

Research

Forest cover and connectivity have pervasive effects on the maintenance of evolutionary distinct interactions in seed dispersal networks

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Seed dispersal by animals is one of the most important ecological processes in tropical forests, entailing millions of years of evolutionary adaptations of plants and frugivorous animals forming networks of interactions that, ultimately, contribute to the resilience of such forests. We analyze 29 seed dispersal networks in the threatened Atlantic Forest biodiversity hotspot, with data on the frequency of feeding visits by birds to fruiting plants to answer: 1) which are the effects of forest cover and landscape connectivity on the maintenance of phylogenetic diversity (PD) of interacting birds and plants and the evolutionary distinctiveness of the interactions (EDi) between them; and 2) how EDi and plant/bird PD affects the robustness of the interaction networks? We found that forest cover positively influences both plant and bird PD and EDi. Landscape connectivity is an important predictor of bird PD, but not plant PD, suggesting that the spatial arrangement of forest remnants is essential for guaranteeing bird movement among forest fragments. Furthermore, interaction networks of areas with higher PD and EDi had great robustness to the simulated extinction of species, which underscore the importance of larger forest blocks for conserving evolutionary information and, consequently, the health and natural resistance of seed dispersal networks against environmental change.

Keywords: Atlantic Forest, ecosystem functioning, frugivory, tropical biodiversity

Abstract summarizing sentences

- Each 1 percent of forest cover loss resulted in the loss of 270 million years of evolutionary distinctiveness in the interactions between plants and frugivorous birds.
- The loss of forest cover and landscape connectivity increases the loss of evolutionary information in plant/bird interactions.
- Evolutionary information is an important indicator of the robustness of mutualistic networks between plants and birds.



Introduction

Much effort has been done to understand how landscape alterations caused by human activities influence ecosystem functioning (Cramer et al. 2007, Srivastava et al. 2012). The pervasive processes of habitat loss and fragmentation, for instance, are among the main threats to the integrity of key ecological processes such as pollination (Fleming et al. 2009, Grab et al. 2019), seed dispersal (Lorts et al. 2008, Pigot et al. 2016) and ecosystem resilience (Pérez-Valera et al. 2018), ultimately affecting the conservation of biodiversity worldwide (Butchart et al. 2010, Johnson et al. 2017). Fragmentation as a process results in patch size reduction and increased habitat isolation, thus magnifying the occurrence of edge effects (Fahrig 2003), all of which affects the persistence of the species most sensitive to habitat alterations. Habitat fragmentation can also reduce landscape connectivity or the ability of the landscape to promote movements (*sensu* Taylor et al. 1993). Such changes impact a myriad of species, but particularly mutualistic interactions, whose effectiveness partially depends on species movement, such as pollination and seed dispersal (Côrtes and Uriarte 2013).

In tropical forest, networks of interactions between frugivorous birds and plants are negatively impacted by fragmentation, which affects particularly large bird species, often the first to disappear from fragmented landscapes (Emer et al. 2019a, Marjakangas et al. 2020). Consequently, the importance of small generalist birds tend to increase in such landscapes (Emer et al. 2018, Carreira et al. 2020), which, in the medium and long-term, can lead to the homogenization of bird–plant interactions (Olden et al. 2004, Tylianakis et al. 2010).

The loss of interactions performed by large animals disproportionately affects large-seeded plants (Galetti et al. 2013). Therefore, most evolutionarily distinct species (ED, *i.e.* species that have appeared longer in evolutionary time and share less evolutionary history with the rest of the community) can be lost, resulting in the loss of millions of years of evolutionary history (Emer et al. 2019b). For this reason, considering evolutionary processes in studies focused on the loss of species and interactions adds an important dimension to conservation, thus going beyond the extinction of taxonomic entities or species (Crandall et al. 2000, Moritz 2002).

