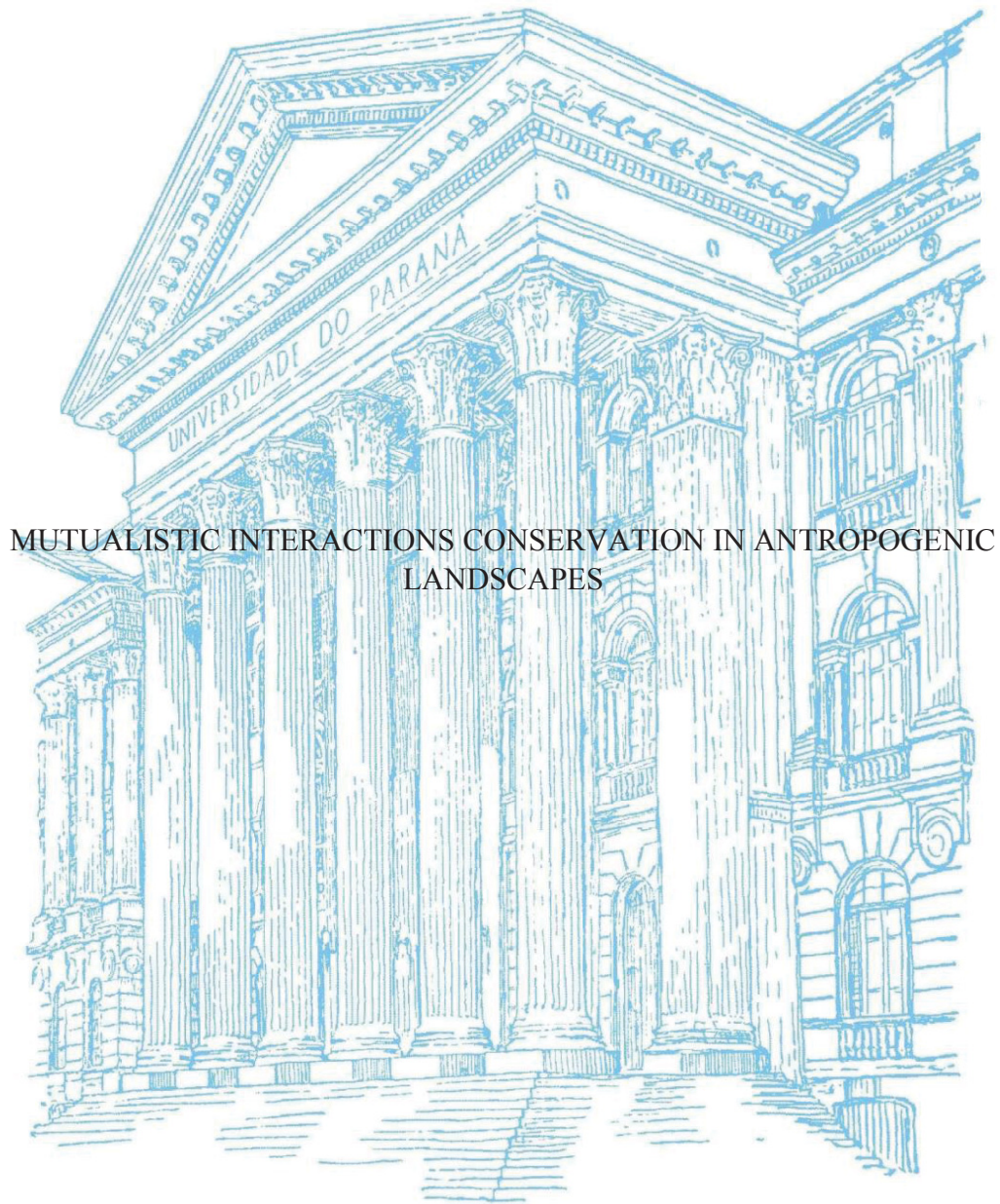


UNIVERSIDADE FEDERAL DO PARANÁ

ISRAEL SCHNEIBERG DE CASTRO LIMA



MUTUALISTIC INTERACTIONS CONSERVATION IN ANTROPOGENIC
LANDSCAPES

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ISRAEL SCHNEIBERG DE CASTRO LIMA

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LANDSCAPES

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RESUMO

Biodiversidade é uma propriedade emergente que surge das interações entre espécies. Infelizmente, nosso planeta está perdendo biodiversidade em uma taxa acelerada, não apenas as espécies, mas também as interações e os serviços ecossistêmicos relacionados com tais interações. Uma das ameaças mais atuais e invasivas para a biodiversidade são as atividades relacionadas à conversão da paisagem. Um grande desafio para compreender as consequências das perdas da biodiversidade é compreender a complexidade dos sistemas naturais e as ações necessárias para conservar os elementos da biodiversidade em um mundo em rápida mudança. Entre as funções que estão sob ameaça, os animais frugívoros e os serviços por eles prestados estão sendo afetados pelas atividades de desmatamento. A perda e a fragmentação florestal podem afetar a persistência das espécies de frugívoros e alterar a composição das redes entre aves e frutos. A persistência de uma espécie pode depender da presença de outras espécies com as quais ela interage e da possibilidade de encontros entre elas, ou como Janzen (1974) pontuou "o tipo mais insidioso de extinção é a extinção das interações ecológicas". No capítulo 1, investiguei os fatores de diversidade taxonômica e funcional em paisagens antropogênicas, ponderando as exigências de habitat das espécies. Descobri que a perda de espécies foi mais acentuada do que a perda de riqueza funcional em todo o conjunto de espécies. Por outro lado, a diversidade funcional das espécies dependentes da floresta foi mais afetada pela estrutura da paisagem do que quando considerado todo o conjunto de espécies. Estes resultados destacam a importância de considerar os requisitos de habitat principalmente em grupos altamente heterogêneos, bem como de tratar os efeitos da paisagem em diferentes níveis de organização biológica. No capítulo 2, investiguei como a estrutura da paisagem afeta o acoplamento morfológico e a congruência filogenética das redes entre aves e frutos. Separei os efeitos das características morfológicas e filogenia nas redes de interações e previ a probabilidade de interação com base nessas dimensões de biodiversidade. Descobri que o acoplamento morfológico aumentou nas paisagens florestais principalmente porque há mais variabilidade de atributos morfológicos, e portanto, mais chances das interações serem mediados pelo acoplamento morfológico. No entanto, a congruência filogenética aumenta em paisagens desmatadas e isoladas. Este padrão não significa o resultado da coevolução *per se*, mas é o resultado da seletividade para habitats alterados pelo homem por linhagens particulares que induzem a co-ocorrência de espécies próximas filogeneticamente. No capítulo 3, investiguei se as redes são mais robustas à extinção secundária de aves em paisagens florestadas por se tratar de locais com maior variabilidade de atributos, permitindo mais oportunidades de reconexão entre as espécies, levando em conta o acoplamento morfológico. Observei que as redes são mais robustas em paisagens florestadas do que em paisagens desmatadas. Este padrão pode ocorrer porque as aves frugívoras são aquelas que apresentam maior variabilidade de atributos (por exemplo, largura e comprimento do bico).

Palavras-chave: cofilogenias, correspondência funcional, interações mutualísticas, isolamento, perda de habitat.

ABSTRACT

Biodiversity is an emergent property that arise from interactions between species. Unfortunately, our planet is losing biodiversity at an accelerating rate, not only losing species but also the interactions between species and the ecosystems services related to interactions. One of the most actual and invasive threats for biodiversity are those activities related to landscape conversion. A major challenge for understanding the consequences of biodiversity losses is to understand the complexity of natural systems and the steps needed to conserve biodiversity elements in a rapidly changing world. Among the functions that are under threat, frugivore animals and the services performed by them are being affected by deforestation activities. Forest loss and fragmentation can affect the persistence of frugivores species and change the composition of plant-frugivores networks. The persistence of a species may depend on the presence of other species with which it interacts and on the possibility of encounters between them, or as Janzen (1974) stated it “the most insidious kind of extinction is the extinction of ecological interactions”. In chapter 1, I investigated the drivers of taxonomic and functional diversity in anthropogenic landscapes by weighing habitat requirements of species. I found that the loss of species was more marked than the loss of functional richness in the entire assemblages. Functional diversity of forest-dependent species was more affected by landscape structure than when analyzing the entire assemblages. These results highlight the importance to consider habitat requirements mainly in high heterogeneous group as well as to addressing landscape effects across different levels of biological organization. In chapter 2, I investigated how landscape structure erodes trait matching and phylogenetic congruence of plant-frugivore networks. I partitioned the effects of traits and phylogeny on interactions networks and predicted the interaction probability based on these biodiversity dimensions. I found that trait matching increased in forested landscapes mainly because there is more trait variability and then more chance to produce trait matching. On the other hand, phylogenetic congruence increases in deforested and isolated landscapes. This pattern does not mean the result of coevolution *per se*, but is a result of selectivity for human altered habitats by particular lineages which induces closely related species to co-occur. In chapter 3, I investigated if networks are more robust to secondary extinction of birds in forested landscape because more trait variability allow more opportunity to species rewire taking into account trait matching. I found that networks were more robust in forested than in deforested landscapes. This pattern may occur because frugivorous birds are those which show more trait variability in traits (e.g., bill width and bill length).

Keywords: Cophylogenies, Habitat loss, Isolation, Morphological matches, Mutualistic interactions.

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GENERAL INTRODUCTION

Anthropogenic activities lie as the main cause underlying contemporary biodiversity loss and represents a ubiquitous threat to the natural world. One of the main results of these activities is the conversion of natural areas to human-modified landscapes, mainly to supply the needs of human population but also for feeding and water to quench livestock thirst (Newbold *et al.* 2015). Thus, extensive areas of pristine landscapes are converted to novel ecosystems (e.g., agricultural landscapes, urban landscapes), without maintaining landscape connectivity and habitat amount (Ribeiro, M *et al.* 2009; Sams *et al.* 2017). However, the response of each species to the loss of natural areas may vary according to its niche requirements (Ferraz *et al.* 2007) and dispersal ability. Local factors such as patch size and patch quality may affect species persistence (Hodgson *et al.* 2011; Beninde *et al.* 2015), while matrix type and the presence of ecological corridors may constrain or enhance species movement through the landscape (Fahrig 2003; Niebuhr *et al.* 2015).

Many studies about the magnitude of the effect of landscape structure on biodiversity dimensions have assumed that all species are functionally equivalent, evolutionary independent and do not interact. Nevertheless, functional traits determine species responses to landscape change (Öckinger *et al.* 2010). On the one hand, forest loss can negatively affect the persistence of habitat specialists. On the other hand, landscape heterogeneity can increase the functional space filled by species that use the resources provided by land cover types (Fahrig *et al.* 2011). Moreover, depending on the magnitude of the effect of landscape change, remaining populations can share similar traits which result in functional homogenization (Devictor *et al.* 2007). For this reason, certain species may have a major impact on ecosystem function and services (Grime 1998).

Due to long-term of intense and invasive anthropogenic activities, Tropical Forest remnants are increasingly isolated, small, irregular and with strong edge effects (Ribeiro, M *et al.* 2009; Rezende *et al.* 2018). These shifts in natural areas drives changes in different dimensions of biodiversity (i.e., taxonomic, functional and phylogenetic) (Bovo *et al.* 2018; Morante-Filho *et al.* 2018a; Püttker *et al.* 2020). In general, it is expected that closely related species (i.e., species which share the same evolutionary history) share more similar traits with each other than with distantly related species (Blomberg & Garland 2002). If species-environmental relationships are mediated by functional traits, habitat loss, fragmentation and isolation can increase the degree of functional and phylogenetic homogenization, because the majority species in disturbed landscapes will be more functionally and phylogenetically similar. For example, habitat loss and fragmentation decrease evolutionary distinctness of frugivores (Monteiro *et al.* 2021). In the same way, large-bodied birds and birds with large-gapes have more chance to be locally extinct in deforested and fragmented landscapes (Emer *et al.* 2020). This homogenization can profoundly affect ecosystem services due to losses of evolutionary distinctness and particular functional traits (Emer *et al.* 2020; Monteiro *et al.* 2021).

One of the most important mechanism of biodiversity and ecosystem services are those that arise from interactions between elements of ecosystems (Norris 2012). Generally, the persistence of a species may depend on the presence of other species with which it interacts and on the possibility of encounters between them (Fortuna & Bascompte 2006; Tylianakis & Morris 2017). Network analyzes put the focus on the patterns of interactions among species, introducing heterogeneity to the system, not only allowing the description of network architecture, but also to investigate the ecological, environmental, and evolutionary consequences (Aizen *et al.* 2016; Guimarães *et al.* 2017). Mutualistic networks are often constrained by traits. For example, frugivory is

constrained by trait matching between bill gape and seed size. Moreover, some interactions can shape coevolutionary responses among species (Galetti *et al.* 2013) when related species of one trophic level preferentially interacting with related species of the other trophic level (Tylianakis & Morris 2017). The disruption of interacting species linked by functional and phylogenetic aspects can erode long-term interactions and increase the occurrence of less reliable mutualisms (Aizen *et al.* 2016; Tylianakis & Morris 2017).

In this way, frugivory is especially appropriate as a study group because of their relatively high taxonomic, functional and phylogenetic diversity involved in both trophic levels (Burin *et al.* 2021). Frugivory emerges as a process of diffuse co-evolution, i.e., many plants interact with many different frugivores, and frugivores depend on many plants for food (Burin *et al.* 2021). Moreover, different lineages converge to the same kind of traits, which can allow the trait matching in different lineages. For this reason, it has been suggested that frugivory is a foraging mode that does not require special adaptation in traits involved in the interactions (Jordano, 2000) as those involved in prime classic examples of co-evolution (e.g., Darwin's sphinx moth, figs and fig wasps). Due to the high complexity involved in plant-frugivore interactions, it is important to take into account different dimensions of biodiversity to understand the effect of landscape change on the network structure and how secondary extinctions can erode interactions (Colwell *et al.* 2012). Here, my goal was to tackle these issues in deforested and fragmented landscapes in Brazilian Atlantic Forest using spatial approaches, functional and phylogenetic inferences.

In Chapter 1, we aim to understand the potential drivers of landscape change on frugivores assemblages, I first selected bird species known to be forest dependent. Using landscape composition and configuration metrics, combined with functional traits and

taxonomic and functional metrics, I found that the loss of species was more marked than the loss of functional richness in the entire assemblages. Functional diversity of forest-dependent species was more affected by landscape structure than when analyzing the entire assemblages. Functional richness of forest-dependent species declines when landscape reaches 40% of forest loss and forest patches became more isolated. In a similar way, forest-dependent species showed higher functional dispersion in landscapes with increased forest cover and less fragmented. Using a multivariate approach, I found a positive relationship between frugivore species with forest cover. These results highlight the importance to consider habitat requirements mainly in high diverse group as well as to addressing landscape effects across different levels of biological organization.

In chapter 2, in order to investigate how landscape structure erodes trait matching and phylogenetic congruence of plant-frugivore networks, I used quantitative networks from Atlantic Frugivore dataset. Then, I partitioned the effects of traits and phylogeny on interactions networks and predicted the interaction probability based on these biodiversity dimensions. I found that trait matching increased in forested landscapes mainly because there is more trait variability and then more chance to produce trait matching. On the other hand, phylogenetic congruence increases in deforested and isolated landscapes. This pattern does not mean the result of coevolution *per se*, but is a result of selectivity for human altered habitats by particular lineages which induces closely related species to co-occur.

In chapter 3, I ask if networks are more robust to secondary extinction of birds in forested landscape because more trait variability allow more opportunity to species rewire taking into account trait matching. To do that, I used the same dataset and some of those functional traits used in chapter 2. Then, I simulated plant extinctions because deforestation and extractivism practices are increasingly common. I found that networks

were more robust in forested than in deforested landscapes. This robustness in forested landscape is linked to trait variability which allow interaction rewire. Moreover, I found a positive relationship between the degree of frugivory and network robustness. This pattern may occur because frugivorous birds are those which show more trait variability in traits (e.g., bill width and bill length).

When viewed as whole, the result of this thesis suggests the effect of landscape not only on taxonomic, but also on functional and phylogenetic dimensions of biodiversity, and shows the importance to conserve continuous forests to maintain the diversity of species, traits and phylogenetic history. In addition, landscape structure can generate more accurate effects when habitat requirements are taken into account. Finally, due to an increase of dismantling of the environmental policies and increase actions against conservation efforts, the previously described as “the most extreme case” the extinction of well-connected species has become possible and point out to strong cascading effects on the interactions partners.

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CHAPTER 1

Forest dependency determines landscape influence on bird diversity

Forest dependency determines landscape influence on bird diversity

ABSTRACT

Landscape conversion modifies the environment at multiple spatial scales, allowing the substitution of forest-dependent species by non-forest species, which impacts ecosystem functioning due to loss of functional groups. The effect of landscape conversion on functional diversity may vary according to the habitat requirements of each species and has been little explored. Our main goal is to identify the drivers of taxonomic and functional diversity in anthropogenic landscapes by weighing habitat requirements of species. We analyzed taxonomic and functional diversities using a comprehensive dataset representing the occurrences of 447 bird species across 86 communities in the southern Atlantic Forest. We used four environmental variables related to landscape composition and configuration at different spatial scales to assess the responses of taxonomic and functional indices along a gradient of habitat loss and fragmentation. The loss of species was more marked than the loss of functional richness in the entire assemblages. Functional diversity of forest-dependent species was more affected by landscape structure than when analyzing the entire assemblages. Functional richness of forest-dependent species declines when landscape reaches 40% of forest loss and forest patches became more isolated. In a similar way, forest-dependent species showed higher functional dispersion in landscapes with increased forest cover and less fragmented. When considering only the entire assemblages, important changes to ecological functions remained undetected. Taxonomic and functional changes were mostly detected when considering forest-dependent species, which are deeply affected by such transformations in the original habitat. Overall, this highlights the importance of addressing landscape effects on biodiversity across different levels of biological organization.

Keywords: Biodiversity dimensions, Functional similarity, Habitat matrix, Human-induced landscape

INTRODUCTION

Anthropogenic activities lie as the main cause underlying contemporary biodiversity loss and represents a ubiquitous threat for the natural world. Amongst these threats, forest loss and fragmentation have been particularly concerning. (Hagen *et al.* 2012; Sutherland *et al.* 2013; Newbold *et al.* 2015). Landscape conversion due to anthropogenic activities leads to the loss and fragmentation of natural ecosystems, complementary processes that commonly occur together (Fahrig 2003; Smith *et al.* 2009), and are the main drivers of species decline and disruption of ecosystem services. Studies about the magnitude of landscape structure effect on biodiversity dimensions have assumed that all species are functionally equivalent (Hubbell 2001); but it is well-known that certain species may have a major impact on ecosystems functions and services (Grime 1998). In addition, some dimensions of biodiversity may be maintained in a gradient of landscape conversion due to compensatory dynamics, as species intolerant to landscape change are compensated by stress-tolerant species, which in turn may maintain taxonomic, functional and phylogenetic diversities (Steiner *et al.* 2011; Morante-Filho *et al.* 2018a; Matuoka *et al.* 2020). Although significant decrease in functional diversity has already been observed in face of landscape conversion (Devictor *et al.* 2008; Gutiérrez-Cánovas *et al.* 2015), some studies have found positive effects (Coster *et al.* 2015; Matuoka *et al.* 2020) or unchanged effects on functional diversity (Magnago *et al.* 2014), some of them related to positive effects of landscape heterogeneity (Fahrig *et al.* 2011), and due to compensatory dynamics (Morante-Filho *et al.* 2018a; Matuoka *et al.* 2020). Here, we investigated the effects of forest spatial structure on bird functional diversity by separating forest-dependent species and the complete assemblages, which includes forest and non-forest depend species. Equal weighting forest-dependent and non-dependent species can generate biases when the habitat requirements are not taken into account.

Species responses to the loss of natural areas may vary according to species requirements (Ferraz *et al.* 2007) and dispersion ability (Burgess *et al.* 2012). Habitat loss influences species persistence, determined by local factors such as forest patch size and quality (Beninde *et al.* 2015), as well as species movements in the landscape, which are affected by landscape elements such as matrix type, habitat amount, and landscape connectivity (Fahrig 2003; Uezu *et al.* 2008). Human-induced landscape changes ultimately cause taxonomic (Crocì *et al.* 2008; Solar *et al.* 2015; Vallejos *et al.* 2016), functional (Devictor *et al.* 2007; Aguirre-Gutiérrez *et al.* 2020), and phylogenetic simplification (Pavoine & Ricotta 2014; Sol *et al.* 2017). This increase in biotic homogenization across areas is a global phenomenon that affects multiple taxa (Smart *et al.* 2006; Gutiérrez-Cánovas *et al.* 2015) and is often characterized by the replacement of specialists to generalist species (Devictor *et al.* 2008; McKinney 2008; Bennett *et al.* 2020). At the same time, the effects of forest loss and fragmentation involve mechanisms that cannot be studied separately because human-induced landscapes are spatially heterogeneous and species perceive this heterogeneity in a complex way (Fahrig *et al.* 2011).

