



# Reconstruction and variability of tropical pollination networks in the Brazilian Atlantic Forest

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## Abstract

Loss of biodiversity comprehends not only the extinction of individual species, but also the loss of the ecological interactions among them. Survival of species, continuation of ecosystem functioning in nature, and ecosystem services to humans depend on the maintenance of well-functioning networks of species interactions (e.g. plant–pollinator networks and food webs). Analyses of ecological networks often rely on biased and incomplete survey data, especially in species-rich areas, such as the tropics. We used a network inference method to reconstruct pollination data compiled from a large tropical rainforest habitat extent. To gain insight into the characteristics of plant–pollinator interactions across the region, we combined the reconstructed pollination network with species distribution modelling to obtain local pollination networks throughout the area. We explored how global network properties relate to natural forest cover and land cover heterogeneity. We found that some network properties (the sum and evenness of link weights, connectance and nestedness) are positively correlated with forest cover, indicating that networks in sites with more natural habitat have greater diversity of interactions. Modularity was not related to forest cover, but seemed to reflect habitat heterogeneity, due to the broad spatial scale of the study. We believe that the methodology suggested here can facilitate the use of incomplete network data in a reliable way and allow us to better understand and protect networks of species interactions in high biodiversity regions of the world.

**Keywords** Blockmodels · Ecological networks · Species co-occurrence · Species interactions

## Introduction

The fast decline in biodiversity currently underway has been called the sixth mass extinction. The loss encompasses not only individual species, but also ecological interactions, often at a higher rate (Valiente-Banuet et al., 2015). Since many key functional aspects and services important for the maintenance of natural biomes and human subsistence depend on biotic interactions, species interactions should be treated as a major component determining the health of ecosystems. For example, plant–animal mutualistic networks,

such as pollination and seed dispersal, sustain terrestrial biodiversity and human food security (Hougnier et al., 2006; Burkle et al., 2017, Guimaraes Porto et al. 2021). However, pollinating insects are declining in many parts of the world because of human disturbances, especially habitat loss (Vanbergen & the Insect Pollinators Initiative, 2013), but also landscape simplification, population subdivision and consequent changes in behaviour and in interspecific interactions (Fischer & Lindenmayer, 2007). Around 70% of the 124 main crops consumed by humans depend on animal pollinators (Klein et al., 2007), and so do most flowering plant species in the wild (NRC, 2007), especially in the tropics (Rech et al., 2016).

Because no species is an island, effective conservation action must protect not only individual species, but the functioning of the whole ecological community, easily represented by the web of interspecies interactions (Tylianakis et al., 2010). This focus on relationships or interactions is at the heart of ecology as a science, and it is therefore not surprising that network tools and concepts have a long tradition in ecological studies (e.g. Elton, 1927). Although various

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interaction types act simultaneously (e.g. pollination combined with competition or seed dispersal, see Fernandez and Fonturbel 2021; Debnam et al., 2021), an important first step is to study homogeneous networks with a single interaction type (e.g. pollination). Studies dealing with species interaction networks often rely on biological survey data, sometimes originally obtained with different goals in mind. These data typically suffer from observation errors, incomplete and biased sampling, particularly when dealing with large geographic extents and species-rich systems. Network inference techniques can help in the reconstruction of incomplete data (Pichler et al., 2020; Young et al., 2019), to identify motifs (Simmons et al., 2019) and key components of complex systems (Kovács-Hostyánszki et al., 2019; Pereira, 2018; Pereira et al., 2017, 2022). Novel algorithms allow us to get data from novel resources (Thouverai et al., 2021), reveal hidden patterns also at large scales (Podani et al., 2014) and gain further insight into ecosystem functioning, and hopefully build better conservation strategies.

In this study, we sought to: (1) construct local plant–pollinator networks across a highly impacted tropical rainforest habitat; (2) examine some structural network properties; and (3) explore how network structure relates to natural forest cover and land cover heterogeneity. For this, we used a database on plant–insect flower visitor interactions from the Atlantic Series data papers collection. We predict that the number of species, number of links, sum and evenness of link weights, connectance and modularity will increase with forest cover, while nestedness and centralization will decrease.

## Materials and methods

### Study area

The neotropical Atlantic Forest is a hotspot of biodiversity that originally covered more than 1.5 million km<sup>2</sup> along the Atlantic coast of South America, including a wide variety of environmental conditions. As a result of centuries of anthropogenic pressure, it has been reduced to around 12% of its original extent and subsists today almost exclusively in small fragments (< 100 ha) (Ribeiro et al., 2009), mostly occupied by pasture and crops (Mapbiomas 2018 data; Souza et al., 2020). Land cover heterogeneity is highest at areas of intermediate forest cover. We divided the Atlantic Forest domain (sensu Ribeiro et al., 2009) within the national continental borders of Brazil in local sites, using hexagonal grids in three scales: 25, 50 and 100 km of site length in the N–S direction, using Albers projection to ensure equal area to all sites, with SIRGAS 2000 datum, in QGIS version 3.4 (QGIS.org, 2020). To each local site (at each scale) corresponds a local plant–pollinator interaction network.