One way to understand how environmental changes lead to the loss of evolutionary information is to consider the phylogenetic diversity (Faith 1992) and the amount of evolutionary divergence accumulated in a community (Emer et al. 2019b). Here, we use the amount of accumulated evolutionary divergence between species interacting in a given location to assess how much of that divergence is lost as habitats shrink, and how such loss influences the robustness of networks of interacting fleshy-fruited plants and frugivorous birds to the extinction of species.

In interaction network theory, robustness allows us to quantify how extinctions in one side of a bipartite network (*e.g.* birds) results in secondary extinctions on the other side (*e.g.* plants), thus allowing us to assess the level of disturbances caused by species extinctions (Mommott et al. 2004). This metric has the

drawback of considering interactions statically as it does not take into account the possibility that interactions might reorganize in response to the extinction of a given species (*rewiring*), or that functional extinction may occur even before local extinction (Säterberg et al. 2013). In addition, the robustness analysis does not take into account the abundance of species or interactions (Morán-López et al. 2020). However, the robustness of an interaction network is a proxy for their resilience to cope with changes in environmental factors such as the reduction of functional landscape connectivity (Dunne et al. 2002, Vieira and Almeida-Neto 2014), habitat loss (Evans et al. 2013) and changes in the behavior of interacting animals (Kaiser-Bunbury et al. 2010). Ultimately, the robustness permits evaluating how networks of ecological interactions are maintained under scenarios of ecological changes (Mommott et al. 2004).

In well-preserved habitats that maintain the complete coterie of interacting species, regarding the networks of interactions, we expect to have more connections among species, which is associated with greater robustness due to the lower likelihood of losing species by coextinction (Dunne et al. 2002, Burgos et al. 2007, Kaiser-Bunbury and Blüthgen, 2015). On the other hand, networks with fewer connections are prone to the coextinction of species partners (Vieira and Almeida-Neto 2014), which can compromise the maintenance of the evolutionary history embedded in interactions that Emer et al. (2019b) called evolutionary distinctness of interactions (EDi). EDi can be defined as ‘the combined ED that both interacting partner species convey to a given interaction, irrespective of how long they have been interacting with one another’. Losing interactions with high EDi should make the recovery of the species composition of disturbed forests even more difficult, for instance, through the limitation in the dispersal of large-seeded plants that generally have a great EDi (Tabarelli and Peres 2002, Costa et al. 2012).

Although many efforts have been made to understand how human-induced modifications impact the occurrence, abundance and species persistence in fragmented landscapes (Johnson et al. 2017), it is of utmost importance to quantify how landscape changes shape the maintenance of phylogenetic diversity of interacting species and how these changes can influence the robustness of interaction networks that are essential to maintain key ecological processes, such as seed-dispersal. In addition, this can allow us to estimate how much of evolutionary history can be lost due to landscape changes affecting only one or both sides of interaction networks. Here, we addressed two questions: 1) how the decrease in forest cover and functional connectivity affects the maintenance of the phylogenetic diversity (PD), and evolutionary distinct interactions (EDi) between plants and frugivorous birds, and 2) how do plant and bird PD and EDi affect the robustness of interaction networks? We expect that: 1) the loss of forest cover and reduction of functional connectivity causes a decline in phylogenetic diversity of birds and plants, and 2) the loss of PD and the loss of interactions between evolutionarily distinct species would lead to the reduction of robustness in mutualistic networks between plants and frugivorous birds (Fig. 1).

Material and methods

Study area

The Atlantic Forest is among the top five global biodiversity hotspots in the world (Myers et al. 2000). It is the second largest rainforest in the Americas, originally covering more than 1.5 million km² encompassing latitudinal, longitudinal and environmental gradients distributed along the Atlantic coast of Brazil and in the continent interior to reach parts of Argentina and Paraguay (Morellato and Haddad 2000, Young 2003, Muylaert et al. 2018). The extensive geographic coverage, combined with extreme heterogeneity in composition and altitudinal gradient (from sea level to 2900 m), favored great species diversification and endemism, with more than 20 000 species of plants and 688 species of birds (Goerck 1997, Mittermeier et al. 1998). As a consequence of intense forest loss and fragmentation, the Atlantic Forest was reduced to less than 16% of its original forest cover (Ribeiro et al. 2009) (Fig. 2).