Species relationships with the surrounding environment are mediated by their traits (Meynard *et al.* 2011; de Bello *et al.* 2017). Overall, specialist species (e.g., diet, habitat specialists) are replaced by generalist species as forest amounts is reduced and fragmented. This substitution affects the variation (rate or frequency) of traits what may have stronger influence in a given ecosystem service (Díaz *et al.* 2013). For example, in a gradient of increasing loss and fragmentation of forested areas, species of large frugivores that use a high proportion of fruits in the diet are replaced by small generalist species (Emer *et al.* 2020). As a result, the seed dispersal service of provisioning of large

fruits is reduced or lost, thereby affecting the forest dynamics in small patches (Emer *et al.* 2018).

Birds are a suitable group to investigate the relationship between forest spatial structure and dimensions of biodiversity because they are highly diverse, both taxonomically (del Hoyo *et al.* 1992) and functionally (Wilman *et al.* 2014), they show variable level of forest dependency (Bregman *et al.* 2014), and are involved in several interaction networks, playing key roles in community and ecosystem dynamics (Sekercioglu 2006). Therefore, addressing how forest spatial structure influences bird diversity across different dimensions of diversity has become essential to determine the degree to which anthropogenic pressures due to habitat conversion have impacted ecosystem functioning. Here we addressed forest influences on bird taxonomic and functional diversity in the Atlantic Forest in southern Brazil, which harbors a large bird diversity and endemism throughout its broad extension (Parker *et al.* 1996). Despite their importance of this hotspot for safeguarding the biological diversity, the Atlantic Forest is strongly fragmented and only around 12% of its original land cover remains due to land-use conversion (Ribeiro, *et al.*, 2009). By integrating data on bird community composition and species traits across a gradient of forest loss and fragmentation, we aimed to answer: how are taxonomic and functional diversity of forest-dependent and the complete bird assemblages are affected by forest spatial structure? We predict that forest loss and fragmentation have little or unchanged effects on complete assemblage due compensatory dynamics, whereas forest loss and fragmentation have a negative role in taxonomic and functional diversity of forest dependent species because both processes can act as ecological filter for forest dependent species like obligate frugivores and insectivorous specialist (e.g., woodcreepers). We expect that the amount of functional space in deforested and fragmented landscapes is filled by compensatory dynamics of non-forest

species in complete assemblages, but not for particular ecosystem functions mainly those made by obligate frugivores

MATERIALS AND METHODS

Background: an overview of the studied system

The study was conducted in the southern Atlantic Forest (Figure 1), characterized by different forest types, including coastal rainforests, *Araucaria* mixed forest, and seasonal forest (Solórzano et al. 2021).

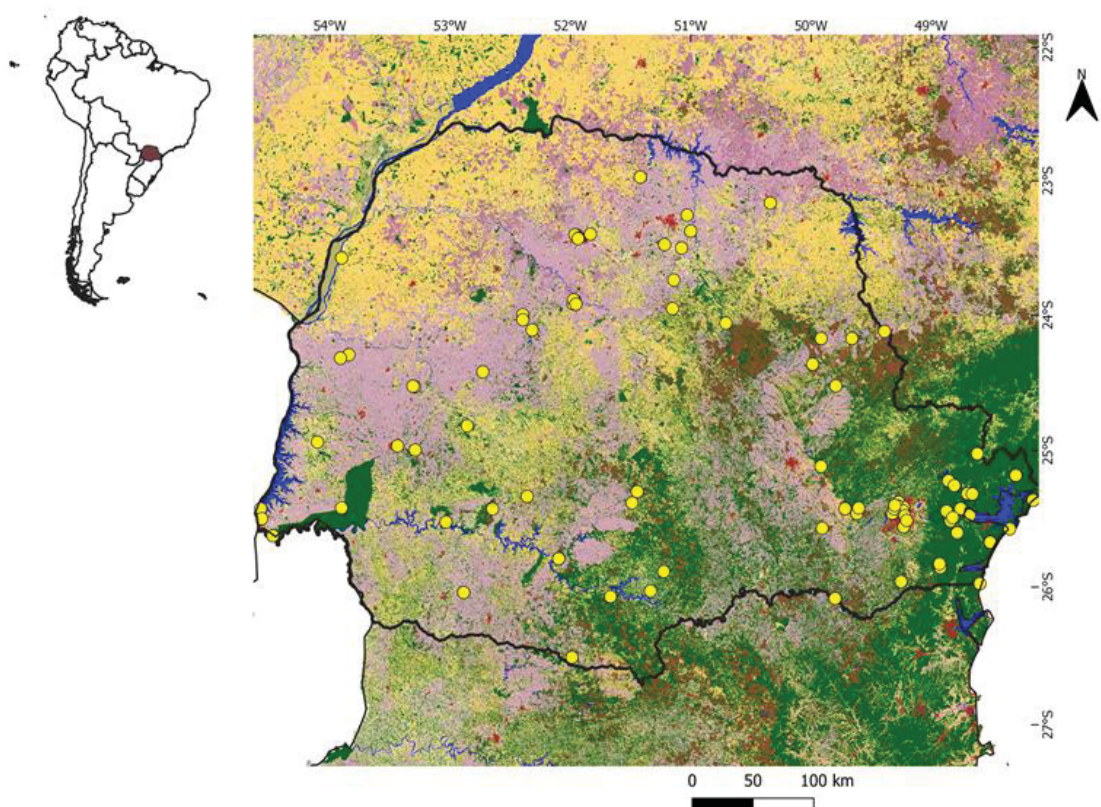


Figure 1 Location of sampling sites in southern Brazil (dots in yellow) overlaid in the land use map for the inventory year (2012). Green areas are Atlantic Forests remnants. Blue areas are water. Other colors represent a gradient of different land use classes (e.g., pasture in orange and agriculture in pink).

The landscape conversion of the southern Atlantic Forest was uneven. Specifically, during the landscape conversion process to the extent of this study (i.e.,

Paraná state), seasonal forest had more loss of forest cover, followed by *Araucaria* mixed forest and rainforest. At the same time, Paraná state is the shelter of one of the most important continuous remnants of Brazilian Atlantic Forest in its eastern portion associated with the Serra do Mar mountain chain (Ribeiro et al., 2009). We did not investigate the differences between phytophysiognomies because the effect of forest loss and fragmentation should be similar regardless of forest type.

Data on bird assemblages

We used citizen science bird data from the Paraná Birds Participatory Inventory (IPAVE) (Straube et al. 2012). In this initiative, professional ornithologists, photographers, students and birdwatchers were advised into a protocol to collect information about the spatial distribution of bird species using visual/auditory methods. All records were evaluated by a group of specialized ornithologists to avoid inconsistencies in species records regarding their distribution and habitats. The inventory took place at the beginning of bird reproductive season, and lasted one week. This data set have been used previously and found to be accurate, specifically when sampling effort has not been shown to strong influence on the response variable (Vallejos et al. 2016). We used the same procedure made by Vallejos et al. (2016) to filtered IPAVE data in order to increase the reliability and to avoid under-representations. The final result of IPAVE procedure was 447 species distributed along 86 sites. For our approach, we performed correlation test between sampling effort and response variables. All correlation were weak (< 0.4). For our analyses, we have divided IPAVE inventory considering the complete assemblages (forest and non-forest species) and forest-dependent bird species (Bregman, Sekercioglu, and Tobias 2014; Stotz, 1996; Sick, 1997). Forest species are

those specialized on structured forest interior (i.e., maximum canopy height, basal area and large forest amount), that resembles the structure of pristine landscapes (Stotz, 1996). Non-forest species do not require large and continuous forested areas, and comprised those species related to the heterogeneity of habitats which include edge environments, secondary forest and open areas (Stotz, 1996).

Landscape structure

We used data from the Mapbiomas project to obtain maps of forest spatial structure for each assemblage. Mapbiomas presents 30-m resolution Landsat collection data and has a time series of land-use variation over time. We obtained images for the 86 sampled areas for the year of the inventory (i.e., 2012).

In order to compare structural forest features between landscapes, we analyzed three landscape metrics that comprised forest structure: (a) edge density - the length (m) of all forest fragment edges divided by the total landscape area; (b) isolation – average Euclidean distance between all forest patches in the landscape; (c) forest cover - proportion of forest in the landscape, and one landscape metric related to composition of different land uses : landscape Shannon's diversity index, used to describe the landscape diversity considering the number and proportion of landscape classes. All landscape metrics were calculated at three spatial extents (radius of 500 m, 1000 m, 2000 m) to investigate environmental relationships (i.e., scale of effect) (Jackson & Fahrig 2015; Miguet *et al.* 2016). We highlight that, although there are some species in the data set that are known to exhibit long distances (i.e., eagles, vultures), studies that have been investigate Atlantic bird-landscapes associations (Coster *et al.* 2015; Morante-Filho *et al.* 2018a; Barros *et al.* 2019; Matuoka *et al.* 2020) indicate that the selected scales are good

indicators to investigate bird movement and represent, at least 90% of registered species. In addition, the inventory took place at the breeding season, which result in less movement across landscapes and increase habitat fidelity. All landscape metrics were calculate using Fragstats v.4 (McGarigal et al. 2012).

Bird functional traits

We characterized bird species using traits data from Elton Traits (Wilman *et al.* 2014) database on proportional use of food types in species diet (invertebrates, mammals or birds, reptiles or amphibians, fish, scavenger, fruit, nectar, seeds, or other plant material); proportional use of foraging stratum (ground, understory, mid to high levels in trees, canopy, aerial); and body mass (log-transformed). We chose these traits because they cover different aspects by which species are related to ecosystems dynamics (Sekercioglu, 2006).

Taxonomic and functional diversity indices

We considered the species richness as a measure of taxonomic diversity at each assemblage. For functional diversity, we used functional richness (FRic), representing the functional trait-space occupied by the species in the community (Cornwell *et al.* 2006; Villéger *et al.* 2008), and functional dispersion (FDis), an index of dispersion of species in the trait space, measured by the mean distance of species to the centroid of the community, which is less sensitive to outliers than FRic (Laliberté & Legendre 2010).

For calculating functional diversity indices we first created an inter-species distance matrix using a modified Gower distance index to compare how species are different to each other using variables of different types all together (e.g. continuous, categorical traits) (Pavoine *et al.* 2009). We converted the fuzzy variables (e.g. diet and

foraging stratum) to proportional variables using *prep.fuzzy* function. Then, we obtained the distance matrix using the *dist.ktab* function of the *ade4* package (Dray & Dufour 2007) and calculated the functional diversity indices using the *dbFD* function in the FD package (Laliberté & Legendre 2010) in R (R Development Core Team, 2020).

Data analysis: landscape effects on bird diversity

To investigate the relationship between landscape structure and taxonomic and functional diversities we used spatial autoregressive models (SAR) (Hoef *et al.* 2018). These models incorporate the spatial structure of residuals, being an effective way to overcome the spatial non-independence among sampling sites. To evaluate the explanatory power of models in the model selection approach, we calculated Nagelkerke *pseudo-R*², as implemented in the R package *spatialreg* version 1.1-5 (Bivand *et al.* 2013).

For each response variable (i.e., taxonomic and functional indices), we defined a set of models representing hypotheses of the effects of land use variables. Because the range of absolute values of landscape metrics are different and varied, we standardized all landscape metrics (mean = 0, standard deviation =1). We evaluated pairwise correlation among explanatory variables using Pearson's correlation to avoid multicollinearity. Landscape variables with strong collinearity ($r > 0.7$) were removed (Figure S1). We constructed models that explored the unique and additive pairwise effects of edge density, isolation, forest cover and landscape diversity in influencing variations in taxonomic and functional indices. All models were composed by variables in their scales with the highest coefficient of variation (i.e., scale of effect) (Figure S2). Then, we contrasted the multiple hypotheses in a model selection framework, comparing competing models using an information theory approach (Burham & Anderson 2002). For each model, we calculated its information criterion (AIC). We created the models according to

the results of the scale of effect analysis. We considered as plausible those models with $\Delta AIC < 2$ values and based on the probabilities of being the best models were measured with the Akaike's weight of evidence (wAIC). We created SAR models using the *spdep* package (Bivand et al. 2017) and performed all model selection analyses using the *MuMIn* package in R (Barton, 2017).

Data analysis: trait-landscape relationships

We investigated the relationship between landscape structure and species traits combining RLQ and fourth-corner analysis (Dray *et al.* 2014). RLQ is an ordination technique that summarizes the relationship between species traits and landscape structure. Fourth-corner analysis is useful to test the significance between these variables. Both analyses require three matrices: landscape structure (R), species composition (L) and species traits (Q). To test the significance, a two-step procedure are required (ter Braak *et al.* 2012). The first step removes the relationship between landscape structure and species composition by permutating species identities in the original matrices. The second removes the relationship between species traits and species composition by randomizing species identities in the original matrices. The result is a fourth matrix (e.g., matrix X) which relates traits and landscape relationships. Our objective in combining these two approaches was to use RLQ scores to summarize traits and landscape structure of a multivariate space, and then test the significance of links between RLQ axes and traits (Q.axes) and landscape structure variables (R.axes). We chose to analyze trait-by-landscape relations only for the entire assemblages because then we can analyze the maximum of variation in species traits composition. This procedure is implemented using the model 6 in *fourthcorner* function in the *ade4* package in R (Dray *et al.* 2014).

RESULTS

Landscape effects on bird taxonomic and functional diversities

We found that bird species richness was highly variable across communities, ranging from 30 to 173 (mean = 71 ± 34.66) for complete assemblages, and 4 to 118 (mean = 33.3 ± 25.2) for forest-dependent species. For complete assemblages, two models were considered equally plausible. The first model encompasses the combined effects of forest cover and isolation. The model prediction described an increase in species richness starting in landscapes with 40% of forest cover and in forest patches isolated between 50 and 100 m (wAIC = 0.41) (Figure 2a; Table 1). The second model was a univariate model containing only forest cover (wAIC = 0.33), predicting an increase in species richness in landscapes with higher forest cover. For forest-dependent species, only one model was considered plausible in describing species richness (wAIC = 0.77) (Figure 2b; Table 1). The model described a higher species richness in landscapes with more than 80% of forest cover than landscape with less forest cover, and higher species richness in landscapes between 30 and 70 meters per hectare of edge density than in more irregular landscapes.

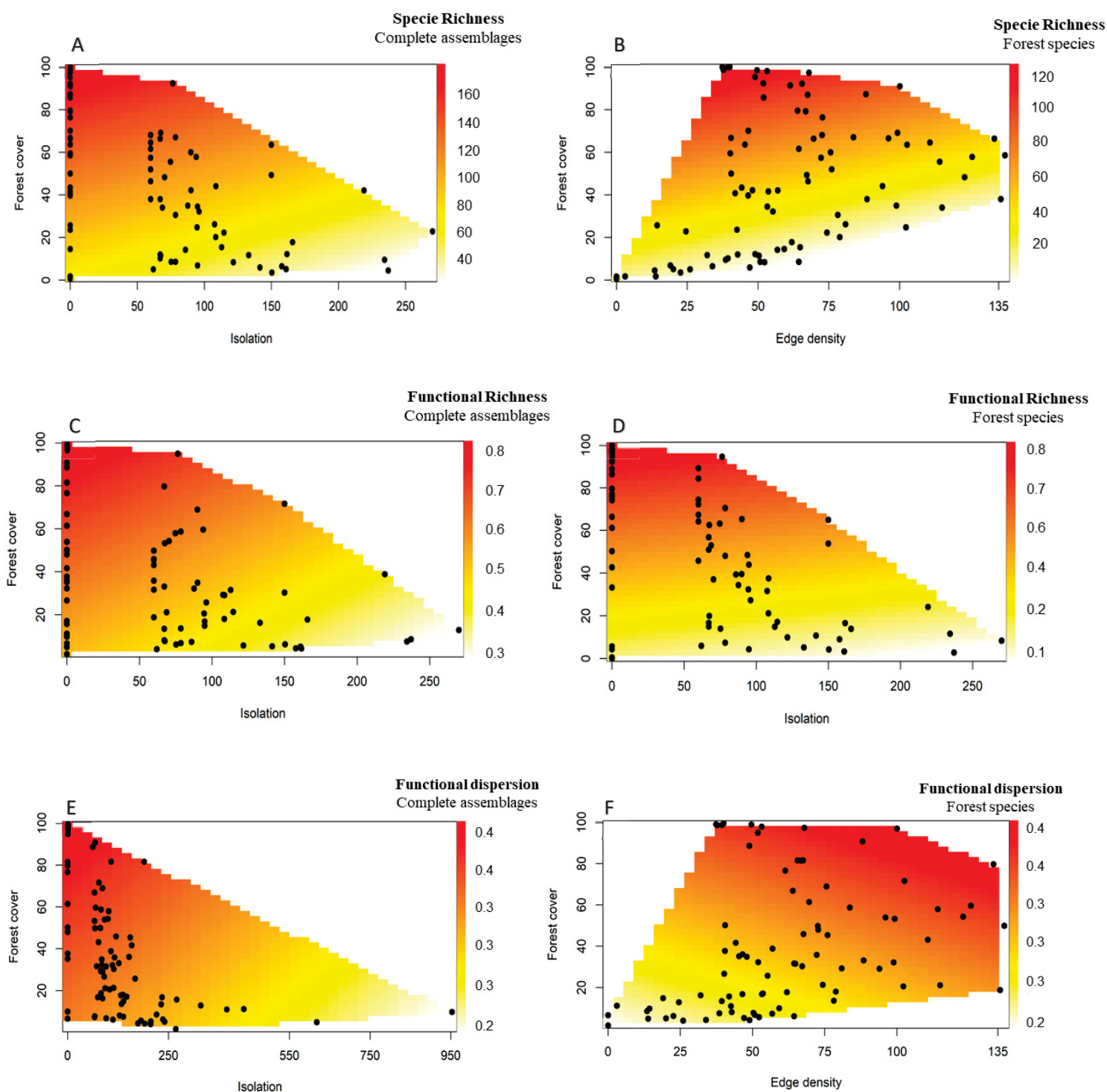


Figure 2 Predicted distribution of diversity indexes of birds in the Brazilian Atlantic Forest following a gradient of combined effects between landscape elements (forest cover, edge density and isolation). Black dots represent sampled units and red colors represent landscapes with a higher diversity.

Table 1 Taxonomic and functional diversity models based on standardized indices ranked from best to worst according to the Akaike's information criterion (AIC). ΔAIC is the difference between AIC from a certain model to the model with the lowest AIC value. $wAIC$ is the probability of each model being the most appropriate one. Species richness (S), functional richness (FRic), functional dispersion (FDis). Models with $\Delta AIC < 2$ are in bold.

Response variable	Model	AIC	ΔAIC	$wAIC$
$S_{complete}$	Forest Cover + Isolation	833.1	0	0.41
	Forest Cover	833.6	0.46	0.33
	no effect (~1)	857.5	24.36	0
$FRic_{complete}$	Forest Cover + Isolation	-107.8	0	0.64
	no effect (~1)	-90.3	17.47	0
$FDis_{complete}$	Forest Cover	-487.3	0	0.19
	Forest Cover + Land.diversity	-487.2	0.17	0.17
	Forest Cover + Edge Density	-487.1	0.28	0.16
	no effect (~1)	-486.1	1.25	0.10
S_{forest}	Forest Cover + Edge density	755.5	0	0.77
	no effect (~1)	800.6	45.17	0
$FRic_{forest}$	Forest Cover	-34.8	0	0.35
	Forest Cover + Isolation	-34.3	0.49	0.28
	Forest Cover + Edge density	-33.4	1.46	0.18
	Forest Cover + Land.diversity	-33.3	1.48	0.17
$FDis_{forest}$	no effect (~1)	6.9	41.70	0
	Forest Cover + Isolation	-386.4	0	0.53
	Forest Cover + Edge density	-384.5	1.94	0.20
	no effect (~1)	-368.3	18.12	0

Functional richness of complete assemblages was best explained by the combined effect of forest cover and isolation. The model described higher values of functional richness of entire assemblages in landscapes with more than 50% of forest cover and less isolation (approximately between 50 and 100 m) ($wAIC = 0.66$) (Figure 2c, Table 1). Four models were equally plausible in describing the functional richness of forest species. The best model was a univariate model containing forest cover ($wAIC = 0.35$), followed by the combined effect of forest cover and isolation ($wAIC = 0.28$) (Figure 2d, Table 1), or forest cover and edge density ($wAIC = 0.18$), or forest cover and landscape diversity ($wAIC = 0.17$).