### Building plant–pollinator networks

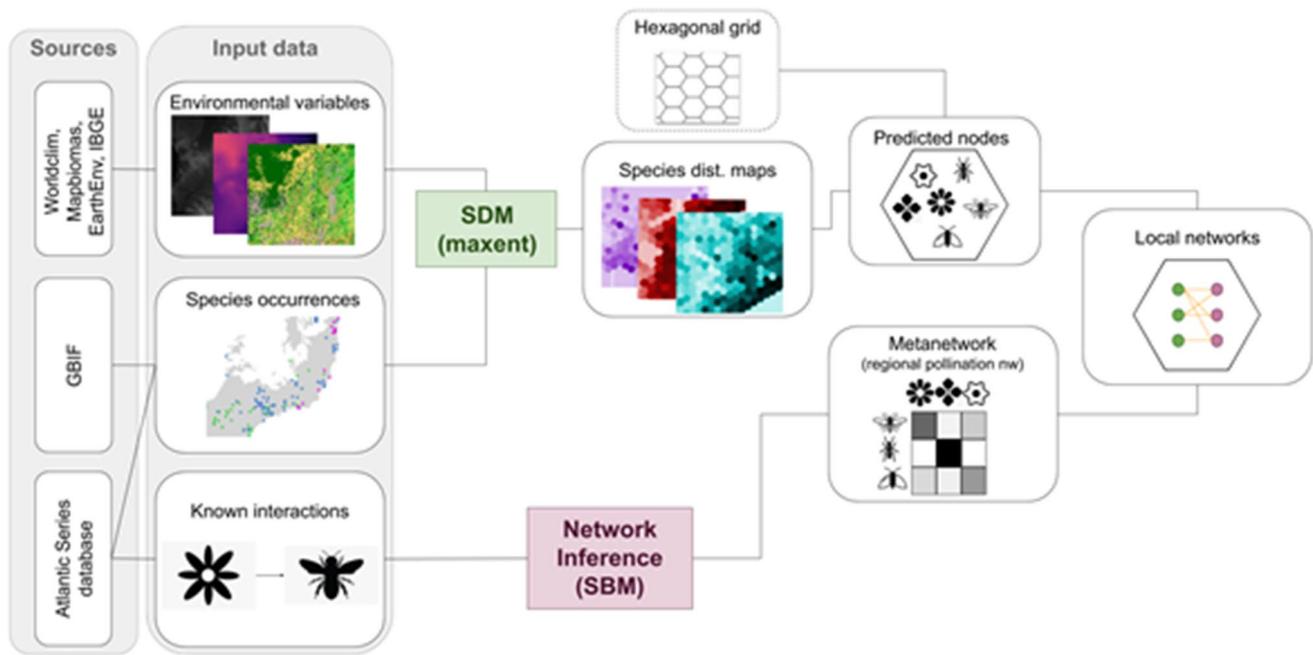
The local interaction networks corresponding to each site combine information on species interactions in general (for methodological challenges, see King et al., 2013) and spatial co-occurrence locally. Following the approach by Marjakangas and colleagues (2020), we first need to obtain these two types of networks separately and then multiply them to obtain the local networks (Fig. 1).

### Interaction network reconstruction

For the regional network of interactions, we used the Atlantic Plant–Insect database, a compilation of georeferenced interaction events observed between plants and insect flower visitors across the Brazilian Atlantic Forest (in prep.; see the complete Atlantic Data Papers series at [https://esajournals.onlinelibrary.wiley.com/doi/toc/10.1002/\(ISSN\)1939-9170.AtlanticPapers](https://esajournals.onlinelibrary.wiley.com/doi/toc/10.1002/(ISSN)1939-9170.AtlanticPapers) and at [https://github.com/LEECLab/Atlantic\\_series](https://github.com/LEECLab/Atlantic_series)). We kept only observations with classification at the species level, within the Brazilian territory and the Atlantic Forest domain. This comprised our initial regional pollination network, or *metanetwork*, with 1273 species (nodes) and 2895 unique interaction pairs (links). We emphasize that local networks describe the communities in the hexagons, while the metanetwork describes the unified plant–pollinator community of the whole region.