Dataset

We searched for studies carried out in the Atlantic Forest with records of interactions between frugivorous birds and plants in scientific journals, data repositories and the gray literature, which included theses and dissertations. We searched the databases Google Scholar, Scopus and Web of Science using the terms 'bird', 'avian', 'frugivory', 'seed dispersal', and their Portuguese and Spanish equivalents. To be considered, the study should have 1) a list of interacting plants, birds and information on visit frequency of frugivorous birds to plants, and 2) at least five plant species with interactions with birds recorded (Supporting information).

Phylogenetic trees of plants and birds

Plants

Considering the regional pool of species, we first obtained the updated species names from the plantminner.com platform

(Carvalho et al. 2019), using The Plant List (2013) as a standard for nomenclature. Then, we obtained the initial mega-phylogeny of plants using the *S.PhyloMaker* function (Qian and Jin 2016) based on 'scenario 1', which places unidentified genera and species within their highest taxonomic level as basal polytomies. We proceeded to solve the polytomies by applying a birth–death model using the *PolytomyResolver* function (Kuhn et al. 2011) to adjust the length of the branches in the BEAST software ver. 1.5.4 (Suchard et al. 2018). A Markov chain Monte Carlo simulation was performed for 106 iterations, sampling trees at 103 iterations. Finally, we randomly selected 100 solved trees, after burning out the first 25% options. We calculated the phylogenetic metrics for all the 100 trees and used the means of these metrics for subsequent analyses.

Birds

We considered all bird species recorded in the 29 studied networks as our regional pool for the bird phylogenetic tree. Furthermore, we standardized species nomenclature using the South American Classification Committee (Remsen et al. 2017) and submitted the corrected names to birdtree.org online database (Jetz et al. 2012). We used the *Hacket* source tree as the master phylogeny of birds containing up to 10 000 phylogenetic hypotheses, which resulted in a multiphylo file ('.tre') containing 100 phylogenetic trees without polytomies and with resolution at the species level. Likewise for the plant phylogeny, we calculated the phylogenetic metrics of all 100 trees and used the mean for subsequent analyses.

Phylogenetic metrics

Based on the phylogenetic trees of our regional pool of bird and plant species, we estimated the evolutionary history involved in the interactions for each studied network using two complementary metrics calculated at the community level: 1) phylogenetic diversity (PD) which accounts for the summed branch lengths of all species within a network (Faith 1992), and 2)

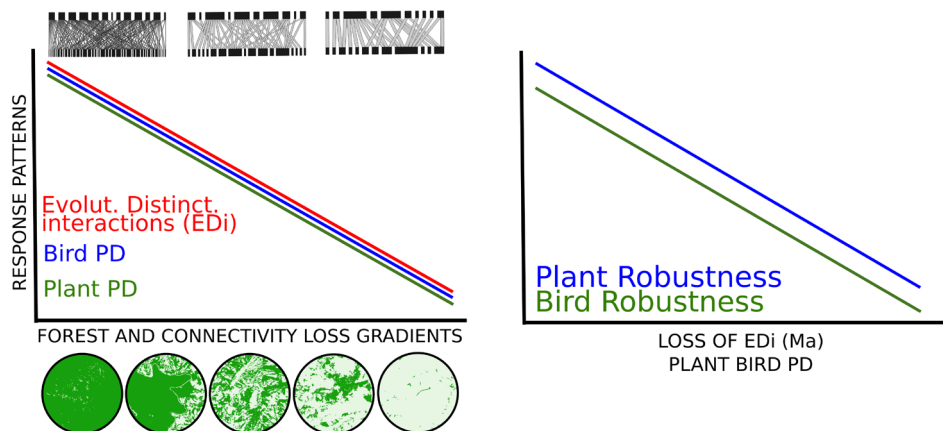


Figure 1. Expected effects of deforestation on the phylogenetic diversity (PD) of interacting birds and plants, and the distinctiveness of interactions (EDi) between them (left panel). The right panel shows the expected consequences of the decrease in PD and EDi on the robustness of interaction network between plants and frugivorous birds.