For functional dispersion of entire assemblages, none of the models were plausible ($\Delta AIC < 2$) to explain variation in functional dispersion in forest structure gradient. However, two models best describing functional dispersion of forest-dependent species. The first model considered the combined effect of forest cover and isolation. The model described a higher functional dispersion in landscapes with more than 60% of forest cover and less isolated landscape (i.e., less than 150 m) ($wAIC = 0.53$) (Figure 2e, Table 1). The second model considered the combined effect of forest cover and edge density. The prediction of the second model described a higher functional dispersion in landscapes with high forest cover and high edge density ($wAIC = 0.20$) (Figure 2f, Table 1).

Relationship between bird traits and landscape variables

The two axes of RLQ analysis explained 98% of the variance (Figure 3a). The fourth-corner analysis identified that the first axis of RLQ ordination and traits (Q.axes) showed a positive correlation with frugivory and negative correlations with granivory and ground-feeding (Figure 3b). However, links between RLQ and landscape structure (R.axes) identified significant relationships of two axes. The first axis was related positively to forest cover and negatively related to isolation, edge density, and landscape diversity. The second axis was only related negatively to the edge density (Figure 3b).

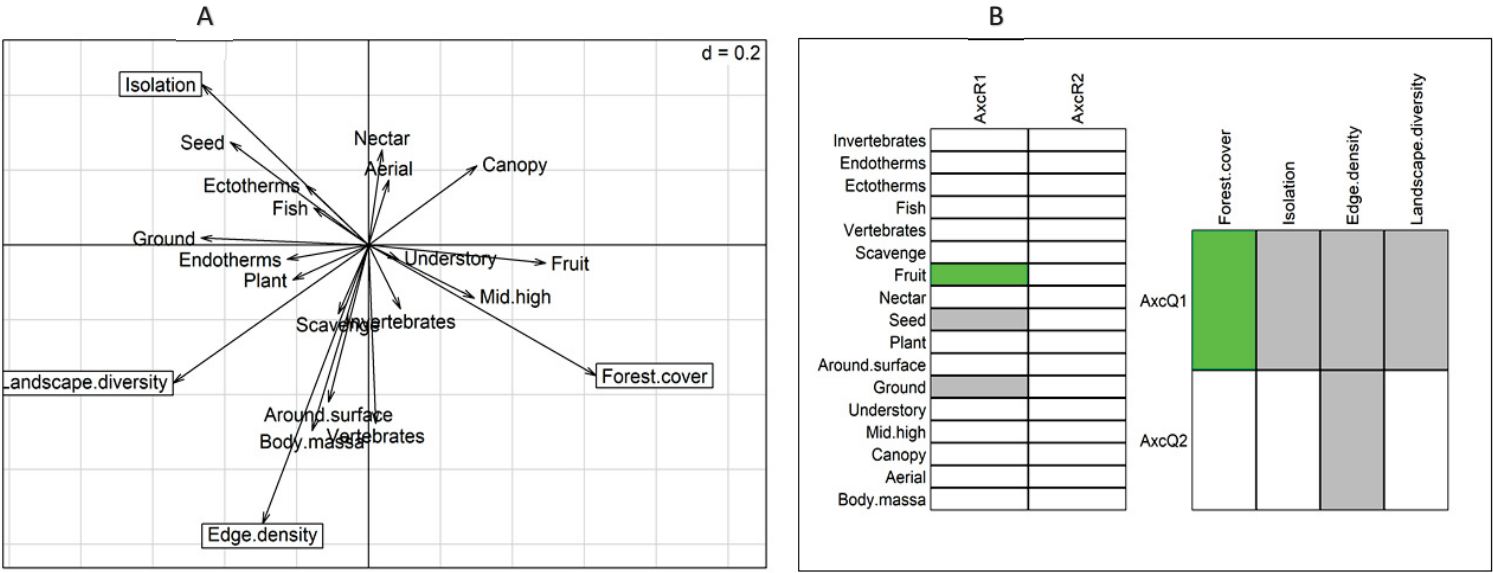


Figure 3 Ordination of landscape elements (rectangle) and functional traits along the two first axes of the RLQ analysis, for Atlantic birds in Southern of Brazil (A). Results of fourth-corner analysis, where green and gray colors represent positive and negative correlations respectively (B). Values of d represent the grid size.

DISCUSSION

By combining extensive data on bird composition and species traits across a gradient of landscape conversion, we were able to untangle the contrasting effects of landscape structures on bird diversity dimensions by weighing habitat requirements of species. We found that the loss of species of forest-dependent assemblages was more marked than in the complete assemblages. Similarly, the reduction of functional richness was higher in forest dependent assemblages than the complete assemblages. This finding may indicate that the complete assemblages are accompanied by compensatory dynamics of species and traits, that is, the reduction in functional spaces due to loss of forest species is filled by non-forested species (Morante-Filho *et al.* 2018a; Matuoka *et al.* 2020). However, in a scenario of intense land-use change, the quality of ecosystem services, mainly those performed by forested species like frugivorous and insectivorous specialist species are not compensated.

The strength of relations was different when both categories of forest dependence was taken into account, reinforcing the importance to consider habitat requirements of species. We found an increase in taxonomic and functional diversity when forest cover

was combined with edge density, landscape diversity, and less isolation. This pattern can be related to landscape heterogeneity theory that predicts higher biodiversity where a greater resource availability can be used by many species with different life histories (Fahrig *et al.* 2011; Redlich *et al.* 2018). However, as we have shown, even when landscape heterogeneity increases biodiversity, a high amount of forest cover is needed to maintain specialist species and landscape connectivity (Redon *et al.* 2014).

The model evidence that describes functional richness was higher for entire assemblages than forest-dependent species. One likely explanation for this result in particular is that complete assemblages are more diverse in terms of responses to landscape contexts and a model that incorporates forest cover and landscape heterogeneity is sufficient to describe the variation in functional richness. Even in landscapes with less forest cover, we found some degree of functional richness for entire assemblages, which increases with higher forest cover and intermediate level of isolation. Moreover, forest-dependent species dynamics require more structural complexity of forest environments. For example, we found positive effects on functional richness of forest-dependent assemblages when forest cover was combined with edge density, or forest cover and landscape diversity, or forest cover and less isolation. Edge environments are related to higher tree productivity, resource persistence, and detectability of fruits (Albrecht *et al.* 2013). At the same time, leaf quality in sunnier edge environments is attractive for defoliating insect larvae, increasing insectivores birds (Barbaro *et al.* 2014). Moreover, we also observed that landscape diversity enables the coexistence of many birds due to the diversity of habitats these environments provide (Fahrig *et al.* 2011; Redlich *et al.* 2018). Finally, less isolated patches can act as stepping stones, while maintaining the movement of species on the landscape (Uezu *et al.* 2008).

Two models were able to describe functional dispersion only for forest-dependent species, combining forest cover with isolation and forest cover with edge density. The lack of relationship between entire assemblage models and functional dispersion might be due to the diversity of niches created by human-activities, enabling the coexistence of a wide range of traits variability, due to the presence of open area species (e.g., Cracidae, Ardeidae, Threskiornithidae, Cathartidae). In contrast, forest-dependent species only shown a wide range of traits in landscapes with higher forest cover in combination with less isolation or edge density. Landscapes with less forest cover and higher isolation were composed mainly by flycatchers (i.e., Tyrannidae) which showed less variation in traits. These important results support the theory of functional homogenization which postulates that habitat loss and fragmentation cause functional similarity because the species able to persist in this new environment, frequently share similar traits (Liang *et al.* 2019).

Trait-landscape relationship

Our trait-by-landscape analyses revealed the effects of landscape structure on functional traits. In fact, some studies have reported that landscape structure act as environmental filters so that species with similar traits tends to co-occur in face of landscape changes (Duflot *et al.* 2014; Newbold *et al.* 2020). Our analyses indicated that frugivorous birds were positively affected by forest cover and negatively by isolation and landscape diversity. Forest loss can negatively impact frugivorous species as a consequence of decreased resource availability and niche conditions availability (Peña *et al.* 2020). For example, large and specialist frugivores are known to be affected by habitat disturbance (Emer *et al.* 2018) and are often replaced by generalist species that tend to perform better in these conditions (Emer *et al.* 2020). These losses negatively impact

ecosystem functions such as seed dispersal and plant recruitment in small forest-patches (Hagen *et al.* 2012; Bovo *et al.* 2018; Emer *et al.* 2018). In addition, forest-dependent species, such as frugivorous birds, are related to smaller re-colonization chances due to reduced abilities to disperse through the open matrix (Boscolo & Metzger 2011; Da Silveira *et al.* 2016).

The landscape heterogeneity indices (i.e., isolation, edge density, and landscape diversity) also showed positive effects on granivores, large-bodied, and ground-species (Figure 3). Increased abundance in granivorous species may result from forest fragmentation (i.e. increase physical isolation across small forest-patches) (Donoso *et al.* 2004), and abundance of resources in croplands and natural grasslands. Small forest-patches have a higher edge density than continuous forests (Fahrig 2003) and this juxtaposition of habitats increases habitat diversity, which may promote the accumulation of species with different traits and habitat requirements. Also, we found a positive relationship between edge density and body mass. An important factor of edge environments is the greater detectability of birds like eagles, vultures, ducks, which may contribute to strong variation in body mass. Overall, our results indicate the important influence of landscape structure in filtering species and specific traits, affecting trait-distribution and the interactions birds are likely to establish in these environments.

CONCLUSION

Our study demonstrates the importance of considering particular sets of traits (forest-dependent species and non-dependent species) to gain insights into the effect of landscape composition and configuration on ecosystem functions. When considering only the entire assemblages, important changes to ecological functions remain undetected. Taxonomic and functional changes were mostly detected when considering forest-

dependent species, which are deeply affected by such transformations in the original habitat. Refining the understanding of the relationship between landscape and biodiversity components, our results provide important advances that can be further used not only to determine the community assembly in anthropogenic landscapes but also to improve and foster conservation actions in such threatened and heterogeneous environments.

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SUPPLEMENTARY MATERIAL

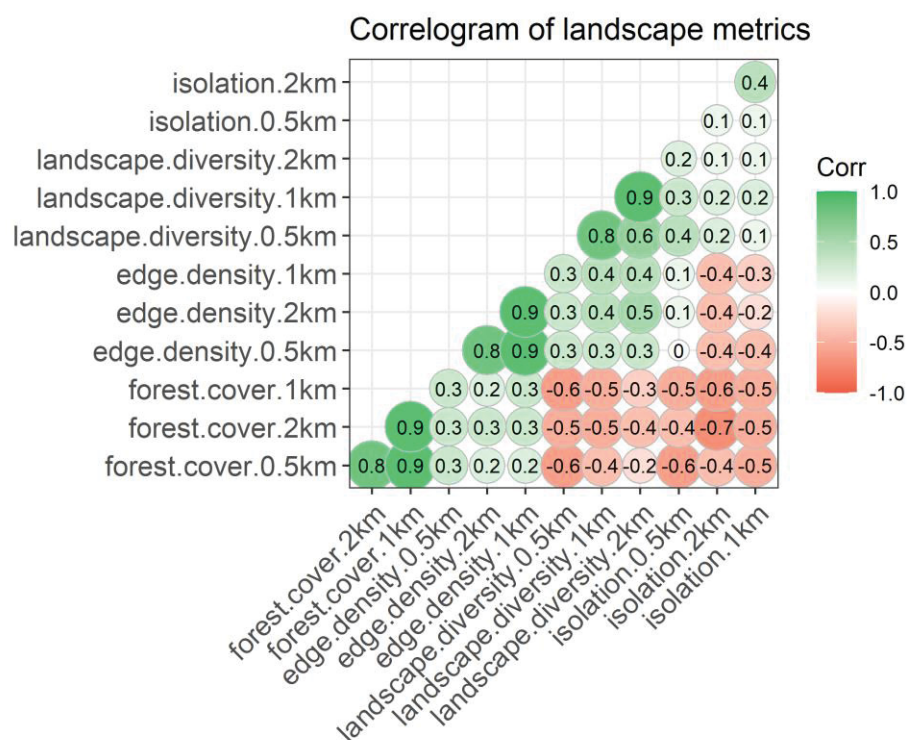


Figure A1 Correlation between landscape metrics. Correlations values above 0.7 were not considered for model selection approach. Numbers next to variables correspond to spatial scales.

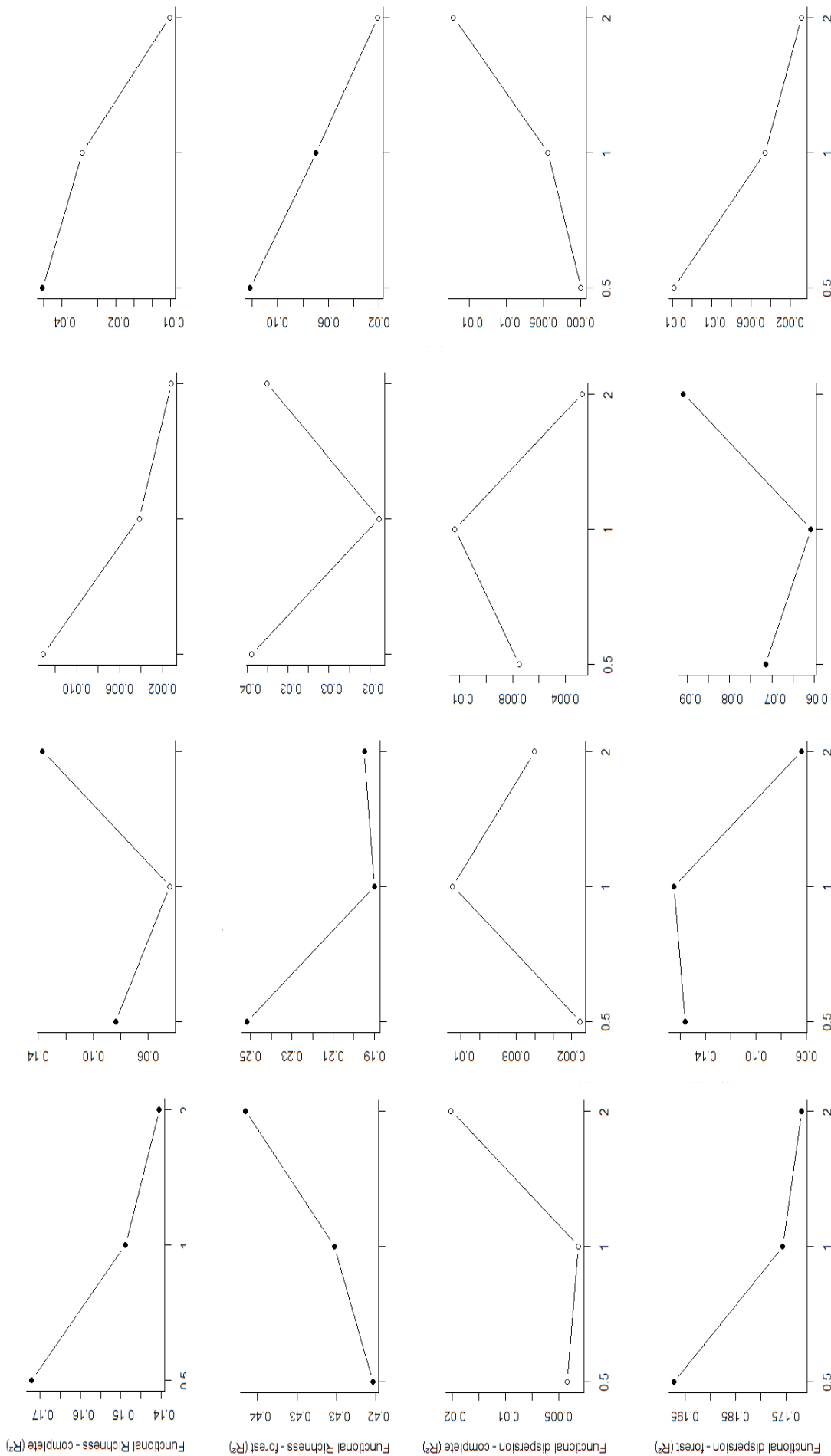


Figure A2 Plots of a set of multi-scale analyses (i.e., scale of effect) using R-square to index of strength of the relationship between three spatial scales (0.5km, 1km, and 2km). Black-filled and white-filled dots represent models with significant and non-significant estimate models coefficients respectively.

Table A1 Bird species found in 86 communities across southern of Brazilian Atlantic Forest. The nomenclature and taxonomic position follow *Comitê Brasileiro de Registros Ornitológicos* CBRO 2015. Habitat preferences following Bregman et al. (2014), and are indicated by forest dependence (1) and non-forest species (2).

Order	Family	Species	English Name	Habitat
Tinamiformes	Tinamidae	<i>Tinamus solitarius</i>	Solitary Tinamou	1
	Tinamidae	<i>Crypturellus obsoletus</i>	Brown Tinamou	1
	Tinamidae	<i>Crypturellus noctivagus</i>	Yellow-legged Tinamou	1
	Tinamidae	<i>Crypturellus parvirostris</i>	Small-billed Tinamou	2
	Tinamidae	<i>Crypturellus tataupa</i>	Tataupa Tinamou	2
	Tinamidae	<i>Rhynchotus rufescens</i>	Red-winged Tinamou	2
	Tinamidae	<i>Nothura maculosa</i>	Spotted Nothura	2
Galliformes	Cracidae	<i>Penelope superciliaris</i>	Rusty-margined Guan	1
	Cracidae	<i>Penelope obscura</i>	Dusky-legged Guan	1
	Cracidae	<i>Aburria jacutinga</i>	Black-fronted Piping-Guan	1
	Cracidae	<i>Ortalis guttata</i>	Speckled Chachalaca	1
Pelecaniformes	Odontophoridae	<i>Odontophorus capueira</i>	Spot-winged Wood-Quail	1
	Ardeidae	<i>Bubulcus ibis</i>	Cattle Egret	2
	Ardeidae	<i>Syrigma sibilatrix</i>	Whistling Heron	2
Cathartiformes	Threskiornithidae	<i>Theristicus caudatus</i>	Buff-necked Ibis	2
	Cathartidae	<i>Cathartes aura</i>	Turkey Vulture	2
	Cathartidae	<i>Coragyps atratus</i>	Black Vulture	2
Accipitriformes	Cathartidae	<i>Sarcorampus papa</i>	King Vulture	1
	Accipitridae	<i>Leptodon cayanensis</i>	Gray-headed Kite	2
	Accipitridae	<i>Elanoides forficatus</i>	Swallow-tailed Kite	2
	Accipitridae	<i>Elanus leucurus</i>	White-tailed Kite	2
	Accipitridae	<i>Harpagus diodon</i>	Rufous-thighed Kite	2
	Accipitridae	<i>Circus buffoni</i>	Long-winged Harrier	2
	Accipitridae	<i>Accipiter poliogaster</i>	Gray-bellied Hawk	1
	Accipitridae	<i>Accipiter superciliosus</i>	Tiny Hawk	1
	Accipitridae	<i>Accipiter striatus</i>	Sharp-shinned Hawk	1
	Accipitridae	<i>Ictinia plumbea</i>	Plumbeous Kite	2
	Accipitridae	<i>Rostrhamus sociabilis</i>	Snail Kite	2
	Accipitridae	<i>Geranoospiza caerulescens</i>	Crane Hawk	2
	Accipitridae	<i>Buteogallus aequinoctialis</i>	Rufous Crab Hawk	2
	Accipitridae	<i>Heterospizias meridionalis</i>	Savanna Hawk	2
	Accipitridae	<i>Amadonastur lacernulatus</i>	White-necked Hawk	1
	Accipitridae	<i>Urubitinga urubitinga</i>	Great Black Hawk	2
	Accipitridae	<i>Rupornis magnirostris</i>	Roadside Hawk	2
	Accipitridae	<i>Geranoaetus albicaudatus</i>	White-tailed Hawk	1
	Accipitridae	<i>Geranoaetus melanoleucus</i>	Black-chested Buzzard-Eagle	2
	Accipitridae	<i>Pseudastur polionotus</i>	Mantled Hawk	1
Charadriiformes	Accipitridae	<i>Buteo brachyurus</i>	Short-tailed Hawk	1
	Accipitridae	<i>Spizaetus tyrannus</i>	Black Hawk-Eagle	1
	Charadriidae	<i>Vanellus chilensis</i>	Southern Lapwing	2
Columbiformes	Columbidae	<i>Columbina talpacoti</i>	Ruddy Ground-Dove	2