As is the case with most empirical networks, sampling of interactions in biological surveys is incomplete in our dataset. Studies show that sampling bias tends to strongly underestimate the number of interactions and overestimate the degree of specialization (Young et al., 2019). To obtain a more reliable picture of pollination interactions across the Atlantic Forest, we applied a method of network reconstruction based on stochastic blockmodels to our metanetwork. Blockmodels are generative models for networks (DiMaggio, 1986), where nodes are classified into blocks according to their profile of interactions. Probabilities are used to describe interactions between blocks. The model is visualized as a block matrix (see Supplementary material Fig. 1 for an illustrative example).

A block matrix can be used to draw network samples. Conversely, we can fit a block matrix to a known incomplete network and, as a second step, infer missing links and network structure based on the blocks and probabilities, in order to reconstruct the network. We did this using the python package *graph-tool* (Peixoto, 2014), which uses Bayesian inference to extract the underlying optimal block structure. First, we fitted a nested stochastic blockmodel to our binary metanetwork. Next, we reconstructed our



**Fig. 1** Reconstruction of local pollination networks from occurrence records of species and interactions

metanetwork using the fitted blockmodel as prior. We used the function `UncertainBlockState`, adequate for cases in which we do not have repeated measurements of each link but can offer extraneous error estimates as independent edge probabilities (Peixoto, 2014). This applies well to our case, because the data are a compilation from many different studies, with different geographical extents, methods of survey and research questions, so that the numbers of observations recorded for each pair are not comparable. We used three error estimates: First, for all forbidden links (i.e. plant–plant or pollinator–pollinator links), we set the uncertainty value to 0, indicating our previous knowledge that these links do not exist. Secondly, we must choose an uncertainty value for the observed links. After testing different values ranging between 0.75 and 0.99, we chose the value 0.98, because it resulted in the best reconstructed network (no forbidden links were created, and the maximum number of the original links was kept). Thirdly, for each non-edge (non-observed plant–pollinator links), we picked a value chosen to preserve the expected connectance of the original network (see Supplementary Material for the code and further details). The resulting reconstructed local networks had 49,406 links, none of which were forbidden, and had lost only 2 of the original edges. Each resulting link has a weight corresponding to its posterior probability (e.g. the probability that this edge exists), which we interpret as the potential of interaction between species.

## Co-occurrences and local networks

We performed species distribution modelling with Maxent to predict the occurrences of species in each site, using the R package `ENMeval` (Muscarella et al., 2014). As labeled data, we included the georeferenced interaction points from the pollination dataset, complemented by additional species occurrence points from the Global Biodiversity Information Facility (dataset available at <https://doi.org/10.15468/dl.by6nuj>; GBIF.org, 2018) filtered with the R package `CoordinateCleaner` (Zizka et al., 2019). We removed any point records of the same species located within the same 1 km × 1 km raster cell of environmental covariates used in the model to avoid causing bias in the distribution modelling. Only species with at least 5 occurrences were included in the analysis. The environmental factors reported to affect plant and insect distributions the most are temperature, precipitation and soil type (Savopoulou-Soultani et al., 2012). For this reason, we used as explanatory environmental variables topographic, soil, climatic and land cover covariates, with final resolution of 1 km (Supplementary Material Table 1). For background points, we used the weighted-target group approach (i.e. occurrence points of all plant or pollinator species other than the one being modeled), which reduces the influence of sampling bias (Muscarella et al., 2014). We selected models with  $\Delta AICc = 0$  and secondarily with maximum AUC on testing data. As final output, we chose the cumulative output maps, which can be interpreted in terms of omission rate, i.e. thresholding the map at a value  $c$

to binarize it into prediction of presence or absence of the species would omit approximately  $c\%$  of presences. We discarded local models that performed poorly ( $AUC < 0.7$ ) and were left with 389 species (297 plants and 92 pollinators, Supplementary Material Table 2). Of these, 223 species' distributions are positively correlated with natural forest cover (%). Since dominant, generalist species (*Apis mellifera*, *Trigona spinipes*, *Bombus morio* and *Plebeia droryana*) are richly connected, they are strongly represented in network analysis, "masking" the network positions and roles of potentially interesting, rare, often specialist species. For this reason, we did not consider them, making it possible to look at the fine structure of the rest of the community and have a quantitative view on the rest of diversity and community structure. This approach has clear disadvantages (i.e. the most important species are not present) but also opens a way to better evaluate others (neighbourhood similarity and redundancy in the community). The absence of the most important species in our networks could considerably alter their structure and mask some of the properties' correlations we expected to find. Therefore, we decided to proceed with the analysis considering, in parallel, networks with all 389 species (all-spp networks) and networks only with the 223 forest species (forest-spp networks) and compare these results. This study is focused on plants and pollinators and explicitly on their interactions in space. We emphasize that the conservation priorities we suggest are relevant only for maintaining pollination as an ecosystem function, but it is also clear that there are many other species important for the maintenance of other ecological processes.