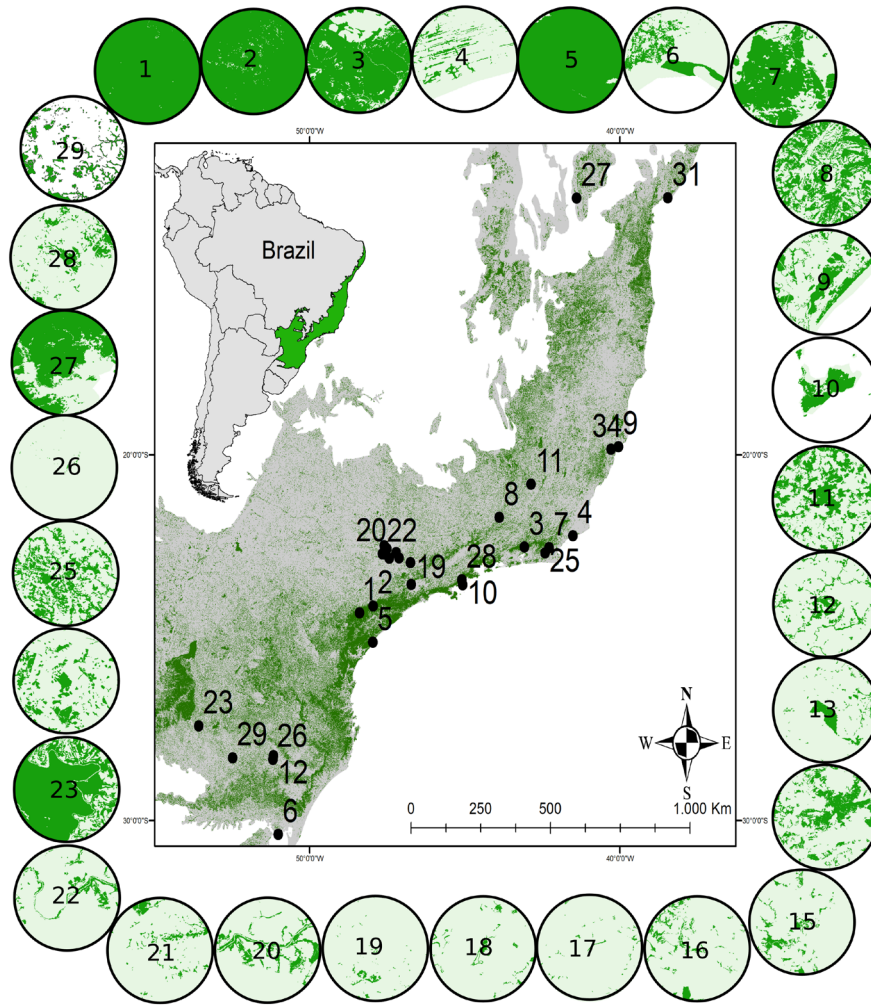


Figure 2. Distribution map of the areas where interaction networks were sampled in the Atlantic Forest with their respective forest cover buffers (4 km radius). Additional information on each area are in the Supporting information.

how unique the frugivory interactions are within each network by calculating the evolutionary distinctness (ED) of birds and plants followed by the evolutionary distinctness of interactions (ED_i, sensu Emer et al. 2019b). ED_i represents how many millions of years of evolutionary history is carried by a given interaction, regardless of how long they have co-evolved. We estimated ED using the equal splits metric in the ‘evol.distinct’ function in the *spicy* package for R (Kembel et al. 2010). Equal splits equally divide the phylogenetic distance between a branch and its roots by the number of nodes between them, given higher values of ED for species placed in clades with lower speciation events. We used the averaged ED of bird and plant species calculated over 100 correspondent phylogenetic trees to calculate ED_i as the sum of the average EDs of plants and birds that interact in each network.