Order	Family	Species	English Name	Habitat
Cuculiformes	Columbidae	<i>Columbina squammata</i>	Scaled Dove	2
	Columbidae	<i>Columbina picui</i>	Picui Ground-Dove	2
	Columbidae	<i>Claravis pretiosa</i>	Blue Ground-Dove	2
	Columbidae	<i>Columba livia</i>	Rock Pigeon	2
	Columbidae	<i>Patagioenas picazuro</i>	Picazuro Pigeon	1
	Columbidae	<i>Patagioenas cayennensis</i>	Pale-vented Pigeon	1
	Columbidae	<i>Patagioenas plumbea</i>	Plumbeous Pigeon	1
	Columbidae	<i>Zenaida auriculata</i>	Eared Dove	2
	Columbidae	<i>Leptotila verreauxi</i>	White-tipped Dove	1
	Columbidae	<i>Leptotila rufaxilla</i>	Gray-fronted Dove	1
	Columbidae	<i>Geotrygon montana</i>	Ruddy Quail-Dove	1
	Cuculidae	<i>Piaya cayana</i>	Squirrel Cuckoo	1
	Cuculidae	<i>Coccyzus melacoryphus</i>	Dark-billed Cuckoo	1
	Cuculidae	<i>Crotophaga major</i>	Greater Ani	1
	Cuculidae	<i>Crotophaga ani</i>	Smooth-billed Ani	2
	Cuculidae	<i>Guira guira</i>	Guira Cuckoo	2
	Cuculidae	<i>Tapera naevia</i>	Striped Cuckoo	1
	Cuculidae	<i>Dromococcyx pavoninus</i>	Pavonine Cuckoo	1
	Tytonidae	<i>Tyto furcata</i>	American Barn Owl	2
	Strigidae	<i>Megascops choliba</i>	Tropical Screech-Owl	2
	Strigidae	<i>Megascops atricapilla</i>	Black-capped Screech-Owl	1
	Strigidae	<i>Megascops sanctaecatarinae</i>	Long-tufted Screech-Owl	1
	Strigidae	<i>Pulsatrix koeniswaldiana</i>	Tawny-browed Owl	1
	Strigidae	<i>Strix hylophila</i>	Rusty-barred Owl	1
	Strigidae	<i>Strix virgata</i>	Mottled Owl	2
	Strigidae	<i>Glaucidium minutissimum</i>	Least Pygmy-Owl	1
	Strigidae	<i>Glaucidium brasilianum</i>	Ferruginous Pygmy-Owl	2
	Strigidae	<i>Athene cunicularia</i>	Burrowing Owl	2
	Strigidae	<i>Asio clamator</i>	Striped Owl	2
	Strigidae	<i>Asio stygius</i>	Stygian Owl	1
	Strigidae	<i>Asio flammeus</i>	Short-eared Owl	2
Caprimulgiformes	Nyctibiidae	<i>Nyctibius griseus</i>	Common Potoo	1
	Caprimulgidae	<i>Lurocalis semitorquatus</i>	Short-tailed Nighthawk	1
	Caprimulgidae	<i>Nyctidromus albicollis</i>	Common Pauraque	2
	Caprimulgidae	<i>Hydropsalis anomala</i>	Sickle-winged Nightjar	1
	Caprimulgidae	<i>Hydropsalis longirostris</i>	Band-winged Nightjar	2
	Caprimulgidae	<i>Hydropsalis torquata</i>	Scissor-tailed Nightjar	2
Apodiformes	Caprimulgidae	<i>Hydropsalis forcipata</i>	Long-trained Nightjar	2
	Apodidae	<i>Cypseloides senex</i>	Great Dusky Swift	2
	Apodidae	<i>Streptoprocne zonaris</i>	White-collared Swift	1
	Apodidae	<i>Streptoprocne biscutata</i>	Biscutate Swift	2
	Apodidae	<i>Chaetura cinereiventris</i>	Gray-rumped Swift	2
	Apodidae	<i>Chaetura meridionalis</i>	Sick's Swift	2
	Apodidae	<i>Panyptila cayennensis</i>	Lesser Swallow-tailed Swift	1
	Trochilidae	<i>Ramphodon naevius</i>	Saw-billed Hermit	1

Order	Family	Species	English Name	Habitat	
	Trochilidae	<i>Glaucis hirsutus</i>	Rufous-breasted Hermit	1	
	Trochilidae	<i>Phaethornis squalidus</i>	Dusky-throated Hermit	1	
	Trochilidae	<i>Phaethornis pretrei</i>	Planalto Hermit	1	
	Trochilidae	<i>Phaethornis eurynome</i>	Scale-throated Hermit	1	
	Trochilidae	<i>Eupetomena macroura</i>	Swallow-tailed Hummingbird	2	
	Trochilidae	<i>Aphantochroa cirrochloris</i>	Sombre Hummingbird	2	
	Trochilidae	<i>Florisuga fusca</i>	Black Jacobin	2	
	Trochilidae	<i>Colibri serrirostris</i>	White-vented Violetear	2	
	Trochilidae	<i>Anthracothorax nigricollis</i>	Black-throated Mango	2	
	Trochilidae	<i>Stephanoxis lalandi</i>	Green-crowned Plovercrest	1	
	Trochilidae	<i>Lophornis chalybeus</i>	Festive Coquette	1	
	Trochilidae	<i>Chlorostilbon lucidus</i>	Glittering-bellied Emerald	2	
	Trochilidae	<i>Thalurania glaucopis</i>	Violet-capped Woodnymph	1	
	Trochilidae	<i>Hylocharis chrysura</i>	Gilded Hummingbird	2	
	Trochilidae	<i>Leucochloris albicollis</i>	White-throated Hummingbird	1	
	Trochilidae	<i>Amazilia versicolor</i>	Versicolored Emerald	1	
	Trochilidae	<i>Amazilia fimbriata</i>	Glittering-throated Emerald	2	
	Trochilidae	<i>Amazilia lactea</i>	Sapphire-spangled Emerald	2	
	Trochilidae	<i>Heliodoxa rubricauda</i>	Brazilian Ruby	2	
	Trochilidae	<i>Calliphlox amethystina</i>	Amethyst Woodstar	2	
	Trogonidae	<i>Trogon viridis</i>	Green-backed Trogon	1	
	Trogoniiformes	Trogonidae	<i>Trogon surrucura</i>	Surucua Trogon	1
		Trogonidae	<i>Trogon rufus</i>	Black-throated Trogon	1
	Coraciiformes	Momotidae	<i>Baryphthengus ruficapillus</i>	Rufous-capped Motmot	1
	Galbuliformes	Bucconidae	<i>Notharchus swainsoni</i>	Buff-bellied Puffbird	1
		Bucconidae	<i>Nystalus chacuru</i>	White-eared Puffbird	2
		Bucconidae	<i>Malacoptila striata</i>	Crescent-chested Puffbird	1
		Bucconidae	<i>Nonnula rubecula</i>	Rusty-breasted Nunlet	1
		Ramphastidae	<i>Ramphastos toco</i>	Toco Toucan	2
		Ramphastidae	<i>Ramphastos vitellinus</i>	Channel-billed Toucan	1
		Ramphastidae	<i>Ramphastos dicolorus</i>	Red-breasted Toucan	1
		Ramphastidae	<i>Selenidera maculirostris</i>	Spot-billed Toucanet	1
		Ramphastidae	<i>Pteroglossus bailloni</i>	Saffron Toucanet	1
		Ramphastidae	<i>Pteroglossus aracari</i>	Black-necked Aracari	1
		Ramphastidae	<i>Pteroglossus castanotis</i>	Chestnut-eared Aracari	1
Picidae		<i>Picumnus cirratus</i>	White-barred Piculet	2	
Piciformes		Picidae	<i>Picumnus temminckii</i>	Ochre-collared Piculet	2
Picidae		<i>Picumnus albosquamatus</i>	White-wedged Piculet	2	
Picidae		<i>Picumnus nebulosus</i>	Mottled Piculet	2	
Picidae		<i>Melanerpes candidus</i>	White Woodpecker	2	
Picidae		<i>Melanerpes flavifrons</i>	Yellow-fronted Woodpecker	1	
Picidae		<i>Veniliornis passerinus</i>	Little Woodpecker	2	
Picidae		<i>Veniliornis spilogaster</i>	White-spotted Woodpecker	1	
Picidae		<i>Piculus flavigula</i>	Yellow-throated Woodpecker	1	
Picidae	<i>Piculus aurulentus</i>	White-browed Woodpecker	1		

Order	Family	Species	English Name	Habitat
Cariamiformes	Picidae	<i>Colaptes melanochloros</i>	Green-barred Woodpecker	2
	Picidae	<i>Colaptes campestris</i>	Campo Flicker	2
	Picidae	<i>Celeus galeatus</i>	Helmeted Woodpecker	1
	Picidae	<i>Celeus flavescens</i>	Blond-crested Woodpecker	1
	Picidae	<i>Dryocopus lineatus</i>	Lineated Woodpecker	1
	Picidae	<i>Campephilus robustus</i>	Robust Woodpecker	1
	Cariamidae	<i>Cariama cristata</i>	Red-legged Seriema	2
	Falconidae	<i>Caracara plancus</i>	Southern Caracara	2
	Falconidae	<i>Milvago chimachima</i>	Yellow-headed Caracara	2
	Falconidae	<i>Milvago chimango</i>	Chimango Caracara	2
Falconiformes	Falconidae	<i>Herpetotheres cachinnans</i>	Laughing Falcon	2
	Falconidae	<i>Micrastur ruficollis</i>	Barred Forest-Falcon	1
	Falconidae	<i>Micrastur semitorquatus</i>	Collared Forest-Falcon	1
	Falconidae	<i>Falco sparverius</i>	American Kestrel	2
	Falconidae	<i>Falco femoralis</i>	Aplomado Falcon	2
	Psittacidae	<i>Psittacara leucophthalmus</i>	White-eyed Parakeet	2
	Psittacidae	<i>Aratinga auricapillus</i>	Golden-capped Parakeet	2
	Psittacidae	<i>Pyrrhura frontalis</i>	Maroon-bellied Parakeet	1
	Psittacidae	<i>Myiopsitta monachus</i>	Monk Parakeet	2
	Psittacidae	<i>Forpus xanthopterygius</i>	Blue-winged Parrotlet	2
Psittaciformes	Psittacidae	<i>Brotogetis tirica</i>	Plain Parakeet	2
	Psittacidae	<i>Brotogetis chiriri</i>	Yellow-chevroned Parakeet	2
	Psittacidae	<i>Touit melanotus</i>	Brown-backed Parrotlet	1
	Psittacidae	<i>Pionopsitta pileata</i>	Pileated Parrot	1
	Psittacidae	<i>Pionus maximiliani</i>	Scaly-headed Parrot	1
	Psittacidae	<i>Amazona vinacea</i>	Vinaceous-breasted Parrot	1
	Psittacidae	<i>Amazona brasiliensis</i>	Red-tailed Parrot	1
	Psittacidae	<i>Amazona aestiva</i>	Turquoise-fronted Parrot	2
	Thamnophilidae	<i>Terenura maculata</i>	Streak-capped Antwren	1
	Thamnophilidae	<i>Myrmotherula unicolor</i>	Unicolored Antwren	1
Passeriformes	Thamnophilidae	<i>Formicivora acutirostris</i>	Parana Antwren	2
	Thamnophilidae	<i>Rhopias gularis</i>	Star-throated Antwren	1
	Thamnophilidae	<i>Dysithamnus stictothorax</i>	Spot-breasted Antwren	1
	Thamnophilidae	<i>Dysithamnus mentalis</i>	Plain Antwren	1
	Thamnophilidae	<i>Dysithamnus xanthopterus</i>	Rufous-backed Antwren	1
	Thamnophilidae	<i>Herpsilochmus rufimarginatus</i>	Rufous-winged Antwren	1
	Thamnophilidae	<i>Thamnophilus doliatus</i>	Barred Antshrike	2
	Thamnophilidae	<i>Thamnophilus ruficapillus</i>	Rufous-capped Antshrike	2
	Thamnophilidae	<i>Thamnophilus pelzelni</i>	Planalto Slaty-Antshrike	1
	Thamnophilidae	<i>Thamnophilus caerulescens</i>	Variable Antshrike	1
	Thamnophilidae	<i>Hypoedaleus guttatus</i>	Spot-backed Antshrike	1
	Thamnophilidae	<i>Batara cinerea</i>	Giant Antshrike	1
	Thamnophilidae	<i>Mackenziaena leachii</i>	Large-tailed Antshrike	1
	Thamnophilidae	<i>Mackenziaena severa</i>	Tufted Antshrike	2
	Thamnophilidae	<i>Biatas nigropectus</i>	White-bearded Antshrike	1

Order	Family	Species	English Name	Habitat
	Thamnophilidae	<i>Myrmoderus squamosus</i>	Squamate Antbird	1
	Thamnophilidae	<i>Pyriglena leucoptera</i>	White-shouldered Fire-eye	1
	Thamnophilidae	<i>Dryophila ferruginea</i>	Ferruginous Antbird	1
	Thamnophilidae	<i>Dryophila rubricollis</i>	Bertoni's Antbird	1
	Thamnophilidae	<i>Dryophila ochropyga</i>	Ochre-rumped Antbird	1
	Thamnophilidae	<i>Dryophila malura</i>	Dusky-tailed Antbird	1
	Thamnophilidae	<i>Dryophila squamata</i>	Scaled Antbird	1
	Conopophagidae	<i>Conopophaga lineata</i>	Rufous Gnateater	1
	Conopophagidae	<i>Conopophaga melanops</i>	Black-cheeked Gnateater	1
	Grallariidae	<i>Grallaria varia</i>	Variegated Antpitta	1
	Grallariidae	<i>Hylopezus nattereri</i>	Speckle-breasted Antpitta	1
	Rhinocryptidae	<i>Merulaxis ater</i>	Slaty Bristlefront	1
	Rhinocryptidae	<i>Eleoscytalopus indigoticus</i>	White-breasted Tapaculo	1
	Rhinocryptidae	<i>Scytalopus speluncae</i>	Mouse-colored Tapaculo	1
	Rhinocryptidae	<i>Psilorhamphus guttatus</i>	Spotted Bamboowren	1
	Formicariidae	<i>Formicarius colma</i>	Rufous-capped Antthrush	1
	Formicariidae	<i>Chamaeza campanisona</i>	Short-tailed Antthrush	1
	Formicariidae	<i>Chamaeza meruloides</i>	Such's Antthrush	1
	Formicariidae	<i>Chamaeza ruficauda</i>	Rufous-tailed Antthrush	1
	Scleruridae	<i>Sclerurus scansor</i>	Rufous-breasted Leaf-tosser	1
	Dendrocolaptidae	<i>Dendrocincla turdina</i>	Plain-winged Woodcreeper	1
	Dendrocolaptidae	<i>Sittasomus griseicapillus</i>	Olivaceous Woodcreeper	1
	Dendrocolaptidae	<i>Xiphorhynchus fuscus</i>	Lesser Woodcreeper	1
	Dendrocolaptidae	<i>Campylorhamphus falcularius</i>	Black-billed Scythebill	1
	Dendrocolaptidae	<i>Lepidocolaptes angustirostris</i>	Narrow-billed Woodcreeper	1
	Dendrocolaptidae	<i>Lepidocolaptes falcinellus</i>	Scalloped Woodcreeper	1
	Dendrocolaptidae	<i>Dendrocolaptes platyrostris</i>	Planalto Woodcreeper	1
	Dendrocolaptidae	<i>Xiphocolaptes albicollis</i>	White-throated Woodcreeper	1
	Xenopidae	<i>Xenops minutus</i>	Plain Xenops	1
	Xenopidae	<i>Xenops rutilans</i>	Streaked Xenops	1
	Furnariidae	<i>Furnarius rufus</i>	Rufous Hornero	2
	Furnariidae	<i>Lochmias nematura</i>	Sharp-tailed Streamcreeper	1
	Furnariidae	<i>Clibanornis dendrocolaptoides</i>	Canebrake Groundcreeper	1
	Furnariidae	<i>Automolus leucophthalmus</i>	White-eyed Foliage-gleaner	1
	Furnariidae	<i>Anabazenops fuscus</i>	White-collared Foliage-gleaner	1
	Furnariidae	<i>Anabacerthia amaurotis</i>	White-browed Foliage-gleaner	1
	Furnariidae	<i>Anabacerthia lichtensteini</i>	Ochre-breasted Foliage-gleaner	1
	Furnariidae	<i>Philydor atricapillus</i>	Black-capped Foliage-gleaner	1
	Furnariidae	<i>Philydor rufum</i>	Buff-fronted Foliage-gleaner	1
	Furnariidae	<i>Heliobletus contaminatus</i>	Sharp-billed Treehunter	1
	Furnariidae	<i>Syndactyla rufosuperciliata</i>	Buff-browed Foliage-gleaner	1
	Furnariidae	<i>Cichlocolaptes leucophrys</i>	Pale-browed Treehunter	1
	Furnariidae	<i>Leptasthenura setaria</i>	Araucaria Tit-Spinetail	1
	Furnariidae	<i>Phacellodomus ruber</i>	Greater Thornbird	2
	Furnariidae	<i>Phacellodomus ferrugineigula</i>	Orange-breasted Thornbird	2

Order	Family	Species	English Name	Habitat
	Furnariidae	<i>Anumbius annumbi</i>	Firewood-Gatherer	2
	Furnariidae	<i>Certhiaxis cinnamomeus</i>	Yellow-chinned Spinetail	2
	Furnariidae	<i>Synallaxis ruficapilla</i>	Rufous-capped Spinetail	1
	Furnariidae	<i>Synallaxis cinerascens</i>	Gray-bellied Spinetail	1
	Furnariidae	<i>Synallaxis frontalis</i>	Sooty-fronted Spinetail	2
	Furnariidae	<i>Synallaxis albescens</i>	Pale-breasted Spinetail	2
	Furnariidae	<i>Synallaxis spixi</i>	Spix's Spinetail	2
	Furnariidae	<i>Cranioleuca vulpina</i>	Rusty-backed Spinetail	2
	Furnariidae	<i>Cranioleuca obsoleta</i>	Olive Spinetail	1
	Furnariidae	<i>Cranioleuca pallida</i>	Pallid Spinetail	1
	Pipridae	<i>Pipra fasciicauda</i>	Band-tailed Manakin	1
	Pipridae	<i>Manacus manacus</i>	White-bearded Manakin	1
	Pipridae	<i>Ilicura militaris</i>	Pin-tailed Manakin	1
	Pipridae	<i>Chiroxiphia caudata</i>	Swallow-tailed Manakin	1
	Oxyruncidae	<i>Oxyruncus cristatus</i>	Sharpbill	1
	Onychorhynchidae	<i>Onychorhynchus swainsoni</i>	Atlantic Royal Flycatcher	1
	Onychorhynchidae	<i>Myiobius barbatus</i>	Whiskered Flycatcher	1
	Tityridae	<i>Schiffornis virescens</i>	Greenish Schiffornis	1
	Tityridae	<i>Tityra inquisitor</i>	Black-crowned Tityra	1
	Tityridae	<i>Tityra cayana</i>	Black-tailed Tityra	2
	Tityridae	<i>Pachyramphus viridis</i>	Green-backed Becard	2
	Tityridae	<i>Pachyramphus castaneus</i>	Chestnut-crowned Becard	1
	Tityridae	<i>Pachyramphus polychropterus</i>	White-winged Becard	2
	Tityridae	<i>Pachyramphus validus</i>	Crested Becard	2
	Cotingidae	<i>Carpornis cucullata</i>	Hooded Berryeater	1
	Cotingidae	<i>Carpornis melanocephala</i>	Black-headed Berryeater	1
	Cotingidae	<i>Pyroderus scutatus</i>	Red-ruffed Fruitcrow	1
	Cotingidae	<i>Lipaugus lanioides</i>	Cinnamon-vented Piha	1
	Cotingidae	<i>Procnias nudicollis</i>	Bare-throated Bellbird	1
	Pipritidae	<i>Piprites chloris</i>	Wing-barred Piprites	1
	Platyrinchidae	<i>Platyrinchus mystaceus</i>	White-throated Spadebill	1
	Rhynchocyclidae	<i>Mionectes rufiventris</i>	Gray-hooded Flycatcher	1
	Rhynchocyclidae	<i>Leptopogon amaurocephalus</i>	Sepia-capped Flycatcher	1
	Rhynchocyclidae	<i>Corythopsis delalandi</i>	Southern Antpipit	1
	Rhynchocyclidae	<i>Phylloscartes eximius</i>	Southern Bristle-Tyrant	1
	Rhynchocyclidae	<i>Phylloscartes ventralis</i>	Mottle-cheeked Tyrannulet	1
	Rhynchocyclidae	<i>Phylloscartes kronei</i>	Restinga Tyrannulet	1
	Rhynchocyclidae	<i>Phylloscartes oustaleti</i>	Oustalet's Tyrannulet	1
	Rhynchocyclidae	<i>Phylloscartes difficilis</i>	Serra do Mar Tyrannulet	1
	Rhynchocyclidae	<i>Phylloscartes sylvioius</i>	Bay-ringed Tyrannulet	1
	Rhynchocyclidae	<i>Tolmomyias sulphurescens</i>	Yellow-olive Flycatcher	1
	Rhynchocyclidae	<i>Todirostrum poliocephalum</i>	Gray-headed Tody-Flycatcher	1
	Rhynchocyclidae	<i>Todirostrum cinereum</i>	Common Tody-Flycatcher	2
	Rhynchocyclidae	<i>Poecilatriccus plumbeiceps</i>	Ochre-faced Tody-Flycatcher	1
	Rhynchocyclidae	<i>Myiornis auricularis</i>	Eared Pygmy-Tyrant	1