From the SDM maps of cumulative occurrence probability, we computed the average occurrence probability of each species in each site, at each scale. In order to interact, two potentially interacting species must co-occur in space (Tylianakis et al., 2010). Therefore, we multiplied the average occurrence probability of all plant–pollinator pairs for each site, to obtain the local probabilities of co-occurrence. Next, we multiplied the probability of co-occurrence of each plant–pollinator pair in each site by the probability of interaction of the pair according to our pollination metanetwork. In this way, we obtained local pollination networks for each site, with probabilistic link weights, at each scale. We did this including all the 389 species for which SDM was successful (all-spp networks) and then repeated it including only the species whose spatial distribution is positively correlated (Spearman's  $\rho > 0$  with  $P < 0.05$ ) with natural forest cover (forest-spp networks).

### Linking network properties with forest and land cover heterogeneity

For each scale, for all-spp and forest-spp networks, we computed measures that provide a quantification of network properties relevant to particular ecological functions:

- (1) number of plant and pollinator nodes, or species ( $N_{pl}$ ,  $N_{po}$ );
- (2) number of links ( $L$ );
- (3) sum of link weights ( $S$ ), informing about the general intensity of interactions in the community;
- (4) evenness of node strengths ( $HS$ ) for plants ( $HS_{pl}$ ) and pollinators ( $HS_{po}$ ), measured by Shannon entropy, where node strength is the sum of the weights of the links connected to it;
- (5) weighted connectance (density), which quantifies how many links are present, in comparison with all possible links, taking weights into account ( $C$ );
- (6) centralization, which shows how much the links are centralized on one or a few nodes, based on eigenvector centrality (Centr; Freeman, 1978);
- (7) bipartite modularity, which shows how much the network is compartmented into dense groups of nodes called modules, using the method by Beckett (2016) ( $M$ );
- (8) number of modules ( $Nb_{mod}$ );
- (9) assortativity based on node strength, which shows how much nodes tend to connect with others of similar strength ( $A$ ); and
- (10) nestedness, which shows how much the neighborhoods of specialist species are subsets of the neighborhoods of generalists, using the spectral radius index and row column totals average null model (Nest; Beckett et al., 2014; Mariani et al., 2019). The use of this null model for the computation of nestedness is important to capture only nestedness beyond what is explained by degree (Lewinsohn et al., 2006).

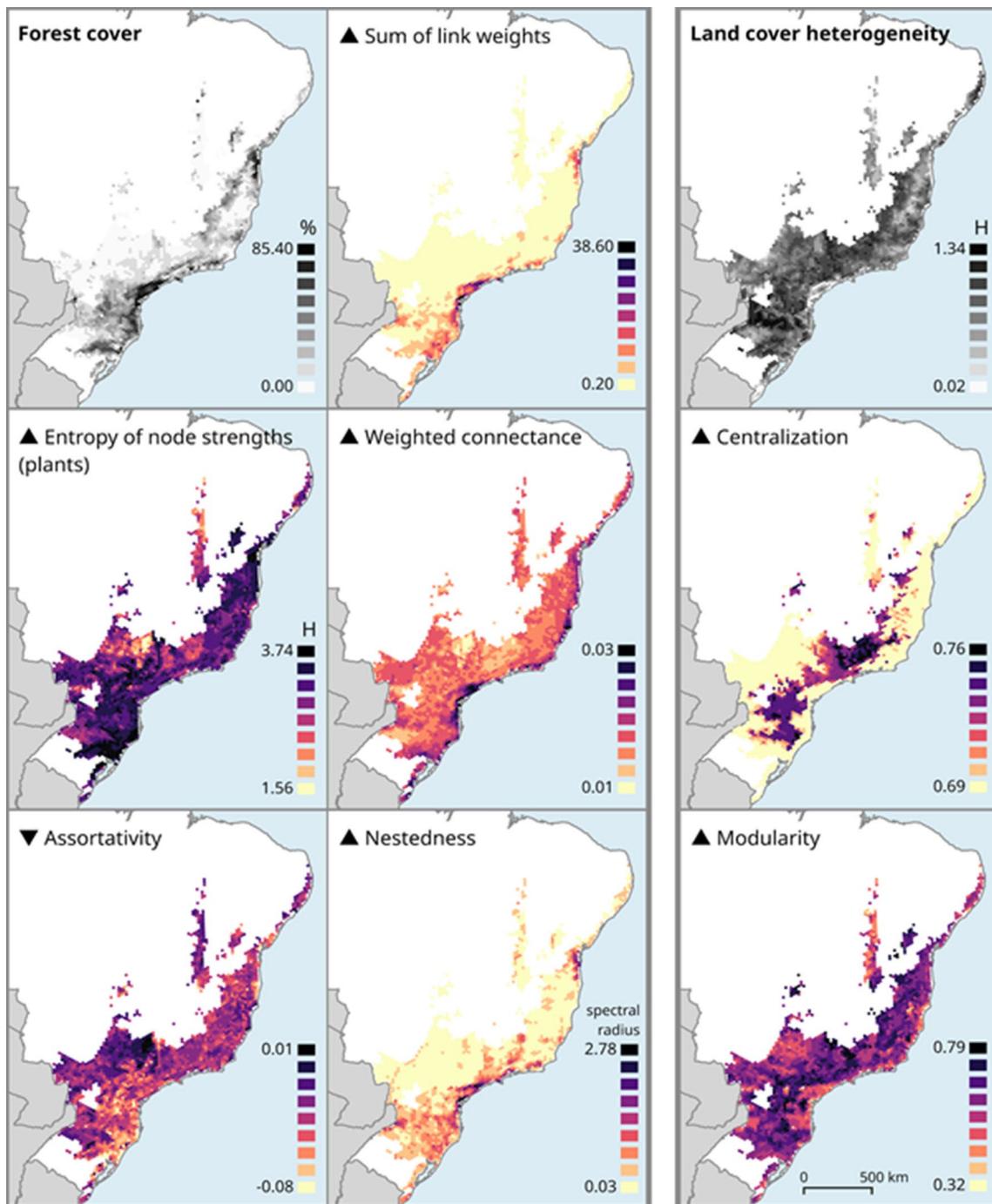
Finally, we tested the correlation of each of these network properties with forest cover (%) and land cover heterogeneity (HLC, Shannon entropy of land cover categories per site) using Spearman's rank correlation. These computations were made using the packages *igraph* (Csardi & Nepusz, 2006), *bipartite* (Dormann et al., 2008), *vegan* (Oksanen et al., 2019) and *Falcon* (Beckett et al., 2014) in R (R Core Team, 2020) with RStudio (RStudio Team, 2019).