Robustness

This metric is calculated from the area under the extinction curve generated by the simulated removal of species from one group of a bipartite network that reflects in secondary

extinctions in the interacting group. The size of this area (from 0 to 1) represents the system tolerance to species loss. Thus, $R=1$ corresponds to a curve that decays slightly until the total extinction of the species in both sides of the network, indicating a robust system, while $R=0$ corresponds to a curve that declines abruptly as soon as the first species is removed from the network, representing a fragile system in which one or multiple extinctions lead to the rapid collapse of the network (Dormann et al. 2009). We calculated robustness via the simulated extinction of birds and plants using a new approach that include the potential of species to replace lost partners (Vizentin-Bugoni et al. 2020) considering rewiring probabilities scenarios of 25, 50 and 75% (Kaiser-Bunbury et al. 2010, Schleuning et al. 2016). Also, we ranked the species in decreasing order of ED and used the lists of plants and birds with external methods into the one. `second.extinct.mod` function modified from *bipartite* package in R (Vizentin-Bugoni et al. 2020). We simulated extinctions using a decreasing order of ED of birds and plants because this is the most realistic scenario for both groups given that large birds and large-seeded plants have in general high ED

and are the most threatened by habitat loss and fragmentation in the Atlantic Forest (Emer et al. 2019a).

Landscape metrics

Vegetation maps were compiled from FBDS (Brazilian Foundation for Sustainable Development, <www.fbds.org.br/>), SOS-Mata Atlântica 2014 (<www.sosma.org.br/>), and Hansen et al. (2000) (using a 95% NDVI limit to determine and delineate forest areas). Using these maps, we generated a binary map (1 = vegetation, 0 = non-vegetation) with 30 m of resolution based on Albers equal area coordinate system and Datum SAD69. The extent of the Atlantic Forest used in this study consists of the consensual limits defined by several previous extent definitions (Muylaert et al. 2018). Then, for each study area we extracted the 1) forest cover (%), considering the percentage of forest cells within two buffers with a radius of 1000 and 4000 m from the centroid coordinate provided in each study, thereby selecting the best representative buffer, and 2) functional connectivity, which represents how much of the vegetation (in ha) is functionally connected to focal forest fragments, given a gap crossing capability of birds. In our case we used a gap crossing of 180 m, which corresponds to the maximum recorded distance for movement between forest fragments by forest-dependent birds of the Atlantic Forest (Awade and Metzger 2008, Martensen et al. 2008). Although these two metrics were correlated (Pearson's correlation = 0.72, $t = 5.52$, $df = 27$, $p < 0.001$), we decided to keep both because they convey different information. While forest cover refers to the percentage of vegetation present in a given landscape, functional connectivity reflects the sum of available forests (in ha) considering that the organisms have the ability to cross over non-forest anthropogenic matrices (such as pasture, agriculture and *Eucalyptus* plantations). Functional connectivity was log-transformed using base 10 (Jorge et al. 2013).

Data analyses

To assess the explanatory power of forest cover and functional connectivity to explain the phylogenetic metrics (PD and EDi) of the interacting plants and birds, we built linear models (LMs) with landscape metrics as predictor variables and PD and EDi as response variables, and used normal error distribution of the residuals during model fitting. To evaluate the effect of phylogenetic metrics on the robustness of networks, we built another model with PD and EDi as predictor variables and robustness as the response variable. The explanatory power of each model was measured using the coefficient of determination (r^2); for beta 1 (b_1) parameter estimates we present both t -value and p -value.

Because our data set put together 29 studies with different sampling effort and number of studied species, we used sampling intensity to control the effect of network sub- and super-sampling using sampling intensity as a weight in all fitted LM models. Sampling intensity was calculated as:

$$\text{Intensity}_{\text{web}} = \frac{\sqrt{N_i}}{\sqrt{\text{size}_i}}$$

where N_i is the total number of interactions, and size is the multiplication of the number of plants by the number of bird species in each network (Schleuning et al. 2012). We used the R language in ver. 3.6.3 for all analyses.

