interactions disappear (Bascompte et al. 2003; Bascompte and Jordano 2007). However, landscapes with higher nestedness are not necessarily better conserved. When comparing environmental quality gradients, higher nestedness can also be a result of network simplification (Soares et al. 2017).

We saw that networks become more nested, but simpler, in landscapes with less remaining forest, with generalist species being relatively more frequent and playing a more critical role in the network, since specialists interact mostly with these generalists (Ferreira et al. 2015; Newton et al. 2018). In landscapes with less forest, the most sensitive species have already disappeared, and the resilient or resistant species (usually the most generalist and frequent) tend to remain and interact more frequently among themselves. Our results agree with Aizen et al. (2012) where true specialist interactions remain only in continuous or large and well-connected forest patches. This probably happens, because landscape changes can affect floral resource availability modulating the foraging behavior of bee individuals (Kunin and Iwasa 1996; Souza 2014; Boscolo et al. 2017; Nery et al. 2018), emerging as landscape-level effects on the networks. Therefore, although forest loss can reduce bee populations (Ferreira et al. 2015), higher landscape connectivity could aid in rescuing the most sensitive species, leading to more specialized networks (Boscolo et al. 2017). Therefore, the proportion of rare species and the less frequent reciprocal specialist interactions in the networks could be important indicators of environmental quality, along with the diversity of species and the network structure itself (see Vázquez and Aizen 2004). In this sense, small networks with higher generalization level may indicate that landscape changes are significantly affecting tropical forest understory and associated key ecosystem processes, such as pollination.

Our results thus indicate that at higher levels of deforestation, species losses may lead to oversimplified plant–pollinator networks. Those networks may be more sensitive to environmental impact, and even small environmental changes could lead to their disruption. For instance, continuous losses of forest implicated in tree diversity reduction below the 30% threshold of forest cover in this region (Rigueira et al. 2013). Moreover, networks that are resistant to random loss of nodes may be very fragile to the extinction of the most well-connected generalist species. For example, a hypothetical loss of *P. shclectendaliana* and *T. braueri* in PTN 15% could lead to the local extinction of eleven other species, five bees, and six plants (see Fig. 2). We believe that when a system undergoes such structural simplification, a threshold situation may have been already reached. Although network nestedness had been considered as a positive characteristic, conferring greater stability or resilience, it is not positive when resulting from species or interaction loss, as in these landscapes. A simplified system is not desirable even if more stable or resilient (see Burkle and Knight 2012; Soares et al. 2017 for further discussion on network resilience). Anthropogenic landscape changes that promote species extinction might lead to sudden changes of pollination networks by affecting the most connected species (Kaiser-Bunbury et al. 2010). The studied networks would

be even more severely impacted by the loss of the most connected species.

Conclusions

We detected that forest loss and patch isolation affected the structure of plant–pollinator networks. In the studied landscapes, an interaction core provided by the generalist species is kept in the networks in situations of high reduction of forest area and increased isolation at the landscape level. However, the modifications in the structure of pollination networks may affect plant populations' performance and local persistence (Kunin 1997; Memmott et al. 2004) as a result of the reduced amount of forest imposing a shortage of resources even for the more generalist pollinator species. This may lead to unexpected and random specialist interactions that may end up in inefficient pollination. The lack of interactions between true specialist plants with true specialist bees (reciprocal specialist interactions) may indicate that all landscapes had already lost the most sensitive species, as highly specialized interactions are expected to be more sensitive to forest loss (Aizen et al. 2012).

In landscapes with less than a third of its area covered by forest, lower nestedness and fewer specialized interactions indicate that generalist species of bees and plants are the ones potentially able to keep the remaining networks. That may represent a fragile situation for plant and pollinators communities at the Brazilian Atlantic Forest, which presently encompasses only about 15% of its original extent, being highly threatened by anthropogenic activities, such as agricultural expansion and urban growth (Ribeiro et al. 2009). In summary, our data show that generalist species, even after the extinction of specialists, maintained the network core of cohesive interactions, keeping the network structure. However, networks were smaller, with fewer species and few reciprocal and truly specialist interactions in landscapes with scarce remaining forest. These results may indicate a tendency to a threshold of modification of the communities and patterns of interaction between plant species and floral visiting bees below 30% of forest in the landscape. Further studies in relation to the thresholds of species extinction as well as changes in patterns of interaction among species in tropical environments are strongly encouraged.

Our findings add a novel perspective to studies of plant–pollinator networks in fragmented landscapes, as we related effects of landscape structural changes with ecological interaction networks topography and structure, showing that forest loss can have nonlinear effects on plant–bee networks structure and community diversity. Interaction networks can also be indicators of the effects of changes in natural environments (Soares et al. 2017). The disruption of

rare mutualistic interactions and those between reciprocal specialists may signal future quick biodiversity loss. In this sense, these interactions should be the main focus of biodiversity monitoring and restoration programs. Finally, we found that network structure is simplified with forest loss. This change can have significant negative effects for pollinators and plant conservation and also for the maintenance of critical ecological processes, such as pollination.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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