Order	Family	Species	English Name	Habitat
	Rhynchocyclidae	<i>Hemitriccus diops</i>	Drab-breasted Pygmy-Tyrant	1
	Rhynchocyclidae	<i>Hemitriccus obsoletus</i>	Brown-breasted Pygmy-Tyrant	1
	Rhynchocyclidae	<i>Hemitriccus orbitatus</i>	Eye-ringed Tody-Tyrant	1
	Rhynchocyclidae	<i>Hemitriccus margaritaceiventer</i>	Pearly-vented Tody-tyrant	1
	Tyrannidae	<i>Hirundinea ferruginea</i>	Cliff Flycatcher	1
	Tyrannidae	<i>Euscarthmus meloryphus</i>	Tawny-crowned Pygmy-Tyrant	2
	Tyrannidae	<i>Tyranniscus burmeisteri</i>	Rough-legged Tyrannulet	1
	Tyrannidae	<i>Camptostoma obsoletum</i>	Southern Beardless-Tyrannulet	2
	Tyrannidae	<i>Elaenia flavogaster</i>	Yellow-bellied Elaenia	1
	Tyrannidae	<i>Elaenia spectabilis</i>	Large Elaenia	1
	Tyrannidae	<i>Elaenia parvirostris</i>	Small-billed Elaenia	2
	Tyrannidae	<i>Elaenia mesoleuca</i>	Olivaceous Elaenia	1
	Tyrannidae	<i>Elaenia chiriquensis</i>	Lesser Elaenia	1
	Tyrannidae	<i>Elaenia obscura</i>	Highland Elaenia	1
	Tyrannidae	<i>Myiopagis caniceps</i>	Gray Elaenia	1
	Tyrannidae	<i>Myiopagis viridicata</i>	Greenish Elaenia	2
	Tyrannidae	<i>Capsiempis flaveola</i>	Yellow Tyrannulet	1
	Tyrannidae	<i>Phaeomyias murina</i>	Mouse-colored Tyrannulet	2
	Tyrannidae	<i>Phyllomyias virescens</i>	Greenish Tyrannulet	1
	Tyrannidae	<i>Phyllomyias fasciatus</i>	Planalto Tyrannulet	1
	Tyrannidae	<i>Phyllomyias griseicapilla</i>	Gray-capped Tyrannulet	1
	Tyrannidae	<i>Culicivora caudacuta</i>	Sharp-tailed Tyrant	2
	Tyrannidae	<i>Serpophaga nigricans</i>	Sooty Tyrannulet	2
	Tyrannidae	<i>Serpophaga subcristata</i>	White-crested Tyrannulet	2
	Tyrannidae	<i>Attila phoenicurus</i>	Rufous-tailed Attila	1
	Tyrannidae	<i>Attila rufus</i>	Gray-hooded Attila	1
	Tyrannidae	<i>Legatus leucophaeus</i>	Piratic Flycatcher	1
	Tyrannidae	<i>Ramphotrigon megacephalum</i>	Large-headed Flatbill	1
	Tyrannidae	<i>Myiarchus swainsoni</i>	Swainson's Flycatcher	2
	Tyrannidae	<i>Myiarchus ferox</i>	Short-crested Flycatcher	2
	Tyrannidae	<i>Myiarchus tyrannulus</i>	Brown-crested Flycatcher	2
	Tyrannidae	<i>Sirystes sibilator</i>	Sibilant Sirystes	1
	Tyrannidae	<i>Pitangus sulphuratus</i>	Great Kiskadee	2
	Tyrannidae	<i>Machetornis rixosa</i>	Cattle Tyrant	2
	Tyrannidae	<i>Myiodynastes maculatus</i>	Streaked Flycatcher	2
	Tyrannidae	<i>Megarynchus pitangua</i>	Boat-billed Flycatcher	2
	Tyrannidae	<i>Myiozetetes similis</i>	Social Flycatcher	2
	Tyrannidae	<i>Tyrannus melancholicus</i>	Tropical Kingbird	2
	Tyrannidae	<i>Tyrannus savana</i>	Fork-tailed Flycatcher	2
	Tyrannidae	<i>Empidonomus varius</i>	Variegated Flycatcher	2
	Tyrannidae	<i>Conopias trivirgatus</i>	Three-striped Flycatcher	1
	Tyrannidae	<i>Colonia colonus</i>	Long-tailed Tyrant	1
	Tyrannidae	<i>Myiophobus fasciatus</i>	Bran-colored Flycatcher	2
	Tyrannidae	<i>Pyrocephalus rubinus</i>	Vermilion Flycatcher	2
	Tyrannidae	<i>Fluvicola nengeta</i>	Masked Water-Tyrant	2

Order	Family	Species	English Name	Habitat
	Tyrannidae	<i>Arundinicola leucocephala</i>	White-headed Marsh Tyrant	2
	Tyrannidae	<i>Gubernetes yetapa</i>	Streamer-tailed Tyrant	2
	Tyrannidae	<i>Cnemotriccus fuscatus</i>	Fuscous Flycatcher	2
	Tyrannidae	<i>Lathrotriccus eulerei</i>	Euler's Flycatcher	2
	Tyrannidae	<i>Contopus cinereus</i>	Tropical Pewee	2
	Tyrannidae	<i>Knipolegus cyanirostris</i>	Blue-billed Black-Tyrant	2
	Tyrannidae	<i>Knipolegus lophotes</i>	Crested Black-Tyrant	1
	Tyrannidae	<i>Knipolegus nigerrimus</i>	Velvety Black-Tyrant	1
	Tyrannidae	<i>Satrapa icterophrys</i>	Yellow-browed Tyrant	2
	Tyrannidae	<i>Xolmis cinereus</i>	Gray Monjita	2
	Tyrannidae	<i>Xolmis velatus</i>	White-rumped Monjita	2
	Tyrannidae	<i>Xolmis dominicanus</i>	Black-and-white Monjita	2
	Tyrannidae	<i>Muscipipra vetula</i>	Shear-tailed Gray Tyrant	1
	Vireonidae	<i>Cyclarhis gujanensis</i>	Rufous-browed Peppershrike	2
	Vireonidae	<i>Hylophilus poicilotis</i>	Rufous-crowned Greenlet	1
	Vireonidae	<i>Vireo olivaceus</i>	Red-eyed Vireo	1
	Corvidae	<i>Cyanocorax caeruleus</i>	Azure Jay	1
	Corvidae	<i>Cyanocorax cristatellus</i>	Curl-crested Jay	2
	Corvidae	<i>Cyanocorax chrysops</i>	Plush-crested Jay	1
	Hirundinidae	<i>Pygochelidon cyanoleuca</i>	Blue-and-white Swallow	2
	Hirundinidae	<i>Stelgidopteryx ruficollis</i>	Southern Rough-winged Swallow	1
	Hirundinidae	<i>Progne tapera</i>	Brown-chested Martin	2
	Hirundinidae	<i>Progne chalybea</i>	Gray-breasted Martin	2
	Hirundinidae	<i>Tachycineta albiventer</i>	White-winged Swallow	2
	Hirundinidae	<i>Tachycineta leucorrhoa</i>	White-rumped Swallow	2
	Hirundinidae	<i>Hirundo rustica</i>	Barn Swallow	2
	Hirundinidae	<i>Petrochelidon pyrrhonota</i>	Cliff Swallow	2
	Troglodytidae	<i>Troglodytes musculus</i>	Southern House Wren	2
	Troglodytidae	<i>Cantorchilus longirostris</i>	Long-billed Wren	2
	Donacobiidae	<i>Donacobius atricapilla</i>	Black-capped Donacobius	2
	Poliopitidae	<i>Ramphocaenus melanurus</i>	Long-billed Gnatwren	2
	Turdidae	<i>Turdus flavipes</i>	Yellow-legged Thrush	1
	Turdidae	<i>Turdus leucomelas</i>	Pale-breasted Thrush	1
	Turdidae	<i>Turdus rufiventris</i>	Rufous-bellied Thrush	2
	Turdidae	<i>Turdus amaurochalinus</i>	Creamy-bellied Thrush	2
	Turdidae	<i>Turdus subalaris</i>	Eastern Slaty Thrush	1
	Turdidae	<i>Turdus albicollis</i>	White-necked Thrush	1
	Mimidae	<i>Mimus saturninus</i>	Chalk-browed Mockingbird	2
	Mimidae	<i>Mimus triurus</i>	White-banded Mockingbird	2
	Motacillidae	<i>Anthus lutescens</i>	Yellowish Pipit	2
	Motacillidae	<i>Anthus hellmayri</i>	Hellmayr's Pipit	2
	Passerellidae	<i>Zonotrichia capensis</i>	Rufous-collared Sparrow	2
	Passerellidae	<i>Ammodramus humeralis</i>	Grassland Sparrow	2
	Passerellidae	<i>Arremon semitorquatus</i>	Half-collared Sparrow	1
	Passerellidae	<i>Arremon flavirostris</i>	Saffron-billed Sparrow	1

Order	Family	Species	English Name	Habitat
	Parulidae	<i>Setophaga pitayumi</i>	Tropical Parula	2
	Parulidae	<i>Geothlypis aequinoctialis</i>	Masked Yellowthroat	2
	Parulidae	<i>Basileuterus culicivorus</i>	Golden-crowned Warbler	1
	Parulidae	<i>Myiothlypis flaveola</i>	Flavescent Warbler	2
	Parulidae	<i>Myiothlypis leucoblephara</i>	White-browed Warbler	1
	Parulidae	<i>Myiothlypis rivularis</i>	Neotropical River Warbler	2
	Icteridae	<i>Procacicus solitarius</i>	Solitary Black Cacique	1
	Icteridae	<i>Cacicus chrysopterus</i>	Golden-winged Cacique	1
	Icteridae	<i>Cacicus haemorrhous</i>	Red-rumped Cacique	1
	Icteridae	<i>Icterus cayanensis</i>	Epaulet Oriole	2
	Icteridae	<i>Gnorimopsar chopi</i>	Chopi Blackbird	2
	Icteridae	<i>Agelasticus cyanopus</i>	Unicolored Blackbird	2
	Icteridae	<i>Chrysomus ruficapillus</i>	Chestnut-capped Blackbird	2
	Icteridae	<i>Pseudoleistes guirahuro</i>	Yellow-rumped Marshbird	2
	Icteridae	<i>Agelaioides badius</i>	Grayish Baywing	2
	Icteridae	<i>Molothrus oryzivorus</i>	Giant Cowbird	2
	Icteridae	<i>Molothrus bonariensis</i>	Shiny Cowbird	2
	Icteridae	<i>Sturnella supercilialis</i>	White-browed Meadowlark	2
	Mitrospingidae	<i>Orthogonys chloricterus</i>	Olive-green Tanager	2
	Thraupidae	<i>Orchesticus abeillei</i>	Brown Tanager	1
	Thraupidae	<i>Pipraeidea melanonota</i>	Fawn-breasted Tanager	1
	Thraupidae	<i>Pipraeidea bonariensis</i>	Blue-and-yellow Tanager	1
	Thraupidae	<i>Stephanophorus diadematus</i>	Diademed Tanager	1
	Thraupidae	<i>Cissopis leverianus</i>	Magpie Tanager	1
	Thraupidae	<i>Schistochlamys ruficapillus</i>	Cinnamon Tanager	2
	Thraupidae	<i>Paroaria coronata</i>	Red-crested Cardinal	2
	Thraupidae	<i>Paroaria capitata</i>	Yellow-billed Cardinal	2
	Thraupidae	<i>Tangara seledon</i>	Green-headed Tanager	1
	Thraupidae	<i>Tangara cyanocephala</i>	Red-necked Tanager	1
	Thraupidae	<i>Tangara desmaresti</i>	Brassy-breasted Tanager	1
	Thraupidae	<i>Tangara sayaca</i>	Sayaca Tanager	2
	Thraupidae	<i>Tangara cyanoptera</i>	Azure-shouldered Tanager	1
	Thraupidae	<i>Tangara palmarum</i>	Palm Tanager	2
	Thraupidae	<i>Tangara ornata</i>	Golden-chevroned Tanager	2
	Thraupidae	<i>Tangara peruviana</i>	Black-backed Tanager	1
	Thraupidae	<i>Tangara preciosa</i>	Chestnut-backed Tanager	1
	Thraupidae	<i>Tangara cayana</i>	Burnished-buff Tanager	2
	Thraupidae	<i>Nemosia pileata</i>	Hooded Tanager	2
	Thraupidae	<i>Conirostrum speciosum</i>	Chestnut-vented Conebill	2
	Thraupidae	<i>Sicalis citrina</i>	Stripe-tailed Yellow-Finch	2
	Thraupidae	<i>Sicalis flaveola</i>	Saffron Finch	2
	Thraupidae	<i>Sicalis luteola</i>	Grassland Yellow-Finch	2
	Thraupidae	<i>Haplospiza unicolor</i>	Uniform Finch	2
	Thraupidae	<i>Chlorophanes spiza</i>	Green Honeycreeper	1
	Thraupidae	<i>Hemithraupis guira</i>	Guira Tanager	1

Order	Family	Species	English Name	Habitat
	Thraupidae	<i>Hemithraupis ruficapilla</i>	Rufous-headed Tanager	1
	Thraupidae	<i>Volatinia jacarina</i>	Blue-black Grassquit	2
	Thraupidae	<i>Trichothraupis melanops</i>	Black-goggled Tanager	1
	Thraupidae	<i>Coryphospingus cucullatus</i>	Red-crested Finch	1
	Thraupidae	<i>Lanio cristatus</i>	Flame-crested Tanager	2
	Thraupidae	<i>Tachyphonus coronatus</i>	Ruby-crowned Tanager	1
	Thraupidae	<i>Ramphocelus bresilius</i>	Brazilian Tanager	2
	Thraupidae	<i>Tersina viridis</i>	Swallow Tanager	2
	Thraupidae	<i>Dacnis cayana</i>	Blue Dacnis	2
	Thraupidae	<i>Coereba flaveola</i>	Bananaquit	2
	Thraupidae	<i>Tiaris fuliginosus</i>	Sooty Grassquit	2
	Thraupidae	<i>Sporophila lineola</i>	Lined Seedeater	2
	Thraupidae	<i>Sporophila frontalis</i>	Buffy-fronted Seedeater	1
	Thraupidae	<i>Sporophila falcirostris</i>	Temminck's Seedeater	1
	Thraupidae	<i>Sporophila collaris</i>	Rusty-collared Seedeater	2
	Thraupidae	<i>Sporophila nigricollis</i>	Yellow-bellied Seedeater	2
	Thraupidae	<i>Sporophila caerulea</i>	Double-collared Seedeater	2
	Thraupidae	<i>Sporophila leucoptera</i>	White-bellied Seedeater	2
	Thraupidae	<i>Sporophila hypoxantha</i>	Tawny-bellied Seedeater	2
	Thraupidae	<i>Sporophila angolensis</i>	Chestnut-bellied Seed-Finch	2
	Thraupidae	<i>Embernagra platensis</i>	Great Pampa-Finch	2
	Thraupidae	<i>Emberizoides herbicola</i>	Wedge-tailed Grass-Finch	2
	Thraupidae	<i>Emberizoides ypiranganus</i>	Lesser Grass-Finch	2
	Thraupidae	<i>Saltator similis</i>	Green-winged Saltator	2
	Thraupidae	<i>Saltator maxillosus</i>	Thick-billed Saltator	2
	Thraupidae	<i>Saltator fuliginosus</i>	Black-throated Grosbeak	1
	Thraupidae	<i>Poospiza nigrorufa</i>	Black-and-rufous Warbling-Finch	1
	Thraupidae	<i>Poospiza thoracica</i>	Bay-chested Warbling-Finch	1
	Thraupidae	<i>Microspingus cabanisi</i>	Gray-throated Warbling-Finch	1
	Thraupidae	<i>Thlypopsis sordida</i>	Orange-headed Tanager	2
	Thraupidae	<i>Pyrrhocomma ruficeps</i>	Chestnut-headed Tanager	1
	Thraupidae	<i>Donacospiza albifrons</i>	Long-tailed Reed Finch	2
	Cardinalidae	<i>Piranga flava</i>	Hepatic Tanager	2
	Cardinalidae	<i>Habia rubica</i>	Red-crowned Ant-Tanager	1
	Cardinalidae	<i>Amaurospiza moesta</i>	Blackish-blue Seedeater	1
	Cardinalidae	<i>Cyanoloxia glaucocerulea</i>	Glaucous-blue Grosbeak	2
	Cardinalidae	<i>Cyanoloxia brissonii</i>	Ultramarine Grosbeak	2
	Fringillidae	<i>Spinus magellanicus</i>	Hooded Siskin	2
	Fringillidae	<i>Euphonia chlorotica</i>	Purple-throated Euphonia	2
	Fringillidae	<i>Euphonia violacea</i>	Violaceous Euphonia	2
	Fringillidae	<i>Euphonia chalybea</i>	Green-throated Euphonia	1
	Fringillidae	<i>Euphonia cyanocephala</i>	Golden-rumped Euphonia	2
	Fringillidae	<i>Euphonia pectoralis</i>	Chestnut-bellied Euphonia	1
	Fringillidae	<i>Chlorophonia cyanea</i>	Blue-naped Chlorophonia	2
	Estrildidae	<i>Estrilda astrild</i>	Common Waxbill	2

Order	Family	Species	English Name	Habitat
	Passeridae	<i>Passer domesticus</i>	House Sparrow	2

CHAPTER 2

Untangling the influence of phylogenetic congruence and trait matching on plant-frugivore interaction in deforested landscapes.

Untangling the influence of phylogenetic congruence and trait matching on plant-frugivore interaction in deforested landscapes.

ABSTRACT

Trait matching is a mechanism that mediates frugivory interactions and that has evolved across the phylogenetic history of plants and frugivores. However, forest fragmentation can erode the evolution of traits relationship. We explored how trait matching and phylogenetic congruence contribute to frugivory interactions along a forest fragmentation gradient using a set of key traits. We found that forest fragmentation erodes trait matching and phylogenetic congruence in different ways. Trait matching decreases in deforested landscapes, potentially affecting the effectiveness of interactions. Moreover, fragmentation causes an increase in phylogenetic distance between frequently interacting species, increasing phylogenetic congruence. Our results show that although trait matching is strongest in non-fragmented landscapes with more close-related species, the congruence between phylogenies of interacting species can arise from environmental filtering associated with fragmented landscapes.

Keywords: Cophylogenies, Deforestation, Morphological match, Mutualistic network,

INTRODUCTION

Landscape changes can strongly influence species interactions and associated ecosystem processes, such as predation or frugivory (Hagen *et al.* 2012; Tylianakis & Morris 2017). However, most of our knowledge about the effects of landscape change on biodiversity derives from variation in species richness across disturbed landscapes (Arnan *et al.* 2017), an approach that assumes that all species are functionally equivalent, evolutionary independent (Swenson 2011), and do not interact. Interactions are often constrained by traits; for example the degree of trait matching between mutualistic partners often influences the quality of interactions (Bender *et al.* 2018; Sonne *et al.* 2019). In addition, traits can be phylogenetically conserved, consequently, species that share a common ancestry tend to interact with a similar set of species (Aizen *et al.* 2016; Peralta *et al.* 2020a). Combining functional aspects and shared evolutionary history between plant and animal species is fundamental for investigating coevolution as a process of reciprocal evolutionary change. However, pairwise coevolution is rare in plant-animal systems, whereas diffuse coevolution occurs when there are multiple species interacting, that is, species are more generalists in the resource lineages use (Bello & Barreto 2021; Burin *et al.* 2021). Landscape change may alter the functional and phylogenetic associations of networks because some lineages become locally extinct due to habitat loss. These changes in network structure can have profound effects on ecosystems services (Schleuning *et al.* 2015; Nowak *et al.* 2019; Peña *et al.* 2020). Here we evaluate how landscape change influences the functional and phylogenetic structure of plant-frugivore network across 16 forest patches in the Brazilian Atlantic Forest. trait matching and phylogenetic congruence.