Results

We found 29 interaction networks in different areas of the Atlantic Forest, spanning a vast latitudinal gradient of 2200 km (Fig. 2) (Supporting information). The oldest study in our data set was published in 1994 and the newest in 2016. Most of the studies were done in south and southeast Brazil, which correspond to the more populated regions of the country. Among the 29 study areas, thirteen are protected areas (44.8%) including state and national parks, five are from restored areas (17.2%), and eleven are non-protected forest fragments (37.9%) ranging from 10 to 380 ha in size.

Networks involved 378 species of plants, 203 species of birds and 3842 interactions between them. The plant species most commonly consumed by birds was *Matayba elaeagnoides* (Sapindaceae) with 788 interactions (i.e. 9.8%), while the bird species most frequently recorded was *Thraupis sayaca* (Thraupidae) with 661 interactions (8.2%).

Areas with high forest cover had greater PD of plants ($b_1 = 1007.11$, $SE = 321.45$, $t = 3.13$, $p = 0.04$, $r^2 = 0.12$) and birds ($b_1 = 403.69$, $SE = 72.55$, $t = 5.56$, $p < 0.01$, $r^2 = 0.33$), maintaining interactions with higher EDi ($b_1 = 7.37$, $SE = 0.21$, $t = 35.69$, $p = 0.002$, $r^2 = 0.27$) (Fig. 3). On average, 270 million years (Ma) of evolutionary distinction in interactions were lost for each 1% of forest cover loss (Supporting information). Likewise, areas with higher functional connectivity had greater PD of birds ($b_1 = 378.2$, $SE = 101.8$, $t = 3.72$, $p = 0.01$, $r^2 = 0.19$), but connectivity was not able to explain the PD of plants nor EDi (Fig. 3).

Networks in areas with higher EDi ($b_1 = 0.03$, $SE = 0.1$, $t = 3.196$, $p = 0.003$, $r^2 = 0.25$) and areas with greater PD of plants ($b_1 = 0.108$, $SE = 0.047$, $t = 2.317$, $p = 0.03$, $r^2 = 0.14$) had greater robustness calculated by the removal of plants with decreasing order of ED. Likewise, networks in areas with higher EDi ($b_1 = 0.051$, $SE = 0.22$, $t = 2.339$, $p = 0.02$, $r^2 = 0.14$) and with greater PD of birds ($b_1 = 0.25$, $SE = 0.078$, $t = 3.17$, $p = 0.003$, $r^2 = 0.24$) presented greater robustness calculated by the removal of birds with decreasing order of ED (Fig. 4). The previews of linear models using robustness rewiring shows that the force of interactions increased with rewiring probability (Table 1, Supporting information).

Discussion

We demonstrated that areas with high forest cover are able to maintain greater phylogenetic diversity of birds and plants, and also maintain interactions between more evolutionarily