## Results

Investigating our local pollination networks at the most detailed scale (25 km), we found that degree and node strength were positively correlated (mean Spearman's  $\rho = 0.57$  and  $0.56$  for all-spp and forest-spp networks, respectively) in agreement with Bascompte et al. (2006). Most link weights were small (average link weight between 0.01 and 0.22 for all-spp and between 0.02 and 0.36 for forest-spp networks). Connectance and assortativity were always below 0.04 (Supplementary Material Table 3), while centralization was between 0.75 and 0.80 for all-spp and 0.66–0.74 for forest-spp networks. Modularity was always positive, and the majority of modules are nested (75.07% in all-spp and 75.04% in forest-spp networks, on average). Nestedness was not correlated with the number of links ( $P = 0.18$  and Spearman's  $\rho = -0.07$  for all-spp and forest-spp, respectively).

We observed similar correlations between network properties and forest cover or land cover heterogeneity, independently of scale (Supplementary Material Table 4 and Fig. 2). In some cases, correlations became stronger with increasing site area (e.g. sum of link weights, evenness of node strengths ~ forest cover in forest-spp networks), while in other cases they became weaker (e.g.

connectance ~ forest cover in forest-spp network). In most instances, the tendencies were also similar between all-spp and forest-spp networks. We observe clearer tendencies in the forest-spp networks: network size (N and L) and centrality appear particularly related to land cover heterogeneity, while the sum of link weights (S), evenness of node strengths (HS), connectance, nestedness and assortativity



**Fig. 2** Pollination network properties correlate to habitat variables. Some network properties are more strongly correlated with forest cover (left) and others with land cover heterogeneity (right), positively (▲) or negatively (▼). Networks of forest species on sites of 25 km are shown

**Table 1** Network properties' correlation with forest cover and land cover heterogeneity were independent of spatial scale.

		$N_{pl}$	$N_{po}$	$L$	$S$	$HS_{pl}$	$HS_{po}$	$C$	Cent r	$M$	$A$	Nest
all-spp	Forest cover	-0.35 ▼	-0.35 ▼	-0.36 ▼	0.27 ■▲	0.09 ■	0.32 ▲	0.19 ■▲	0.36 ▲	-0.12 ■▼	n.s. ■	0.22 ■▲
	HLC	-0.08 ■	-0.46 ▼	-0.44 ▼	-0.14 ■▼	n.s. ■	n.s. ■	n.s. ■	0.46 ▲	n.s. ■	n.s. ■	-0.09 ■
forest-spp	Forest cover	n.s. ■	-0.27 ■▼	-0.25 ■▼	0.78 ▲	0.58 ▲	0.56 ▲	0.33 ▲	0.21 ■▲	0.17 ■▲	-0.60 ▼	0.66 ▲
	HLC	n.s. ■	-0.47 ▼	-0.48 ▼	0.18 ■▲	0.16 ■▲	0.12 ■▲	-0.17 ■▼	0.47 ▲	0.25 ■▲	-0.11 ■▼	0.10 ■

