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Short Note

# Priority areas for protection of plant-pollinator interaction networks in the Atlantic Forest

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ABSTRACT

Quantitative methods of prioritization are necessary to optimize the selection of protected areas for biodiversity conservation. Reserve selection is traditionally based on single species, considers representative habitats or, occasionally, spatial configuration but mostly the needs of the society. However, protecting particular species as independent entities is not enough to ensure effective conservation of ecological communities, since their functioning depends on the interactions between species. We propose a strategy to identify priority areas for protection based on species interaction networks. Similar local networks are grouped according to two different sets of network features: interacting species pairs and overall network structure. These groups or clusters of networks are used to delimitate ecological subregions, which are then compared to current nature reserves. Subregions with a lower proportion of protected area are given higher priority. Results from species pairs and network structure are finally combined to obtain the *network protection priority index*. We present a case study applying this strategy to the Brazilian Atlantic Forest, using plant-pollinator networks. We found that subregions based on network structure show a more grainy pattern, and approach spatial patterns related to forest formation types, while subregions based on species pairs show more distinct patches and a higher level of detail in the division, especially for interior forests. Highest priority is given to portions of the seasonal semi-deciduous and deciduous forest, especially NE São Paulo, NW Paraná, N Rio Grande do Sul and E Minas Gerais and, secondarily, W São Paulo and the São Francisco region. The approach we suggest here goes beyond the level of species, seeking to perpetuate the ecological interactions and networks that make up biological communities. It is our hope and conviction that this strategy contributes to the development of more effective conservation planning.

## 1. Introduction

The loss of biodiversity our planet is experiencing at present has been compared to prehistoric mass extinctions in rate and amount (Barnosky et al., 2011). Among the most important strategies used to curb and reverse this trend are the designation of protected areas to preserve remaining habitat (Margules and Pressey, 2000), restoration efforts to recover lost habitat (Miller and Hobbs, 2007) and linking remaining habitat patches by ecological corridors (Krosby et al., 2010). In the face of limited resources for conservation and competition with other land uses, it is necessary to carefully select which areas to set apart for protection or restoration. Quantitative methods of prioritization are helpful in optimizing such choices. Criteria used in prioritization for reserve design range from representativeness or diversity of species (or other conservation features) to social and economic concerns, and spatial configuration (Pereira, 2018). In the case of representativeness and diversity, we frequently see individual species, sets of species, or habitat types as criteria (Margules and Pressey, 2000; Pereira et al., 2017; Pereira and Jordán, 2017; Williams et al., 2005). However, biodiversity loss encompasses not only species, but also ecological interactions, often at a higher rate (Kovács-Hostyánszki et al., 2019; Valiente-Banuet et al., 2015). Many key functional aspects and services important for the maintenance of natural biomes and human subsistence depend on biotic interactions, therefore they should be treated as a major criterion in reserve selection and design (Okuyama and Holland, 2008; Tylianakis et al., 2010; Valiente-Banuet et al., 2015).

We suggest that species interaction networks may be used as a basis for selecting priority areas for protection and restoration. Networks represent the complex interactions among coexisting species, offering multiple features we could look at. From the point of view of

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conservation, two sets of network features may be of special interest: (1) global network structure and (2) pairwise interspecific interactions. Network structure considers only the topology of the network, without taking into account what species are present and what position they occupy. This is important because network structure is related to function, can be altered by environmental drivers, and may have important ecosystem-level consequences (Tylianakis et al., 2010). However, even networks with similar structure may include different species or interaction pairs. The loss of interactions may have pervasive effects accelerating the local extinction of species and decay of ecosystem functions (Valiente-Banuet et al., 2015). Therefore, we include pairwise interactions as a second feature to be considered. Based on structure and linked species pairs, we describe the diversity of networks found in a given region and assign protection priorities with the goal of representing that diversity. For this, we define a *network protection priority index*, which ranks locations according to priority.