Trait matching and phylogenetic congruence both influence the structure of interaction networks and are expected to be impacted by landscape change. Phylogenetic

congruence occurs when groups of related species preferentially interact with each other (Rezende *et al.* 2007; Tylianakis & Morris 2017). Landscape changes can erode the phylogenetic congruence of interacting species because species of specific lineages may become locally extinct, thereby increasing phylogenetic distances between species. due to stress-induced reduction in phylogenetic breadth (Tylianakis & Morris 2017; Segar *et al.* 2020) A decrease in phylogenetic congruence could be linked with facultative interactions and inconsistent coevolutionary change (Aizen *et al.* 2016). The loss of shared evolutionary history is especially informative given that closely related species preferentially tend to interact with each other (Gómez *et al.* 2010), and functional traits can restrict the range of possible interactions (Díaz *et al.* 2013; Dehling *et al.* 2016a).

Plant-frugivore bird networks show variable levels of trait matching and phylogenetic congruence across gradients (Rezende *et al.* 2007; Bender *et al.* 2018; Schleuning *et al.* 2020). For instance, in plant-frugivore bird networks, large-bodied birds and large-seeded plants have the most unique traits and are often evolutionary distinct from co-occurring species (Emer *et al.* 2019). In disturbed landscapes, large species are replaced by small-bodied bird species with more limited movement capacity and by plant species that tend to have smaller seeds (Emer *et al.* 2018). The shift in interacting partners results in reduced trait matching (Emer *et al.* 2018; Marjakangas *et al.* 2019), and less reliable mutualism due to the loss of phylogenetically distinct lineages of obligate frugivores (Aizen *et al.* 2016; Emer *et al.* 2019).

Here we assess the contribution of trait matching and phylogenetic congruence to plant-frugivore bird networks along a gradient of forest loss and fragmentation, defined in terms fragment area, forest structure and landscape context, in the Atlantic Forest of Brazil. Plant-frugivore bird interactions provide an important ecosystem service for biodiversity management (Schleuning *et al.* 2011, 2015; Emer *et al.* 2018), influencing

energy flows and forest dynamics (i.e., plant demography and recruitment). For instance, in Brazilian Atlantic Forest, about 45-90% tree species depend on frugivorous birds to disperse their seeds, thus frugivore-plant interactions contribute to plant recruitment and forest regeneration (Almeida-Neto *et al.* 2008). For birds, plant-frugivore interactions are essential for 25-30% of birds which include fruit in their diet (Pizo and Galetti 2010). Despite being considered a hotspot of biodiversity and an important area of endemism (Myers *et al.* 2000; Cardoso da Silva *et al.* 2004), the extent of the Brazilian Atlantic Forest has been reduced to only 12% of its original area (Ribeiro *et al.* 2009), mainly due to agricultural intensification and expansion of cities, which shelter more than 120 million people (Pinto *et al.* 2014). As a result of this forest loss the Atlantic Forest provides an excellent system to investigate how trait matching and phylogenetic congruence are affected by forest loss and fragmentation.

By using a gradient of forest loss and fragmentation (i.e., variation in forest cover, forest patch, isolation, and edge density), we first evaluated the response of plant and bird traits to landscape structure. We expected a decrease in trait values in forested landscapes because small fruits and small seeds are linked to secondary forest habitats (Cramer *et al.* 2007), whereas large-bodied and large bill are expected to be extinct or rare in deforested landscapes (Bovo *et al.* 2018). Second, we assessed the variation of phylogenetic structure along a gradient of forest loss. We expected more species per genus or lineages due to niche conservatism in forested landscapes (Wiens & Graham 2005). Third, we investigated whether plant-frugivore interactions are the result of trait-matching or phylogenetic congruence along a gradient of forest loss and fragmentation. We expected an increase in trait matching in forested landscapes due a higher trait variability and no change in phylogenetic congruence because frugivory is described to be an example of megadiverse interaction system (i.e., diffuse coevolution) (Janzen 1980, Howe 1984,

Jordano 1987, Charles-Dominique 1993). For this, we compiled 16 plant-frugivore studies related to fruit consumption by birds in the Brazilian Atlantic Forest (Table S1), on a gradient of forest loss and fragmentation (Figure 1).

MATERIAL AND METHODS

Study site and landscapes metrics

The landscapes of our study area constitute a mosaic of small forest patches (< 50 ha) with 200 m mean distance between them (Ribeiro, M *et al.* 2009). The sampling unit areas (yellow dots in Figure.1) have suffered different levels of anthropogenic land use, resulting in variation in forest cover, degree of forest fragmentation, isolation, and edge density (Table 1). To capture landscape structure in the Brazilian Atlantic Forest, we used a time series Landsat images of land use classification with 30 m and 89% global accuracy (Mapbiomas, collection 4.1).

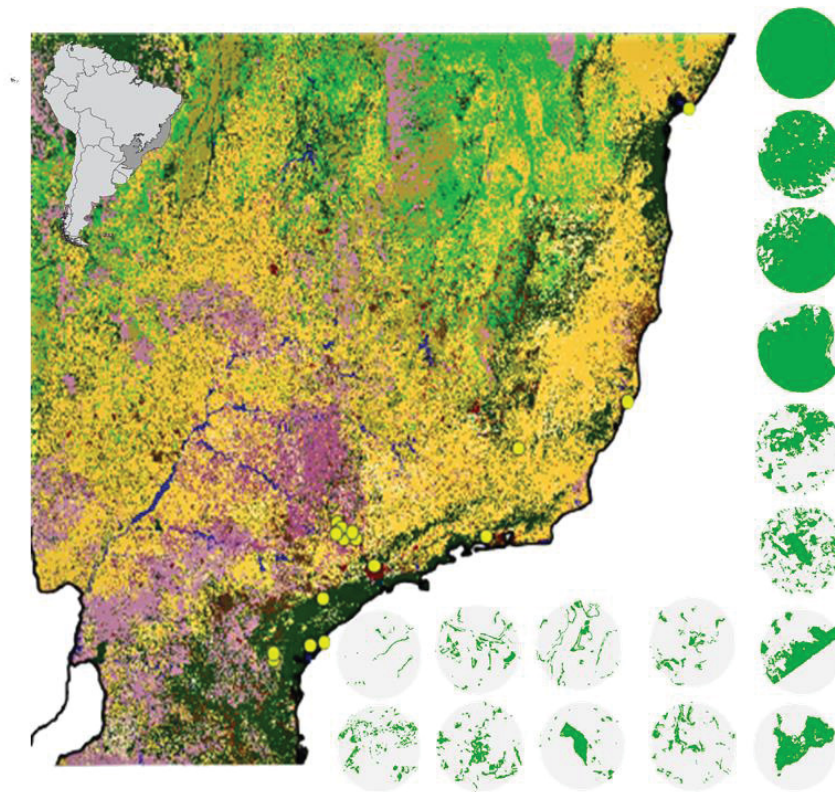


Figure 1 Location of the sampling units in the Brazilian Atlantic Forest. In the center, Atlantic Forest (green areas) distribution in Brazil, South America. The predominant areas in orange and pink are agriculture and pasture respectively. Yellow dots represent the sampling units. For each sampling unit, circles represent forest cover (in green) for each landscape. Numbers on the top of each sampling units are described in Appendices 1.

In order to compare structural forest features between landscapes, we calculated four landscape metrics: (a) forest cover – the proportion of forest in the landscape; (b) the number of patches – the total amount of forest patches in the landscape; (c) isolation – the average distance between all forest fragments in the landscape and (d) edge density – the length (m) of all forest fragment edges divided by the total landscape area. These metrics reflect landscape composition and configuration (Fahrig 2003; Boscolo & Metzger 2009) and are expected to affect plant and bird composition, as well as the interactions between species (Moreira *et al.* 2015; Marjakangas *et al.* 2019; Schneiberg *et al.* 2020). All landscape metrics were calculated at three spatial extents (radius of 500 m, 1000 m, 2000 m) to investigate possible scale effects associated with environmental relationships (i.e., scale of effect) (Jackson & Fahrig 2015; Miguet *et al.* 2016). These

scales were previously tested and are adequate for predicting bird movement (Coster *et al.* 2015; Morante-Filho *et al.* 2015). All landscape metrics were calculated using Fragstats v.4 (McGarigal *et al.* 2014). In order to investigate similarities between forest cover, fragmentation, isolation and edge density, all landscape metrics were standardized and used in a multivariate cluster analysis, considering the average of dissimilarities, based on Euclidian distances using function “vegdist” and “hclust” in R (Table 1).

Table 1 Landscape metrics associated with forest class with cluster analysis results based on standardized data. Two main groups can be identified at cluster dendrogram on the left side. See Appendices 1 for network code reference.

	Landscapes	Forest cover	Forest patches	Isolation	Edge density
	1	99.94	1	0	8.37
	2	79.83	10	79.02	17.84
	3	88.56	6	66.18	28.86
	4	85.06	9	104.09	31.89
	5	10.13	126	111.32	37.42
	6	27.68	93	106.62	57.33
	7	29.37	50	144.32	42.37
	8	9.61	24	329.56	11.59
	9	13.11	53	157.25	31.76
	10	8.42	52	142.44	29.44
	11	7.63	48	151.01	28.44
	12	9.08	47	142.97	28.17
	13	26.10	25	124.84	22.88
	14	6.61	37	145.53	20.43
	15	1.92	27	180.96	9.46
	16	25.42	3	105.32	16.26

Interaction data

We used an updated dataset of Atlantic frugivory interactions (Bello *et al.* 2017) and a dataset from (Machado-de-Souza *et al.* 2019). The dataset includes 9637 interactions between 232 plant species and 168 bird species across 16 plant-frugivore quantitative networks.

Phylogenetic data

We used the angiosperm mega-tree, which has a backbone that comprises 74,533 species distributed in 479 monophyletic families of vascular plant species (Jin & Qian 2019) as the basis of our phylogeny. Using this backbone we built phylogenetic trees including the species of each network to close relatives with dated edges lengths using the function “phylo.maker” in R package “V.PhyloMaker” (Jin & Qian 2019). For every bird assemblage in each network, we used the most complete phylogeny of birds (BirdTree online dataset) to create phylogenetic hypotheses, using the Stage2 MayrParSho Ericson source. The phylogenetic information uses genetic data from 6,663 taxa. Bird species that were identified at the genus level were randomly grafted in their respective clades based on genera using the “add.species.to.genus” function in the phytools package (Revell 2012). From 100 phylogenetic hypothesis trees, we then built a consensus tree using the consensus.edges function in the phytools R-package (Revell, 2012), and calculated pairwise phylogenetic distances using the same procedure for plants.

Trait data

We selected morphological traits known to determine plant-frugivore interactions (Dehling *et al.* 2016a; Bello *et al.* 2017; Bender *et al.* 2018). Plant traits included fruit/seed diameter (mm) and fruit/seed length (mm). Bird traits included bill diameter (mm), bill length (mm) and body mass (g).

Analyses

In order to investigate potential changes in phylogenetic and functional network structure of plant and bird assemblages we created a community abundance matrix using species identity and frequency of interactions (i.e., we considered frequency rate as a proxy for abundance (Vázquez *et al.* 2007). We assessed phylogenetic structure for both trophic levels using the nearest taxon index (NTI) (Webb *et al.* 2002). NTI quantifies the mean minimum distance using all possible pairs of species in a community. Positive NTI indicates phylogenetic clustering, while negative values indicate phylogenetic evenness. Then, we performed linear regression models with forest cover, forest patches, isolation, and edge density as predictors variables.

To investigate the relationship between species, functional traits and landscape variables, we performed RLQ analysis using the community matrix derived from networks. Three matrices were required to access trait variation across landscapes: species weighted by abundance (R), traits (L) and landscape structure (Q). In order to identify functional traits of plant and bird groups, we combined RLQ with cluster analysis as suggested by Kleyer *et al.* (2012). All analyses were performed in the R 3.6.2 environment (R Core Team, 2019).

Finally, to investigate if closely related species from one trophic level interacted with more frequency with related species from the other trophic level and if trait matching shape interactions, we used an integrative analytical framework to partition the effects of phylogeny and functional traits on the structure of plant-frugivore network (Bastazini *et al.* 2017). This tool has been used in previous studies which investigated the contribution of traits (Pillar *et al.* 2009), phylogenetic structure (Pillar & Duarte 2010) on community assembly patterns, and more recently, the influence of phylogeny and traits on

interactions (Bastazini *et al.* 2017; Vizentin-Bugoni *et al.* 2019; Peralta *et al.* 2020a). The method combines fuzzy set theory and matrix correlation, implemented under a Monte Carlo framework to assess the significance of matrix correlations. Three matrices are required: interaction frequency matrix (N_{AB}), functional trait distances for plants (S_A) and birds (S_B), and phylogenetic distances of plants (A_A) and birds (A_B). Based on trait and phylogenetic similarity, every species in each trophic level is used to define a fuzzy set to which every species in the same trophic level belongs with a certain degree of belonging, ranging between 0 and 1 as follows:

$$U_{ij} = \frac{S_{ij}}{\sum_{k=1}^S S_{kj}}$$

where U_{ij} is the degree of belonging matrix of trophic level ij , and S_{ij} is the pairwise similarity, in this case, Gower's similarity ranging 0-1. To estimate the probability of interaction (Y_A and Y_B) of a species in one trophic level interacting with species in the other trophic level, we multiplied the resulting fuzzy matrices $Y_A = U_A N_{AB}$ and $Y_B = U_B N_{AB}$ with the quantitative interaction matrix. We then calculated the matrix correlation (ρ) between trait probability matrices for both trophic levels to assess trait matching. Phylogenetic congruence was assessed by correlation (ρ) between phylogenetic probability matrices using high-order partial mantel correlations to exclude the influence of phylogenetic signal in traits (see details in Bastazini *et al.* 2017).

To test for the correspondence of trait matching and phylogenetic congruence along a gradient of forest spatial structure, we fitted linear regression models with forest cover, forest patches, isolation, and edge density as predictors and the trait-matching and phylogenetic congruence as response. All analyses were performed in the R 3.6.2 environment (R Core Team, 2019).

RESULTS

The networks under study fall into two groups of spatial landscape structure according to the cophenetic correlation coefficient of cluster analysis ($CCC = 0.90$). Less forested landscapes presented small fragments and higher mean isolation when compared with the group of higher forest cover (Table.1).

Species richness in each network ranged from 6 to 73 plants (mean = 22.25, SD = 17.32), and from 12 to 68 birds (mean = 32.37, SD = 15.90). The phylogenetic structure of plants and birds was similar for forest cover and habitat fragmentation (Figure 2, A to D) but showed a different trend for isolation and edge density (Figure 2, E to H). For plants, the direct effect of forest patches had the strongest influence on phylogenetic structure. The model described low values of NTI in more fragmented landscapes (Figure 2). Conversely, both forest cover, isolation and edge density had no effect on the phylogenetic structure of plants. For the birds, forest cover was the main driver of the phylogenetic structure. The model described high values of NTI in landscapes with higher forest cover. However, the number of forest patches, isolation and edge density had no effect on the phylogenetic structure of birds (Figure 2).

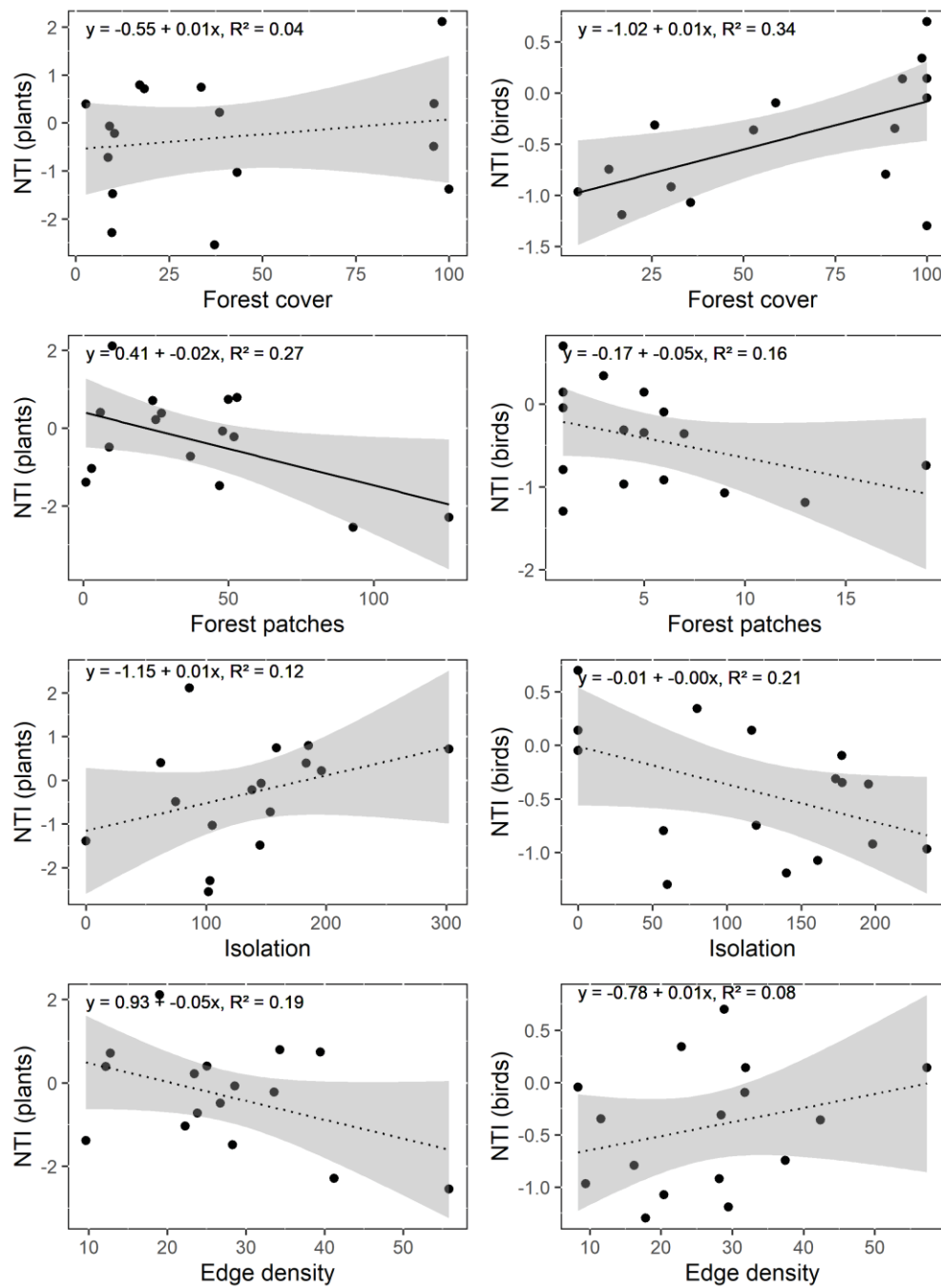


Figure 2 Relationships of phylogenetic structure (NTI) with of forest spatial structure. Left panels show the relationship for plants and right panels for birds. Univariate regression coefficients β are given with their P-values: significant relationships ($P < 0.05$) are indicated by solid lines.

The first two RLQ axes for plants explained 92.85% and 6.09% of total inertia (i.e., maximized covariance). The first axis identified a positive relationship between forest patches and edge density with seed length, fruit length and fruit diameter, as well

as forest cover with seed diameter. For birds, the first two RLQ axes explained 98.39 and 1.40% respectively. The first axis identified a negative correlation between bill length and bill width with fragmented landscapes represented by edge density, forest patches and isolation (Figure 3).

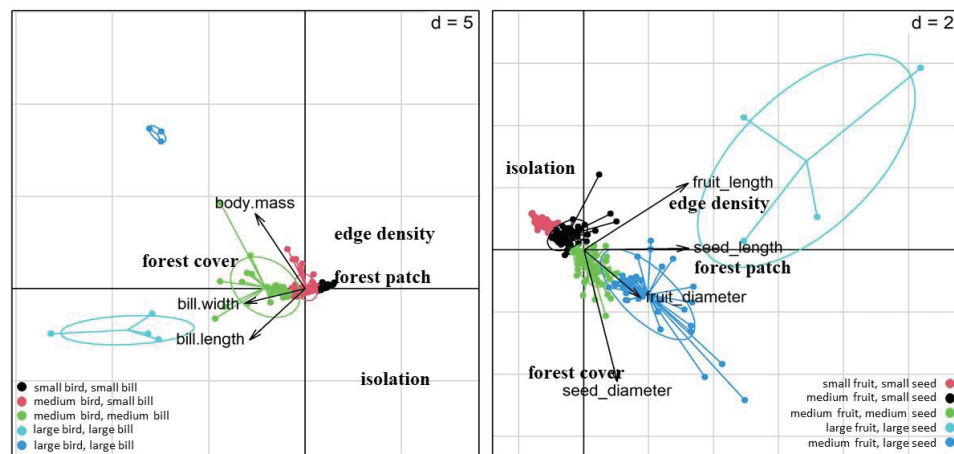


Figure 3 RLQ analysis between species traits and landscape variables. Left side: five groups of bird species clustered according to their functional traits related to landscape structure. Right side: six groups of plant species clustered according to their functional traits. Different colors represent different groups.