$N_{pl}/N_{po}$  number of plant/pollinator species,  $L$  number of links,  $S$  sum of link weights,  $HS_{pl}/HS_{po}$  entropy of plant/pollinator node strengths,  $C$  weighted connectance, Centr: centralization based on eigenvector centrality,  $M$  bipartite modularity,  $A$  assortativity,  $Nest$  spectral radius index of nestedness. Values are average Spearman's rho correlation index across three scales (site N-S length of 25, 50 and 100 km) for all-spp and forest-spp networks. The symbols show positive i.e.  $\rho > 0.3$  (▲), negative i.e.  $\rho < -0.3$  (▼), weak positive i.e.  $0.1 < \rho < 0.3$  (■▲), weak negative i.e.  $-0.3 < \rho < -0.1$  (■▼) or no correlation i.e.  $-0.1 < \rho < 0.1$  or  $P > 0.05$  (■). When at least two out of the three correlations were non-significant, we show them as *n.s.* When one of the three was non-significant, we show the smallest absolute significant value. Cases of opposite correlation between all-spp and forest-spp are highlighted in grey

are shown to be more related to forest cover. These patterns are not very clear when we look at all-spp networks. Modularity and the number of modules showed weak to no correlation in all cases, although modularity seems more related to land cover heterogeneity than to forest cover, when looking at forest-spp networks.

We concentrate now on the average correlation across the different scales for each situation (Table 1). All-spp networks are smaller (few species,  $N$ , and interactions,  $L$ ) both with increasing forest cover and land cover heterogeneity. Forest-spp networks' sizes seem more related to land cover heterogeneity (HLC), and the smaller size is only due to fewer insect species. We observed that only high forest cover sites are characterized by networks with higher  $S$ , while  $L$  is basically independent of forest cover (Supplementary Material Fig. 3). In fact, looking at forest-spp networks, it is clear that high forest cover sites have networks with stronger (although not necessarily more numerous) links (sum of link weights and weighted connectance), as well as more evenly distributed link strengths (HS). Nestedness increases and

assortativity decreases with forest cover, for forest-spp networks. No clear trend is visible for all-spp networks. Centralization, on the other hand, seems more associated with land cover heterogeneity (HLC, Table 1, Fig. 2).

There are two cases in which forest-spp and all-spp networks show opposite results, both involving only very weak correlations. First, modularity seems to decrease with forest cover for all-spp and increase for forest-spp networks. We should however keep in mind that, for forest-spp, modularity was more associated with land cover heterogeneity (HLC) than with forest cover (Supplementary Material Table 4). Secondly, the sum of link weights ( $S$ ) in function of land cover heterogeneity (HLC) decreases for all-spp, but increases for forest-spp. That is, in homogeneous sites, networks of forest species have weaker links, and networks of all-spp have stronger links. It is interesting to note that most homogeneous sites in the study area are occupied by agriculture rather than forest.

## Discussion

In general, sites with large and continuous natural forest host more species and interaction links than deforested or fragmented areas (Marjakangas et al., 2020). Yet, in order to better understand the functioning of both natural and human-impacted forest communities, we need to better understand the principles of their interaction networks, and whether they contain fewer species or interactions. Since our local networks are the result of multiplying two networks with probabilistic links (co-occurrence and potential of interaction), the weights of most links are extremely small, while nodes' strengths and link weights are rarely equal to zero, making both the number of species,  $N$ , and the number of links,  $L$ , very high. Especially in sites with little forest cover, the distribution of interaction weight was quite biased, with a large number of almost zero weights. Therefore, although the number of nodes and links seems to decrease with forest cover, these values carry little meaning in our context. Instead, it is by looking at node strengths (sum of link weights,  $S$ , and evenness of node strengths,  $HS$ ) that we can observe relevant patterns. Indeed, network size may be strongly affected by sampling effort (Ings et al., 2009) and should be regarded with care. Moreover, habitat disturbance may affect link weights more than species richness, as observed for host–parasitoid networks (Tylianakis et al., 2007). Link weights play an important role in stability, with many weak and few strong links, as we observe here, being commonly observed and leading to stable but potentially complex webs (Jordano, 1987). We have found the sum of link weights to be higher in more forested sites. The decrease in interaction richness is generally expected where there is loss of habitat (although rewiring may lead to exceptions, Valiente-Banuet et al., 2015). We have also found node strengths to be more evenly distributed in sites with high forest cover, in agreement with Tokumoto (2015). This may be due to the fact that networks in degraded or fragmented areas rely more heavily on super-generalist species such as the honeybee *Apis mellifera* (Rathcke & Jules, 1993), which have disproportionately high node degree and strength, through establishing a large number of weaker links, and thus increasing interaction asymmetry (Tylianakis et al., 2010). The centralization index did not indicate the same tendency, being instead larger for high land cover heterogeneity. The exclusion of the most generalist species from the analysis may lead to either quantitative (see centralization and forest cover) or qualitative differences in the results (reversed sign for correlations, see modularity and forest cover). We have nevertheless observed high absolute values of network centralization (expected in pollination webs: Martín González et al., 2010), especially in the all-spp networks, indicating that species indifferent to or negatively