In this study, we introduce the suggested strategy with a case study in a tropical rainforest habitat, using pollination networks. This approach considers only a subset of species and one interaction type out of many, but the intimate pairwise relationship between plants and pollinators has been shown to be of crucial importance. We (1) group local plant-pollinator networks to define subregions according to network structure and pairwise interactions; (2) examine the level of coverage of network subregions by current protected areas; and (3) define priority areas for protection targeting the conservation of pollination networks.

## 2. Material and methods

### 2.1. Study area and data

The Atlantic Forest (AF) is a hotspot of biodiversity, originally extending through more than 1.5 million km$^2$ along the Atlantic coast of South America (Ribeiro et al., 2011). The Atlantic Forest may be regarded as an island, because it is isolated from other large forest tracts by a corridor of open or semi open formations, namely Cerrado, Chaco and Caatinga (Ab'Saber, 1977). Because of this isolation, the biota of the Atlantic Forest is quite unique, and includes many endemic taxa (da Silva et al., 2004). After centuries of clearing for timber industry, agriculture and urban settlement, 12% of its original extent has survived, comprising almost exclusively small fragments (<100 ha) (Ribeiro et al., 2009). We consider for this study the AF domain (sensu Ribeiro et al., 2009) within the national continental borders of Brazil.

We used the forest plant-pollinator networks modelled by Pereira et al. (submitted): for the regional interaction network, we used the Atlantic Plant-Insect database containing georeferenced flower visiting interactions observed across the Brazilian Atlantic Forest (https://esajournals.onlinelibrary.wiley.com/doi/toc/10.1002/(ISSN)1939–9170.AtlanticPapers). We kept only observations with classification at the species level, within the Brazilian territory and the Atlantic Forest domain. There are 2247 weighted networks, each corresponding to a local hexagonal site measuring 25 km in the N-S direction. Network sizes vary between 159 and 163 plant nodes and 42 to 58 insect pollinator nodes. Link weights correspond to probability of interaction between species.

### 2.2. Grouping similar networks to form subregions

We compared the networks and grouped similar ones to form subregions within the AF. For this, we used clustering methods. Two different criteria were used for clustering: network structure and edge correspondence.

When considering network structure, a set of global network properties was used for the comparison, so that networks with similar topology, regardless of species pairs, are grouped together. There is a recent interest in considering (Baranyi et al., 2011; Ortiz et al., 2017) and combining (Gouveia et al., 2021) multiple measures of network topology in order to extract as much information from networks as possible. The network properties considered were: (1) sum of link weights (SLW); (2) Shannon entropy of node strength (HS); (3) weighted connectance, which quantifies how many links are present in comparison to all possible links, taking weights into account (C); (4) centralization, which shows how much the links are centralized on one or a few nodes, based on eigenvector centrality (Centr; Freeman, 1978); (5) an implementation of modularity for bipartite networks, which shows how much the network is compartmented into dense groups of nodes called modules, using the method by Beckett, 2016 (M); and (6) 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). We chose these features because they were the most relevant ones for representing the variability of our set of networks (Pereira et al., submitted). We applied model-based clustering, specifically a finite Gaussian mixture modeling using the mclust R package (Scrucca et al., 2016), to group our networks. The optimal number of clusters is computed by the modeling algorithm. We obtained 9 clusters, which we refer to as *structural subregions*.

When considering edge correspondence, the identity of the species in each interaction pair is taken into consideration, so that networks where the same species pairs are connected are more similar to each other. We did this using hierarchical clustering with the weighted Jaccard index as a similarity measure. We flattened the incidence matrices of all networks, turning them into vectors, and compared them pairwise using the R package proxy (Meyer and Buchta, 2020). We built the clustering dendrogram using Ward distance, and cut it to obtain 9 clusters, in order to better compare it with the structural subregions. We refer to the 9 clusters based on edge correspondence as *species pairs subregions*.