We found a significant correlation between plant and bird traits (Table 2), showing that for some interactions, birds must have specific traits to consume their resources. However, the relationship between trait-matching depended on landscape structure. The model described an increase in the contribution of trait matching in shaping interactions in landscapes with higher forest cover ($R^2 = 0.28$, $p = 0.03$, Figure 4A) and a decrease in more fragmented landscapes ($R^2 = 0.41$, $p < 0.01$, Figure 4B). We found no significant association between trait-matching and isolation or edge density (Figure 4E, H). In contrast to the functional component, the contribution of phylogenetic component

associated with interactions decreased in higher forest cover landscapes ($R^2 = 0.52$, $p < 0.01$), and increased in more fragmented ($R^2 = 0.48$, $p < 0.01$) and isolated landscapes ($R^2 = 0.34$, $p = 0.01$) (Figure 4B, D and F).

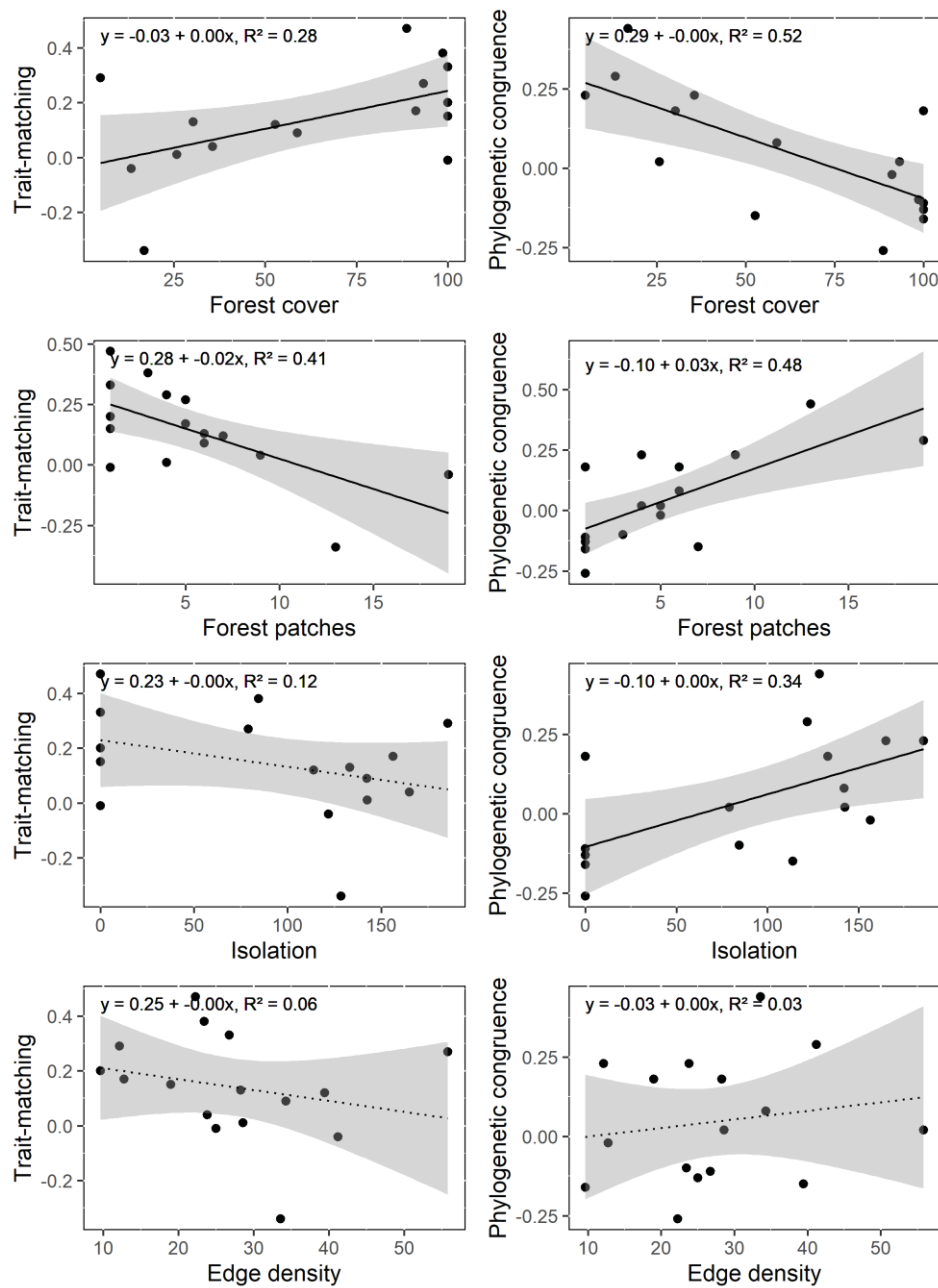


Figure 4 Linear models depicting trait-matching (left) and phylogenetic congruence (right) on the interactions between plant and bird as function of forest cover, number of forest patch, isolation and edge density. Solid line ($p < 0.05$) dotted line ($p > 0.05$).

Table 2 Results from matrix correlation showing the effects of trait matching and phylogenetic congruence in plant-frugivore networks. Networks 1-16 follow a gradient from high to less forest cover. Bold values represent significant values of matrix correlation. Network number refers to networks are listed in Appendices 1.

Network	Functional component	p-value	Phylogenetic component	p-value
1	0.20	0.08	-0.16	0.06
2	0.15	0.03	0.18	0.14
3	-0.01	0.91	-0.13	0.42
4	0.33	0.01	-0.11	0.55
5	-0.04	0.57	0.29	0.09
6	0.27	0.07	0.02	0.9
7	0.12	0.42	-0.15	0.62
8	0.17	0.12	-0.02	0.88
9	0.09	0.61	0.08	0.67
10	-0.34	0.37	0.44	0.14
11	0.01	0.91	0.02	0.81
12	0.13	0.67	0.18	0.64
13	0.38	0.03	-0.10	0.66
14	0.04	0.87	0.23	0.18
15	0.29	0.30	0.23	0.39
16	0.43	0.01	-0.26	0.19

DISCUSSION

We show that the strength of trait-matching and phylogenetic congruence depends on landscape structure. On one hand, forest cover was the main driver for trait-matching in shaping plant-frugivore interactions. This supports the expectation that some degree of trait matching is needed for interactions (Dehling *et al.* 2016b; Marjakangas *et al.* 2019). On the other hand, the strength of phylogenetic congruence increases in more fragmented and isolated landscapes. This pattern probably arises from environmental filtering that sorts more distantly-related species, which increases phylogenetic evenness (Arroyo-Rodríguez *et al.* 2012). Overall, the integrative framework used in this study contributes in four principal ways to our understanding of the organization of plant-frugivore interactions across a gradient of forest spatial structure.

First, phylogenetic clustering was greater in landscapes with less forest patches for plants. Phylogenetic clustering was greater in landscape with higher forest cover for birds. and a higher amount of forest for birds. These results indicate that forest cover is important to maintain several lineages of bird species, which are related to forested landscapes (e.g., long bill, large bodied species) involved in the frugivore system, and some clades were overrepresented. In addition, forest loss and fragmentation can filter out species within some clades but not entire lineages. As a consequence, communities in deforested and fragmented landscapes are composed of species that are relatively evenly spread across the phylogeny. This phylogenetic evenness is more evident when matrix quality (i.e., higher forest cover, less isolation) favors species persistence facilitating movement between forest patches. For example, birds can use forest patches as stepping stones (Uezu *et al.* 2008), which contribute to maintaining lineages from across the phylogeny resulting in patterns of phylogenetic evenness (Rezende *et al.* 2007; Aizen *et al.* 2016). Less competition may be the ecological response of communities composed of species evenly distributed across phylogeny, where members of these communities can concentrate different interactions because some species are open-area exploiters and can be abundant in the landscape.

Second, our trait-by-landscape analysis revealed weak correlations between functional traits and forest spatial structure and not very distinct functional groups. In our study, the scenario of heterogeneous landscapes created by human activities is able to maintain a wide range of trait variability within communities due to elements of landscape heterogeneity like corridors (Ribeiro *et al.* 2017) and/or stepping stones (Uezu *et al.* 2008). Yet, some bird species with particular traits like large bill (toucans) and large-bodied (guans) can be found in fragmented landscapes when matrix condition favors animal movement (Ribeiro, *et al.* 2009; Boscolo and Metzger 2011). Similarly, a wide

range of plant trait variability was found across landscapes. Some of the extreme traits arise from cultivated species like pome fruits, stone fruits, or pods fruits. Although some studies have found functional similarity in disturbed environments (Warring *et al.* 2016; Liang *et al.* 2019), our results showed that bird movement and cultivated species can maintain functional diversity in fragmented landscapes. The presence of large-billed and large-bodied birds in landscapes with higher forest cover is expected since there is an increase in body mass in highly forested landscapes (Morante-Filho *et al.* 2015; Emer *et al.* 2019). In addition, large-seeded plants are more common in more conserved landscapes (Liebsch *et al.* 2008; Warring *et al.* 2016). Our results support, in part, these expectations, as large billed, large-bodied species, as well as large seeds, were founded in landscapes with higher forest cover.

Third, plant-frugivore interactions were associated with phylogenetic and functional components. Phylogenetic congruence increases when communities are composed of species evenly distributed across the phylogeny and those species can concentrate interactions. A key assumption in community ecology predicts that the more closely related species are, the more strongly they will compete (Adler *et al.* 2013). So, clustered phylogenies had overrepresented lineages that use similar resources. As a consequence, competition can cause a dilution of interactions across co-occurring species. In addition, distant relatives can concentrate interactions in plant resources due to less competition or just because these species are favored by landscape context and become abundant species (Figure A1).

Finally, we found that the strength of trait matching increased in more forested landscapes. We could argue three possible explanations: (i) there is more trait variability and more possibility to match morphological traits in forested landscapes, (ii) our results indicate that highly forested landscape had less cultivated species, which are known to

show extreme fruit length like pods fruits and require specific traits, supporting the expectation that the degree of trait matching is weakened in modified landscapes that are dominated by small-bodied bird species (Saavedra *et al.* 2014) and, (iii) a higher correspondence in traits in more conserved landscapes, due to an increase in trait complementarity. Indeed, the increased plant reproductive trait divergence in more conserved forests (Warring *et al.* 2016) may result in a finer interaction partition and higher trait congruence in plant-frugivore interactions.

Ecological interactions can shape coevolutionary responses among interacting species, where the evolution of one trophic level can be highly dependent on that of their partners. This pattern of phylogenetic congruence has been well described in the literature, and we can observe groups of related species that preferentially interact with other ones (Cruaud *et al.* 2012; Tylianakis & Morris 2017). However, we highlight that phylogenetic congruence is not only associated with coevolutionary aspects, but can also emerge as a result of environmental filtering. In human-altered landscapes, obligate frugivore species (e.g., toucans, guans) may become locally extinct. These remaining species can concentrate interactions leading to a pattern of phylogenetic congruence. The absence of phylogenetic congruence in forested landscapes reinforces the assumption that in frugivory, closely related bird species do not necessarily specialize on specific lineages of plant species. As a result, a wide range of plant species was eaten by a large range of bird species.

Although morphological or life-history traits can be conserved along the phylogeny, trait matching does not necessarily need coevolution *per se*. The highest likelihood of interactions being associated with trait matching is at sites where there is a wide range of trait variability of plant and bird species. In human-altered landscapes, several species are filtered out, decreasing the range of variation in ecological traits. In

these landscapes, the presence of species with peculiar traits, such as large fruits, are cultivated by human beings reduces the likelihood of interactions associated with trait matching.

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SUPPLEMENTARY MATERIAL

Table A1 Code, locality and the number of plant and bird in plant-frugivore networks data used in this study

Code	Latitude	Longitude	Nº Plant	Nº Bird
1	-25.1033	-48.1743	73	68
2	-25.1278	-47.9575	49	16
3	-24.1314	-47.9492	28	56
4	-22.5363	-42.2777	13	45
5	-22.7674	-43.6944	20	18
6	-20.8026	-42.8587	22	28
7	-22.9433	-46.7499	15	49
8	-22.8181	-47.1138	33	29
9	-28.2231	-51.1669	11	21
10	-22.7087	-47.6102	6	28
11	-22.6716	-47.2046	23	29
12	-22.5683	-47.505	11	12
13	-19.7415	-39.9961	19	44
14	-22.481	-47.5923	9	30
15	-22.8252	-47.4278	11	15
16	-23.5484	-45.0625	13	30

Network reference:

1. Fadini, R.F. and Marco Jr., P. de. (2004). Interações entre aves frugívoras e plantas em um fragmento de Mata Atlântica de Minas Gerais. *Ararajuba* 12: 97-103.
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CHAPTER 3

Forest loss and fragmentation drive changes in network robustness in tropical forest remnants

Forest loss and fragmentation drive changes in network robustness in tropical forest remnants

ABSTRACT

How species loss affects the extinction risk of the remaining species is one of the 100 fundamental questions in ecology. Anthropogenic activities are increasingly invasive and extensive areas of pristine landscapes are converted by human-induced landscapes. Forest loss and fragmentation can trigger secondary extinctions changing the compositions of interacting species and the ecosystems services. Using 16 quantitative plant-frugivore networks along a gradient of forest cover, fragmentation and isolation, we investigate changes in network composition and robustness. Here, we estimate robustness taking into account interaction rewiring in accordance with abundance and morphological matches. We found that the degree of frugivory increase in forested landscapes. Network robustness is higher when network composition show more degree of frugivory. Finally, network robustness collapses when well-connected species go extinct first. Although this scenario is known as the worst case and often unlikely, increasing uncontrolled deforestation and intense extractivism threaten these species with key roles in mutualistic networks.

Keywords: Coextinctions, Fragmentation, Habitat loss, Secondary extinction, Network stability, Tropical Forest

INTRODUCTION

Biodiversity is an emergent property that arises from interactions between species, and biodiversity maintenance is directly related to the way in which species are linked (Norris 2012; Albrecht *et al.* 2014). However, recent anthropogenic activities erode long-term coevolutionary processes (Colwell *et al.* 2012). Alteration in interactions represents an insidious hidden effect on secondary extinctions (Tylianakis *et al.* 2007), and one way to assess community stability is through network robustness, which measures the resistance of interacting species to change after a local species extinction (Dunne *et al.* 2002). To date, most studies have assessed networks robustness without the possibility of interactions rewiring, that is, partner switching. Rewiring in ecological networks is influenced and/or depends on various aspects, as such as trait matching, phenological matching, and is related to network stability, resilience, and to ecosystem services (Kaiser-Bunbury *et al.* 2010; Pires 2017; Bastazini *et al.* 2019; Vizentin-Bugoni *et al.* 2019). Here, we investigate network robustness along a gradient of forest loss and fragmentation including rewiring taking into account the match of traits, allowing the possibility of interaction rewiring between remaining species.

Habitat loss and fragmentation imposes one of the most negative effects on biodiversity, not only on species richness but also on functional and phylogenetic dimensions of biodiversity as well as on interacting species (Hagen *et al.* 2012; Tylianakis & Morris 2017). The way in which biodiversity dimensions and processes relate to the influence of spatial, temporal, and biotic drivers in interaction networks are complex and require an integrative approach. For example, traits (e.g., bill width, body mass, dispersal ability) often constrain interactions and may show different trends in response to landscape structure (Bartomeus *et al.* 2016; Bender *et al.* 2018). The loss of functional and phylogenetic associations between interacting species can increase less reliable

mutualism (Aizen *et al.* 2016; Bastazini *et al.* 2019). These losses change the network structure and result in a simplification of interactions as well as decrease the network robustness (Bastazini *et al.* 2019; Morrison *et al.* 2020; Pinto *et al.* 2021).

Robustness is a mechanism related to community stability and is linked to network structure (Dunne *et al.* 2002; Memmott *et al.* 2004; Bascompte 2007; Mello *et al.* 2011a). Some studies have reported that redundancy of interacting partners enhances network robustness (Dunne *et al.* 2002). Moreover, nestedness is an inherently characteristic of mutualistic networks which reflect the tendency of species with few interactions to interact with subsets of highly species connected species (Almeida-Neto *et al.* 2007; Burgos *et al.* 2007). These network properties are expected to be affected by habitat loss and fragmentation (Hagen *et al.* 2012; Marjakangas *et al.* 2019), mainly because anthropogenic activities are increasingly common and more negative to biodiversity conservation. Thus, the order in which species go extinct may affect the network structure in face of species loss (Dunne *et al.* 2002; Memmott *et al.* 2004). Some studies have been reported that the more realistic way to simulate species extinction occurs when species with few interactions are extinct first. Actually, intense deforestation activities may cause the extinction of species with many interactions.

Frugivory is a foraging mode that emerges as a process of diffuse co-evolution where many plants interact with many frugivores for seed dispersal, and frugivores depend on many plants for resource (Bello & Barreto 2021). In fact, it has been accepted that obligate frugivores are rare or even locally extinct in deforested landscapes (Bello *et al.* 2015; Egerer *et al.* 2018; Emer *et al.* 2018). Moreover, plants are sessile and are expected to be more vulnerable to forest loss and fragmentation (Arroyo-Rodríguez *et al.* 2012; Hagen *et al.* 2012). In addition, the sensitivity of plant-frugivore interactions to landscape change is unclear, some studies suggest that plant-frugivore networks should

be less robust when animal species are lost (Mello *et al.* 2011b) or plant extinctions are more harmful to collapse networks than animal extinctions (Schleuning *et al.* 2016).

Here, we investigated the effects of forest loss and fragmentation on network robustness. In our model, we allowed interactions to rewire taking into account trait matching between plants and birds. We explored network robustness using 16 quantitative plant-frugivore networks located along a gradient of forest cover and fragmentation in the Brazilian Atlantic Forest. We simulated different scenarios of plant species extinction to address three questions: (i) How does the degree of frugivory change along the gradient? We expected a decrease in importance of fruit in the birds diet in deforested and fragmented landscapes due to the absence of obligate frugivores and an increase in omnivorous birds; (ii) Is there a relationship between robustness and the degree of frugivory? Because frugivores have greater variation in traits related to interactions than omnivorous birds, we expect an increase in network robustness due to greater capacity of rewire; (iii) How do different scenarios of robustness change along the gradient? We expected no changes in network robustness when species with few interactions are extinct first because these species do not have many interactions to propagate disturbances independent of landscape structure. However, when plants with many interactions are extinct first, or random, we expected a negative effect on network structure in deforested and fragmented landscapes. This negative effect will be more strong in deforested landscapes due to functional similarity (Devictor *et al.* 2008) and do not have many opportunities (functional redundancy) to rewire.

MATERIAL AND METHODS

Study site and landscapes metrics

The landscapes of our study area constitute a mosaic of small forest patches (< 50 ha) with 200 m mean distance between them (Ribeiro, M *et al.* 2009). The sampling unit areas (yellow dots in Figure 1) have suffered different levels of anthropogenic land use, which show variation in forest cover, degree of forest fragmentation (i.e., the number of forest patches), and isolation (Table 1). To capture landscape structure of our study system, we used a time series Landsat images of land use classification with 30 m and 89% global accuracy (Mapbiomas, collection 4.1).