associated with forest increase network centralization in our system. The difference between the two approaches (all-spp vs forest-spp) can be considered as providing a more general vs more forest-specific description for the system.

Networks in more forested areas had also higher connectance, in agreement with Morales and Vázquez (2008). High connectance is reportedly associated with stability in mutualistic networks, both in the sense of robustness to the loss of species and fast return to equilibrium after perturbations (Thebault & Fontaine, 2010). Connectance may be strongly influenced by sampling effort, but we could observe a clear correlation, possibly due to network reconstruction.

Nestedness is very common in plant–animal mutualistic networks (Bascompte & Jordano, 2007), especially when coevolutionary selection is weak (Segar et al., 2020). Some studies report nestedness to be robust to sampling effort (Bascompte & Jordano, 2007; Casas et al., 2018), although there are exceptions (Trøjelsgaard & Olesen, 2013). Nestedness has been reported to increase with the number of links in a study with binary networks (Bascompte et al., 2003). Conversely, we did not observe any correlation between these network properties, possibly because we used weighted measures. Nestedness reflects a network structure where many specialist species are reliant on a few persistent generalist species (Segar et al., 2020) and may be generated by differential dispersal, abundance, spatial distribution or similar ecological processes (Lewinsohn et al., 2006). An advantage of nestedness is that it facilitates successful responses to perturbation (Jordano, 1987): in a nested network, it is unlikely that a species ends up isolated, unless it is a very poorly connected species, whose loss will not strongly affect the functioning of the network (Tylianakis et al., 2010). Moreover, the pattern of generalist-with-specialist links provides ways for rare species to persist for a longer time (Bascompte et al., 2003). We found a clear relationship between nestedness and forest cover only when considering forest-spp only. This is quite intuitive, suggesting that forest-living species develop more specialized interaction systems, cross-connected by the more generalist species. Some studies suggest that nested networks, being more resilient, are associated with areas that suffered high impact or very variable climate (Tylianakis et al., 2010), while others report the opposite. For example, Dupont and collaborators (2009) found pollination networks in lower latitudes to be more nested. We found nestedness to increase with forest cover, agreeing with the latter. In any case, the Atlantic Forest as a whole has suffered severe anthropogenic disturbance, and even sites that still retain a large proportion of natural forest today are affected by environmental degradation and fragmentation, and host more resilient communities which are quite different from those of pristine areas (Marjakangas et al., 2020).

Plant–animal mutualistic networks have been reported to be disassortative, which makes the entire network more

resistant to secondary extinctions (Jordano, 1987). One study found mutualistic networks to be more disassortative where there is more connected natural habitat (Tokumoto, 2015), and another where habitat is more fragmented (Morales & Vázquez, 2008). Our results are in line with the former. Disassortativity is also correlated with nestedness (Tylianakis et al., 2010), as we have observed.