### 2.3. Protection status of subregions

Polygons of the current protected areas in the AF region were obtained from the World Database of Protected Areas (UNEP-WCMC and IUCN, 2020). We overlaid the protected area polygons to both sets of subregions and computed the proportion of area covered for each subregion. For conservation goals, we take as a reference the 30 by 30 initiative, which is based on estimates that 30 percent of the surface of the planet and each type of habitat needs to be protected to curb species loss and climate change. As a measure of priority level for protection for subregions, we computed what proportion of each subregion still needs to be protected to complete 30%. This amount was mapped for structural and species pairs subregions separately. We then rasterized both maps, and summed them pixel by pixel, obtaining the final network protection priority index. In cases where the user has a reason to give more emphasis to one of the modalities (structural or species pairs), a weighted sum may be chosen instead. With the advanced applications of remote sensing methods in biodiversity research (Thouverai et al., 2021), a variety of software is available for analyses. Spatial analyses were done with SIRGAS 2000 datum, in QGIS version 3.4 (QGIS.org, 2020) and packages sf (Pebesma, 2018) and raster (Hijmans, 2020) in R (R Core Team, 2020) with RStudio (RStudio Team, 2019).

## 3. Results

Overall, the subregions based on network structure show a more fragmented, grainy pattern, while the subregions based on species pairs form more distinct patches, indicating higher spatial autocorrelation in the case of species pairs (Fig. 1). By visual inspection, we see that there is a partial correspondence between the two divisions, e.g. subregion #1 is similar in the two cases. We can also observe that some subregions with different species pairs have similar network structure, e.g. species pairs subregions #2 and 8 overlap structural subregion #2. Also, species pairs subregions #5 to 7 overlap structural subregion #6. Conversely, some areas host different kinds of network structure, while species pairs are

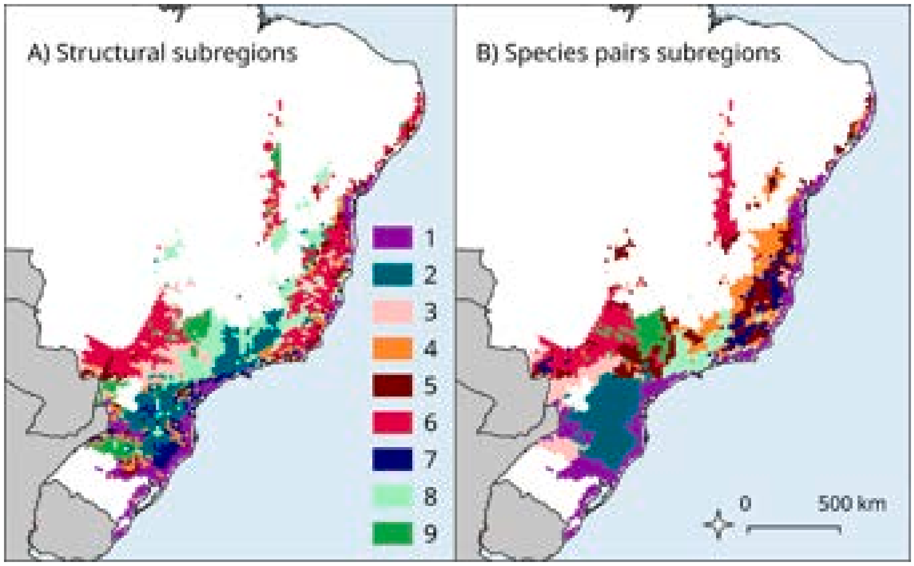


**Fig. 1.** Subregions of pollination networks in the Atlantic Forest, obtained by hierarchical clustering based on (A) network structure and (B) linked species pairs (i.e. edge correspondence). Color legend and scale refer to both maps.

similar, e.g. portions of structural subregions #6, 8 and 9 are contained in the large northern patch of species pairs subregion #6. Additionally, in the South we have portions of structural subregions #2, 4, 7 and 8 within species pairs subregion #2.

Current protected area for the structural subregions varies between 2 and 22%, and for the species pairs subregions, between 1 and 26% (Table 1). The region that bridges the southern and northeastern portions of the Atlantic Forest (Serra do Mar and adjacent areas) is relatively well protected, and this can be seen especially in the species pairs subregions priority map (Fig. 2A and C). The south is low in priority as far as network structure is concerned, since it falls into the same subregion as the Serra do Mar (Fig. 2B). Two large areas are highlighted as most in need of further protection: 1) the wider part of the northeastern portion, including parts of four states (eastern Minas Gerais, Espírito Santo, Rio de Janeiro and south of Bahia) and 2) the west portion, including parts of three states (interior of São Paulo, NW Paraná and S Mato Grosso do Sul). For network structure protection, the isolated patch in the north (São Francisco area) is also very important. There is also a small portion in the south (N Rio Grande do Sul) with high priority for both types of subregions.