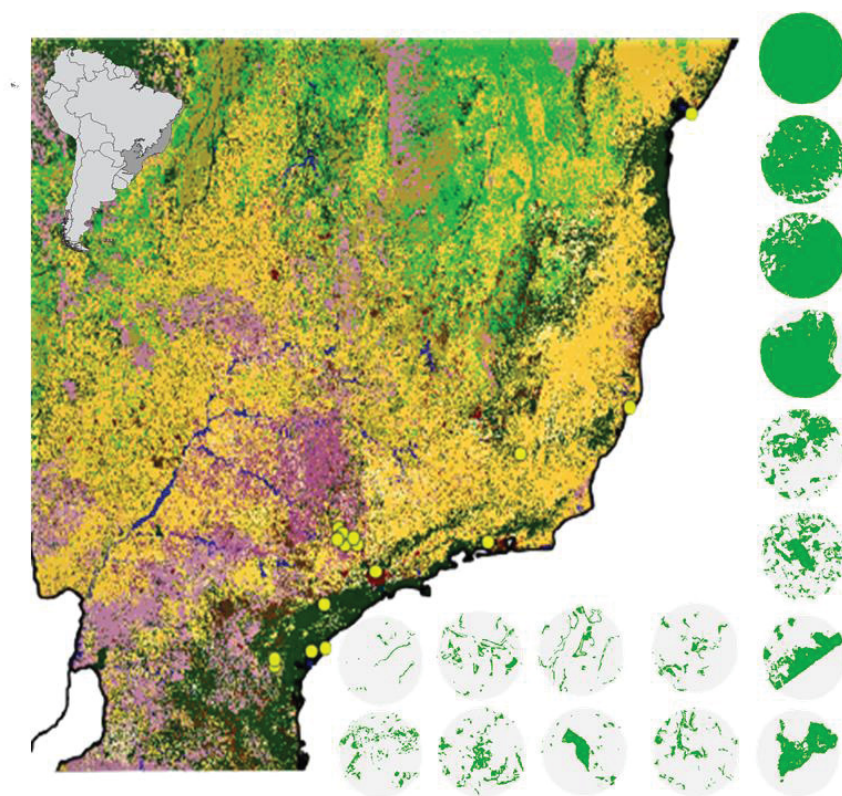


Figure 1 Location of the sampling units in the Brazilian Atlantic Forest. In the center, Atlantic Forest (green areas) distribution in Brazil, South America. The predominant areas in orange and pink are agriculture and pasture respectively. Yellow dots represent the sampling units. For each sampling unit, circles represent forest cover (in green) for each landscape.

In order to compare structural forest features between landscapes, we calculated three landscape metrics: (a) forest cover – the proportion of forest in the landscape; (b) the number of patches – the total amount of forest patches in the landscape; and (c) isolation – the average distance between all forest patches in the landscape. These metrics reflect landscape composition and configuration (Fahrig 2003; Boscolo & Metzger 2009) and are expected to affect plant and bird composition, as well as the interactions between species (Hagen *et al.* 2012; Moreira *et al.* 2015). All landscape metrics were calculated at three spatial extents (radius of 500 m, 1000 m, 2000 m) to investigate possible scale effects associated with environmental relationships (i.e., the scale of effect) (Jackson & Fahrig 2015; Miguet *et al.* 2016). All landscape metrics were calculated using Fragstats v.4 (McGarigal *et al.* 2014). In order to investigate similarities between the structure of the landscapes, all landscape metrics were standardized and used in a multivariate cluster analysis, considering the average of dissimilarities, based on Euclidian distances using the function “vegdist” and “hclust” in R version 3.5.3 (R Core Team 2019).

Interaction data

We used an updated dataset of Atlantic frugivory interactions (Bello *et al.* 2017) and a dataset from Machado-de-Souza *et al.* (2019) to explore the impacts of landscape structure on network robustness through the gradient of forest loss and fragmentation. These studies represent long-term data of frugivory, however, none of the studies recorded the quality of seed dispersion (Bello *et al.* 2017; Emer *et al.* 2018, 2020). The dataset includes 9637 interactions between 232 plant species and 168 bird species.

Frugivore classification

From 168 bird species recorded in the data set, we classified frugivores based on the percentage of fruit consumption following (Wilman *et al.* 2014). In each network, we assessed the degree of frugivory of each species by averaging the proportion of fruit in diet and the proportion of other food items as invertebrates and small vertebrates.

Trait Data

We selected morphological traits known to determine plant-frugivore interactions (Eklöf *et al.* 2013; Dehling *et al.* 2016a; Bello *et al.* 2017; Bender *et al.* 2018). Plant traits included fruit/seed diameter (mm), fruit/seed length (mm). Bird traits included bill diameter (mm), bill length (mm), and body mass (g). We primarily used trait data from Bello *et al.* (2017), but supplemented it with additional sources (Table S1).

Measuring robustness

We used the method proposed by Vizentin-Bugoni *et al.* (2019) to simulate coextinctions based on the possibility that species that lose partners rewire in accordance with their morphological matching. Robustness (R_w) estimates the proportion of species in a trophic level that remains in a network after sequential losses of species in the other trophic level. The method proposed by Vizentin-Bugoni *et al.* (2019) considers a probability of rewiring its interactions to the persisting potential partners. Although some

rules to create the probabilities of interactions are available (see Vizentin-Bugoni *et al.* 2019), we used abundance and matching of traits to create a range of possible interactions rewiring. Here, abundance was assumed to be equivalent to the frequency of interactions (Vázquez *et al.* 2005, 2007). Abundance may determine the probability of species interactions due to the fact that abundant species have more chance to receive new partners than a rare species (Vázquez *et al.* 2009). Moreover, interactions are often constrained by traits (Bender *et al.* 2018; Sonne *et al.* 2019; Peralta *et al.* 2020b). However, if species are functionally similar, the probability to rewire will be higher. To assess the probability of rewiring, we used fuzzy set theory to scale up trait data from plants and frugivorous birds to the network level (Bastazini *et al.* 2017). Three matrices are required: interaction frequency matrix (N_{AB}), functional trait distances between plants (S_A), and bird (S_B). Based on trait similarity, every species in each trophic level is used to define a fuzzy set to which every species in the same trophic level belongs with a certain degree of belonging, ranging between 0 and 1 as follow:

$$U_{ij} = \frac{S_{ij}}{\sum_{k=1}^S S_{kj}}$$

where U_{ij} is the degree of belonging matrix of trophic level ij , S_{ij} is the pairwise similarity, in this case, Euclidean distance. In order to estimate the probability of interaction of a species in one trophic level in the other trophic level, the fuzzy matrix is then multiplied by interaction frequency matrix.

Analyses

The degree to which forest loss and fragmentation affects birds is specific for each species, therefore, the use of landscape may vary among species. To select the spatial

extent at which each landscape metric best predict the degree of frugivory and robustness (R_w), we performed univariate models for each landscape metric and extent and selected the spatial scale with the highest coefficient of determination (R^2) using the function `multifit` in `MultiFit` package (Huais 2018).

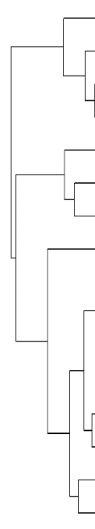
We calculate network robustness (R_r) without possibility of rewiring (i.e., raw robustness) and network robustness while considering rewiring (R_w) for multiple scenarios following three sequences of plant species extinction (i) from the plant species with few interactions (e.g., rare species) to the one with many interactions (e.g., generalists), (ii) from the plant species with many interactions to the one with few interactions and, (iii) at random extinctions. Yet, we selected the criteria for partner's choice which allows multiple attempts with multiple partners, taking into account trait similarity of interacting species. For example, one species could choose more than one partner to rewire due to trait resemblance, Although the exclusion of species with many interactions has been described as the most extreme case (Memmott *et al.* 2004), actually, it makes sense in a scenario of intense global deforestation.

Finally, to investigate the effect of forest spatial structure on biodiversity aspects, general linear regression models were run to assess whether the degree of frugivory and robustness were affected by the proportion of forest cover, fragmentation, and isolation. All landscape variables with the highest coefficient of determinations were selected. All statistical analyses were carried out in R version 3.5.3 (R Core Team 2019).

RESULTS

The networks under study belong to two groups of spatial landscape structure according to the cophenetic correlation coefficient of cluster analysis ($CCC = 0.92$). Less forested landscapes presented small fragments and higher mean isolation when compared with the group of higher forest cover (Table 1).

Table 1 Landscape metrics associated with forest class with cluster analysis results based on standardized data. Two main groups can be identified at cluster dendrogram on the left side. See Appendices 1 for network code reference.

	Landscapes	Forest cover	Forest patches	Isolation
	1	99.94	1	0
	2	79.83	10	79.02
	3	88.56	6	66.18
	4	85.06	9	104.09
	5	10.13	126	111.32
	6	27.68	93	106.62
	7	29.37	50	144.32
	8	9.61	24	329.56
	9	13.11	53	157.25
	11	7.63	48	151.01
	12	9.08	47	142.97
	13	26.10	25	124.84
	14	6.61	37	145.53
	15	1.92	27	180.96
	16	25.42	3	105.32

Species richness in each network was highly variable, ranging from 6 to 73 plants (mean = 22.25, SD = 17.32), and from 12 to 68 birds (mean = 32.37, SD = 15.90). Moreover, we found a decrease in mean frugivory and an increase in omnivory in deforested landscapes (Figure 2).

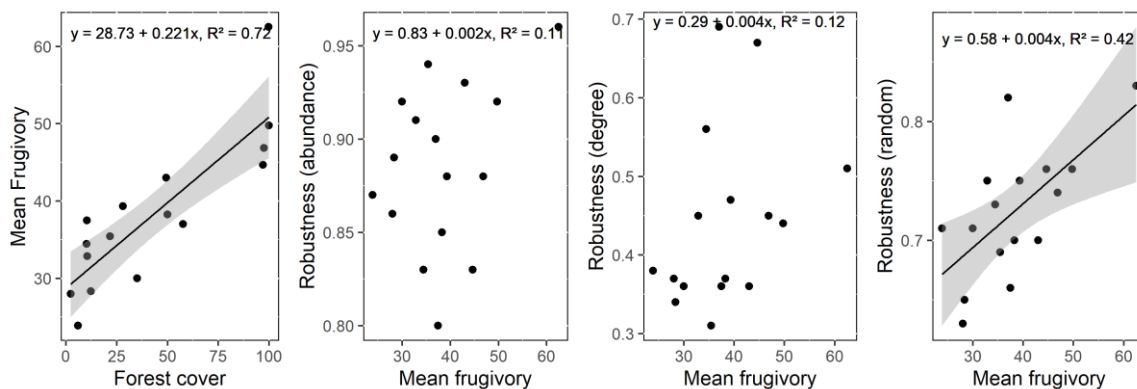


Figure 2 Relationship between the degree of frugivory and forest cover and relationship between network robustness and mean frugivory.

In general, Rw was higher when compared with raw robustness, Rr (Table 2). Networks were more robust to the loss of rare species (species with few interactions) than to random losses of interacting species or when deletion of the generalist species occurs first. When we investigated the relationship between Rw and the mean frugivory, we found that only robustness with random extinctions was significantly related to the degree of frugivory ($R^2 = 0.42$, $p < 0.05$) (Figure 2).

Table 2 The values of network robustness including rewiring (Rw) and network robustness without rewiring (Rr). Rw was estimate taking into account abundance, trait matching and multiple partners choice.

Network	Rw abund	Rr abund	Rw degree	Rr degree	Rw random	Rr random
1	0.92	0.92	0.44	0.43	0.76	0.75
2	0.96	0.96	0.51	0.5	0.83	0.82
3	0.88	0.88	0.45	0.44	0.74	0.73
4	0.83	0.82	0.67	0.64	0.76	0.75
5	0.87	0.87	0.38	0.35	0.71	0.69
6	0.93	0.93	0.36	0.34	0.7	0.69
7	0.92	0.91	0.36	0.34	0.71	0.69
8	0.88	0.87	0.47	0.46	0.75	0.74
9	0.94	0.94	0.31	0.28	0.69	0.67
10	0.89	0.89	0.34	0.28	0.65	0.61
11	0.86	0.85	0.37	0.34	0.63	0.61
12	0.8	0.78	0.36	0.33	0.66	0.64
13	0.85	0.85	0.37	0.35	0.7	0.68
14	0.83	0.81	0.56	0.51	0.73	0.7
15	0.86	0.85	0.37	0.34	0.63	0.61
16	0.9	0.89	0.69	0.66	0.82	0.8

Our results demonstrate that forest loss and fragmentation act in a negative way on network robustness (R_w) especially, when plant species with many interactions or random exclusions were extinct first. Networks were more robust in landscapes with higher forest cover, whereas networks were more susceptible to collapse in deforested, fragmented, and isolated landscapes (Figure 3). Lastly, the effect of forest loss, fragmentation, and isolation were strongest when species were extinct in a random way (Figure 3).

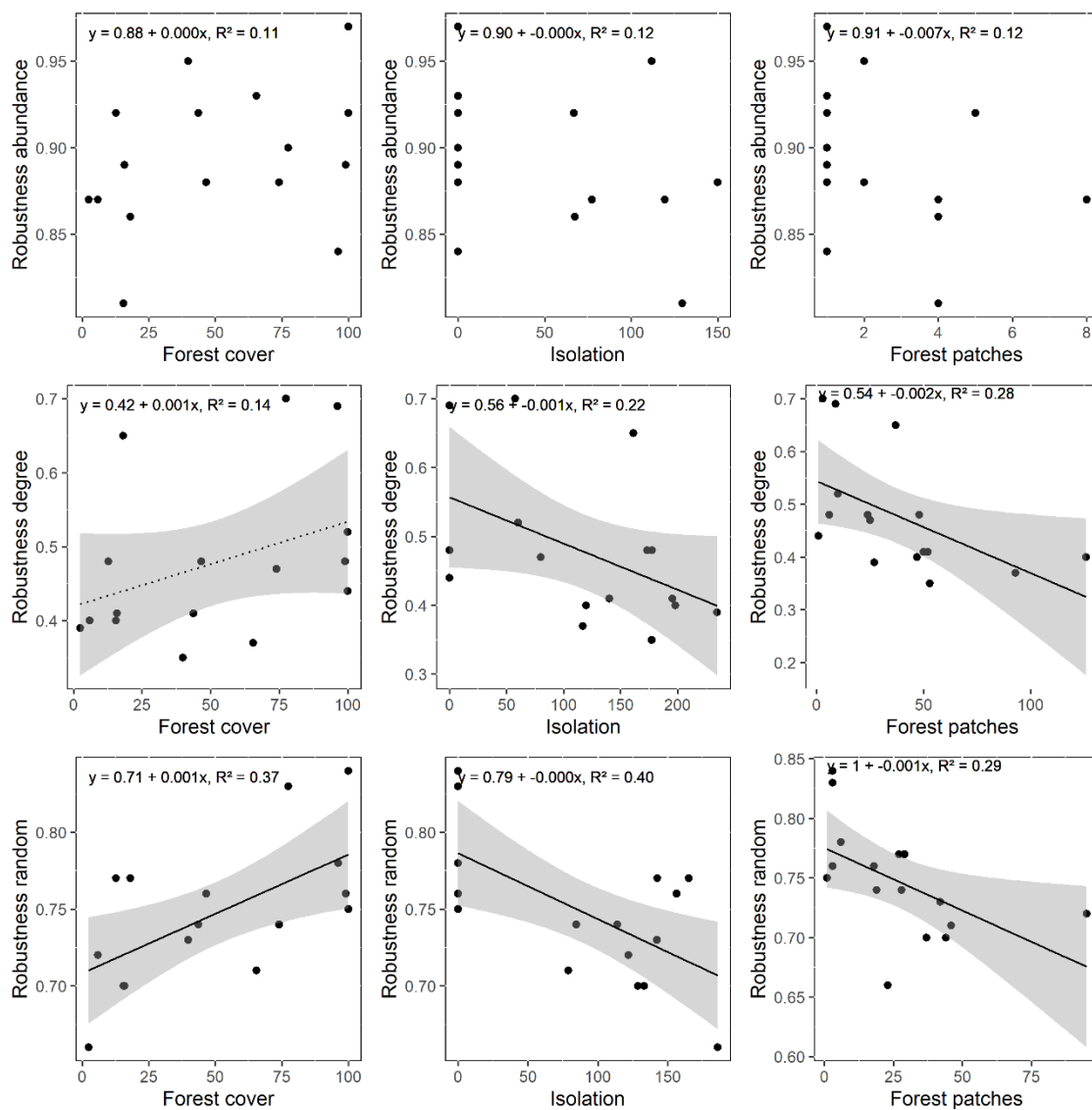


Figure 3 Changes in network robustness (R_w) along forest loss and fragmentation gradient. Dotted lines represent marginally significant relationships ($p = 0.08$)

DISCUSSION

Our results highlight that the network robustness is related to the conservation of continuous forest in landscapes to maintain plants and frugivorous assemblages, as well as alternative routes to rewiring. We show that when forest cover was reduced approximately to less than 40% of the entire landscapes, network compositions lose plant and bird species, which includes obligate frugivores, and decrease drastically the network robustness even when interactions rewiring is taken into account. The intense deforestation, unfortunately increasingly common, causes the extirpation of tree species, regardless of whether plant species have few or many connections with the other trophic level. Overall, the framework used in this study contributes in three principal ways to our understanding of the effect of intense deforestation common nowadays.

First, we found that bird richness, which use a higher proportion of fruits in their diet, decrease in deforested landscapes. The reduced vegetation complexity in deforested landscapes (Morante-Filho *et al.* 2018b; Bonfim *et al.* 2021), results in a decrease in niche width, food availability, and refuge for obligate frugivorous and the interactions they perform (Mariana Morais *et al.* 2019). Such changes in network composition can affect seed dispersal service due to less reliable interactions (Aizen *et al.* 2016; Emer *et al.* 2018). Forest dynamics are also affected by reductions in obligate frugivores. When forest cover was reduced obligate frugivores become rare. Because omnivorous birds show limited effectiveness as dispersers, that is, they occasionally eating fruit, and perform seed deposition inappropriately (Saavedra *et al.* 2014), the loss of frugivorous birds will have cascading effects on their interacting partners (Colwell *et al.* 2012). The relationship between network robustness and the degree of frugivory depends on which species were extinct first. When less connected plant species were locally extinct, no effect was found.

This may occur because robustness is not directly linked with frugivory but is related to the variability of traits that result in more options to rewiring. When more connected plant species were extinct first, the secondary extinct affect omnivorous birds which are more common in deforested and fragmented landscapes and are more likely to perform interactions with well-connected plant species. Lastly, when extinctions occur randomly, frugivorous birds can maintain robustness because frugivorous birds show more trait variability and show more options to rewiring.

Second, in the scenario where the less connected plant species were lost first, most networks are seen to be robust and were not affected by forest spatial structure. This way to simulate coextinctions is described to be more realistic because less-connected species are more vulnerable to stochastic extinctions (Kaiser-Bunbury *et al.* 2010). The higher robustness to the loss of less connected species first is related to network connectance (i.e., the ratio of realized links to potential links) and nestedness (i.e, tendency of species with few interactions to interact with subsets of high connected species). Connectance increases robustness due to the increase in redundancy of interacting species. Yet, nestedness increases network robustness against the loss of fewer connected species, as long as the well-connected species is maintained. However, intense deforestation has the strongest and massive effects on plants species because birds can move to adjacent areas. For this reason, plants are more detrimental than animals in mutualistic networks (Schleuning *et al.* 2016).

Third, the scenarios of generalist species or random extinctions is likely to occur due to the intensification of anthropogenic activities like deforestation. We found that the higher robustness to loss of generalist and/or random deletion of plant species were found in more forested than in deforested and fragmented landscapes. Networks in forested landscapes have more options to rewiring their interactions due to higher trait variability

than deforested landscapes. Two mechanisms can be used to explain our results (i) intense deforestation as discussed above and (ii) extractivism of well-connected plant species (e.g., *Euterpes edulis*) and plant species for the timber industry. The first mechanism, unfortunately, is increasingly common and a vast area of forest is converted to rural areas, pasture, or even urban expansion. In fact, actions against sustainability have led to an increase in human pressure on biodiversity (Barbosa *et al.* 2021). The result of forest loss affects not only species richness but also the emergent properties that arise from interactions between species. For example, deforestations can homogenize interactions increasing reliable interactions (Tylianakis *et al.* 2007; Laliberté & Tylianakis 2010; Schneiberg *et al.* 2020) and reduces trait variability (Magnago *et al.* 2014). The second mechanisms arise when specific plant species are used for food (e.g, palms) or logging. Although palm trees are not present in all networks because some of our networks occur in deforested and fragmented landscapes and therefore palm trees may have been exploited in the past, some studies have found that palm trees are key elements in ecological networks (Galetti & Aleixo 1998; Fadini *et al.* 2009; Muler *et al.* 2014).

Finally, our result shows the importance to conserve continuous forests to maintain the diversity of species and traits which allows more options for rewiring in face of some environmental disturbance. Although some studies have pointed that the exclusion of generalist species represents the worst scenario to simulate coextinctions, anthropic activities which contribute to deforestation and fragmentation, like landscape conversion, represent one of the most invasive threats for biodiversity. Many animals can move across habitat-matrix, however, trees are sessile and extremely vulnerable to dismantling of the environmental policies and increase actions against conservation efforts.

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