For mutualistic networks, modularity is associated with instability, because it means reduced functional redundancy, increasing the chances of secondary extinctions (Dalsgaard et al., 2013). Nevertheless, while one-to-one specialization is extremely rare in mutualistic communities (Jordano, 1987), more specificity in large networks may lead to the formation of separate groups, leading to high modularity (Olesen et al., 2007). Three main explanations have been proposed for modular structure in mutualistic networks. First, modular networks may, in view of this structural fragility, be associated with areas of great environmental stability, which have been left undisturbed for long periods (Dalsgaard et al., 2013). This is because, in such areas, modules corresponding to coevolutionary units with convergent traits (e.g. pollination syndromes; Jordano, 1987) and/or phylogenetically close species (Bascompte & Jordano, 2007) have had the opportunity to evolve unperturbed (Dalsgaard et al., 2013). Tropical habitats are an example of that, with their slow Quaternary climate change, and rich networks associated with high specialization (Dalsgaard et al., 2011). In accordance with this, we found relatively high modularity values in our networks. However, we did not find a strong correlation between modularity and the quality (forest cover) of sites, probably because of the history of high environmental impact in the region, affecting even the most preserved habitat fragments. Secondly, modular structures may be due to the loss of native supergeneralists (Tylianakis et al., 2010), possibly caused by the presence of highly competitive alien species like the honeybee (Valido et al., 2019). Although we know the honeybee and a few native supergeneralists are present in our study area, we were unable to include these species in our analysis because of poor performance of SDM modelling, probably due to their ubiquity. Finally, modularity may also reflect habitat heterogeneity (Tokumoto, 2015), divergent selection regimes, and phylogenetic splits or clustering of closely related species (Olesen et al., 2007), giving rise to compartments that are more perceptible at a large scale or regional level (Lewinsohn et al., 2006). Due to the coarse spatial scale of our study, it is likely that the modules we found are best accounted for by habitat heterogeneity (e.g. species associated with forest and farmland species coexisting in the same site, but in fairly separate parts of the network). Indeed, the highest correlation we obtained for modularity was with land cover heterogeneity for the forest-living species. This suggests that an intuitively understandable relationship is masked, again, by generalist

species that are less sensitive to the actual land cover. Concerning modularity and forest cover, we have seen contrasting results: they are negatively correlated for all-spp networks and positively for forest-spp only. This could be an indication that the non-forest species create bridges between modules of forest species in forested sites, decreasing modularity, and create modules of their own in other sites.

Nestedness and modularity may show opposite geographical patterns, but they are not necessarily mutually exclusive, appearing together especially in large (> 150 species) networks (Lewinsohn et al., 2006). Often modular networks may be nested as a whole and have modules that are themselves nested (Lewinsohn et al., 2006), as we have observed. Such networks may be structured as a core of generalist species that connect modules to each other (Olesen et al., 2007). This structure can be a result of specializations that confine species in modules, while within modules nestedness can emerge (Lewinsohn et al., 2006).

Our work sought to propose a methodological strategy to reconstruct interactions networks in high-diversity regions with incomplete sampling, and to present an example case study exploring the relationship between network structure, forest cover and land cover heterogeneity in the Atlantic Forest. Our results call for some considerations and suggest some avenues for future investigations. First, pollination networks are highly dynamical in species composition and interactions through time. Interactions may also change with location (Lewinsohn et al., 2006), depending on the assemblage and conditions of each habitat site. Similarly, rewiring may occur in ecological networks, increasing resilience even in the face of species loss (Vizentin-Bugoni et al., 2020). However, the structure of the network (e.g. connectance, nestedness, modularity, centralization) remains fairly constant (Dupont et al., 2009). Therefore, although in this study we have not examined how networks change over time, the results concerning network structure should still be valid. Moreover, we used probabilistic links along with network reconstruction, which should signal the possibility of connections that did not exist at the time or place of sampling but may arise via rewiring. In further investigations involving network dynamics, node and module level properties, time series network data would be most valuable, and we would encourage field surveys in this direction. Secondly, our networks are based on potential species distribution, i.e. they are built on abiotic factors, such as climate, land cover and topographic variables. Here we focused on interaction similarity and explored the advantages of blockmodelling but it is an important direction for future work is to include species interactions themselves and their phylogenetic history in the modelling of species distribution (Carnaval et al., 2014), leading to more realistic networks. Finally, flower visitation webs, as the ones used here, may give an inaccurate impression of pollination interactions, because flower

visitors can exhibit specialist behaviour when collecting pollen but generalist behaviour when collecting nectar (Ings et al., 2009). New sampling techniques and molecular methods may hopefully bring a breakthrough here with better data.

## Conclusion

Networks of species interactions need to be targeted for conservation, because the long-term survival of species in the wild, as well as ecosystem functioning and services, depend on biotic interactions. In species-rich regions like the tropics, complete and detailed network data over large geographic extents is often rare. We have shown how network reconstruction, combined with species distribution modelling, can be used to infer local interaction networks in a tropical rainforest habitat. We have examined how some global network properties correlate with forest cover and land cover heterogeneity, finding that nestedness and the sum of interaction strengths are strongly associated with greater forest cover. We believe that our results bring further insight into the structure of pollination networks across the Atlantic Forest, which is important for conservation planning focused on ecological interactions. We hope our work can be helpful for further studies aiming to understand and protect species interaction networks, particularly in regions of the world where the very wealth of biological diversity that motivates conservation action also makes it difficult to obtain complete data.

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**Data archive** We intend to archive our data on the institutional website of the first and last author (Department of Network and Data Science, Central European University).

## Declarations

**Conflict of interest** The authors declare no conflict of interest.

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