Summarizing priority recommendations with a summed map, we find that, overall, the areas with most need of protection for pollination networks are NE of São Paulo state (A in Fig. 3), two portions in the south (B in Fig. 3), and E Minas Gerais, with adjacent portions of S Bahia, Espírito Santo and Rio de Janeiro (C in Fig. 3). Secondarily, W São Paulo and the São Francisco region also call for attention (D and E in Fig. 3).

**Table 1**
Proportion of current protected area for network subregions according to structure and species pairs.

| Subregion | | Proportion protected | |
|---|---|---|---|
| | | Structural | Species pairs |
| (purple) | 1 | 0.15 | 0.16 |
| (teal) | 2 | 0.13 | 0.06 |
| (light pink) | 3 | 0.06 | 0.01 |
| (orange) | 4 | 0.12 | 0.09 |
| (dark red) | 5 | 0.17 | 0.05 |
| (crimson) | 6 | 0.05 | 0.09 |
| (navy) | 7 | 0.22 | 0.03 |
| (light green) | 8 | 0.06 | 0.26 |
| (green) | 9 | 0.02 | 0.02 |

## 4. Discussion

The division of the AF into species pairs subregions resembles other divisions, such as the official mapping of forest formation types and associated ecosystems, developed by the Brazilian Institute of Geography and Statistics (IBGE, 2008). Species pairs subregion #1 largely corresponds to dense ombrophilous forest; subregion #2, to mixed ombrophilous forest and steppe; subregions #4, 5 and 7, to seasonal semi-deciduous forest; and subregion #6 to seasonal semideciduous forest in its southern portion (W São Paulo) and to seasonal deciduous forest in its northern portion (São Francisco area). We also see similarities between the species pairs subregions and the division by (da Silva et al., 2003), based on forest butterflies, primates and birds: subregion #1 approximately corresponds to Serra do Mar and Bahia; subregion #2 to *Araucaria*; subregions #4, 5, 7, 8 and 9, as well as the southern portion of subregion #6, to Interior and Diamantina; and, finally, the northern portion of subregion #6, to São Francisco. We see, therefore, that the division based on network species pairs is more detailed in the interior areas, in comparison with the other studies mentioned here.

We also see some interesting coincidences between the forest formation types (IBGE, 2008) and the structural subregions. For example, structural subregion #7 appears to correspond partially to steppe. Also, the two largest portions of subregion #6 (western São Paulo and eastern Minas Gerais) coincide with semi-deciduous forest. Here we can see that the structural subregions were able to discern some aspects of forest formation types, which refer to structure of ecosystems, that were missed by the species pairs division, both in terms of further detail (steppe) and wide scale similarity (subregion #7). Note that, although western São Paulo and eastern Minas are quite different in terms of species pairs, they are similar in terms of network structure (Fig. 1), and

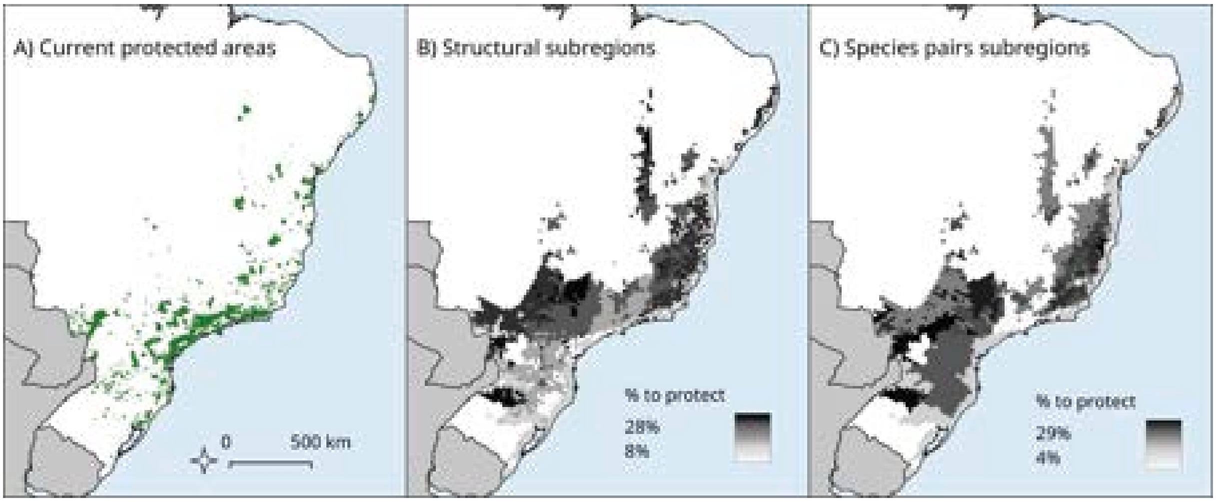


**Fig. 2.** Current protected areas (A) and priority of protection for pollination networks (B and C) in the Atlantic Forest. Priority maps show how much of each subregion still needs to be protected to reach the target of 30% protection for all subregions.

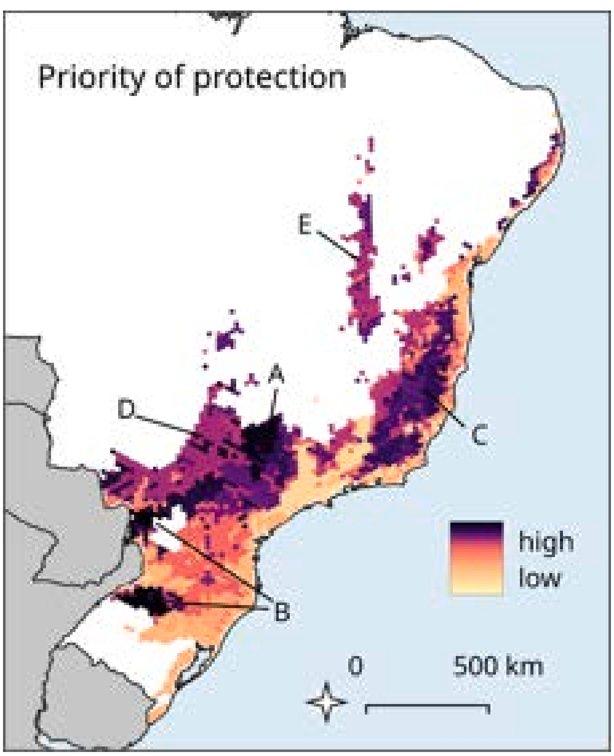


**Fig. 3.** Level of protection priority for pollination networks in the Atlantic Forest. Both network structure and linked species pairs are considered. Seven color classes with quantile intervals are used. Highlighted portions: NE São Paulo (A), NW Paraná and N Rio Grande do Sul (B), E Minas Gerais (C), W São Paulo (D), São Francisco region (E).

both are covered by semi-deciduous forest. On the other hand, in the south, we have a large subregion characterized by *Araucaria* forest with its own species pairs (species pairs #2), but within that habitat we have some portions of steppe, with networks of a different type of structure (structural #7). This shows the importance of accounting for the wider network structure, in addition to species pairs, for a more complete understanding of the communities.

Semi-deciduous forest is the most degraded portion of the AF, due to its flat, fertile soils of high agricultural value (Galetti et al., 2009). It covers most of the priority areas for protection we identified based on networks. Semi-deciduous and the interior AF in general have also been pointed out as a priority for different species groups, such as large mammals (Galetti et al., 2009), tiger moths (Ferro et al., 2014) and felids (Crouzeilles et al., 2015), as well as for optimized restoration (Tambosi et al., 2014). Additionally, this central and southern portion of the AF may be especially affected by climate change in the future, which calls for the inclusion of climate models in the planning of new reserves (Ferro et al., 2014). On the other hand, different or additional priorities have been identified in other studies. For example, priority sites for amphibians are mostly located in northern AF (Trindade-Filho et al., 2012). For woody plants, restoration is needed along the coast, from Bahia to Rio de Janeiro (Zwiener et al., 2017). The *Araucaria* forests, in the south, need special attention in the cases of beta diversity of trees (Bergamin et al., 2017) and felids (Crouzeilles et al., 2015). The official program of the Brazilian Ministry of Environment for conservation and sustainable use of biodiversity (BRASIL, 2004, 2002) defined as priority areas patches mostly near the coast, especially in the central (Bahia) and southern portions (MMA, 2018), based on criteria of biological diversity, ecosystem integrity and opportunities for conservation action and sustainable use.

If, on the one hand, highly degraded areas such as the semi-deciduous forest deserve special care, it may also be argued that landscapes in better condition (Ribeiro et al., 2009) and with recent habitat loss should be prioritized. The reason for this is that they may harbor species that have not yet disappeared but could be lost in the near future, what is called extinction debt (Rappaport et al., 2015). The reason can be, for example, that beyond the number of species, also higher-level structures (such as the interaction network) are damaged (Galiana et al., 2022). Indeed, Serra do Mar, being the best-preserved part of the AF, is also frequently set apart as priority, e.g. for large mammals (Galetti et al., 2009), amphibians (Lemes et al., 2013), optimized restoration (Tambosi et al., 2014), and large carnivores (Castilho et al., 2015). In our study, Serra do Mar is not highlighted because it is already well covered by protected areas, containing the largest conservation units of the AF.

Prioritisation of targets for conservation is important for effective planning of biodiversity protection, but in many cases it is not based on ecological knowledge (Zwiener et al., 2017). Creation of protected areas in Brazil is, at least on paper, chiefly motivated by conflicts at the local level, especially control of irregular occupations and protection of forest remnants, in the case of the AF (Roque et al., 2019). Where ecological criteria are applied in the AF, present species distribution of various taxonomic groups, centres of endemism, projected climate change and the condition of forest remnants have been used as basis for prioritization (Zwiener et al., 2017). Initiatives concentrating on the protection of threatened and flagship species have a long history in the region, including cases of success such as the conservation programs for lion tamarins *Leontopithecus* and muriqui monkeys *Brachyteles*. We can also perceive a shift to multidisciplinary programs targeting broad scale conservation corridors in the past 40 years (Tabarelli et al., 2005). However, to our knowledge, there is no initiative to intentionally protect webs of species interactions, on which the existence and maintenance of ecological communities depend. It is clear that protecting interactions is a more abstract approach than protecting species or areas. For this reason, there are not too many attempts for this. Difficulties emerge especially from the multiplicity and interdependence of interactions. In this study, we have proposed a strategy to identify conservation priorities based on networks of species interactions, so that not only species richness and diversity, but also interdependence between species is preserved. We emphasize that the functioning of ecological communities depends on multiple interaction types, including potentially even more relevant interactions like predation. As a first step towards the direction of protecting interactions, we think that it is appropriate to start with a single interaction types. Methods of network analysis are quite different for multigraphs. Yet, one of the key future challenges is to handle multigraphs representing several interaction types (Vasas and Jordán 2006; Fontaine et al., 2011). For efficient conservation management, large and standardized databases are clearly needed if species interactions are considered: studying co-occurrence networks enriched with trait and habitat type data is one way how to ensure this (Elo et al., 2021). Moreover, we note that some organisms and some interactions (Kandori 2002) as well as some habitat patches (Pereira et al. 2017) are more important than others, so understanding ecosystem functioning and efficient management both profit a lot from system-level approaches focusing on these key system components.

Despite the fast decline in the rainforests of the Brazilian Atlantic coast, the remaining still represents the second-largest area of humid tropical forest in South America (Murray-Smith et al., 2009). We hope this work may contribute to more effective protection of ecological communities in this invaluable biodiversity hotspot, as well as other threatened ecosystems of the world.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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