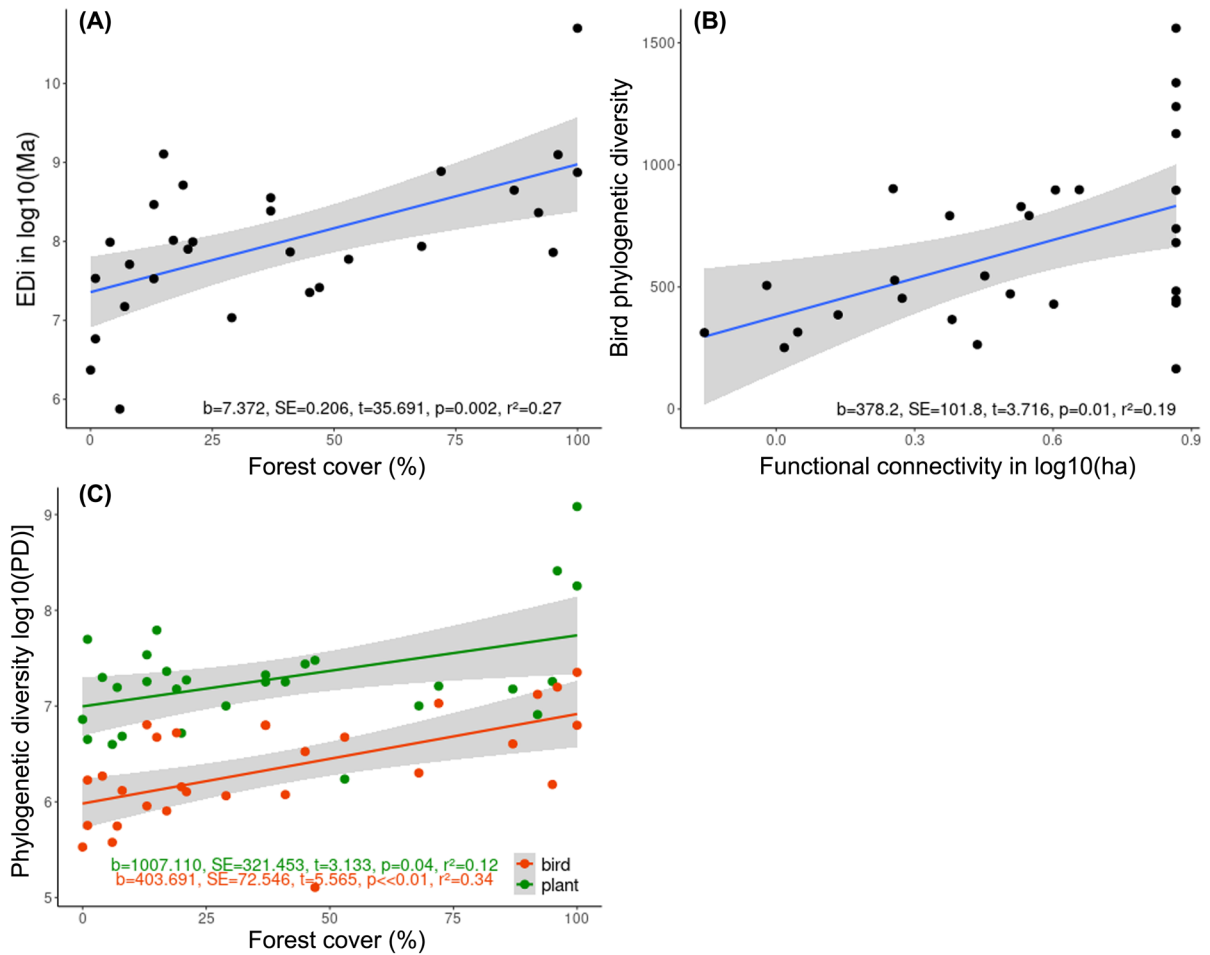


Figure 3. Linear models showing that areas with greater forest coverage in a 4-km radius presented greater distinctiveness of interactions (EDi) (A), greater phylogenetic diversity of both plants and frugivorous birds (B) and that more connected areas maintain greater phylogenetic diversity of frugivorous birds (C). The gray band represents the 95% confidence interval.

distinct species (i.e. high PD and EDi). We also have shown that when 1% of forest cover is lost, on average 270 million years (Ma) of evolutionary distinction in the interactions between plants and frugivorous birds are also lost which means a difference of 19 045 Ma of evolutionary distinction from the three most forested areas (1, 3 and 5 in Fig. 1) to the three most deforested areas (17, 19 and 26). Phylogenetic diversity, in conjunction or not with functional diversity, is known to be an important predictor to biodiversity and ecosystem function (Thompson et al. 2015, Faith 2018, Qin et al. 2020). Here, we highlight the importance of taking a step forward in unifying evolutionary biology with ecosystem ecology and interactions to improve the understanding of biodiversity loss and its consequences especially in high diverse ecosystems (Flynn et al. 2011, Srivastava et al. 2012). These findings reinforce the importance of maintaining large and well-connected forest blocks as key sources of phylogenetic/evolutionary information (Ribeiro et al. 2009, Cadotte et al. 2012). This also emphasizes the great importance of forest restoration projects, particularly those that aim to increase functional connectivity between areas with high levels of integrity of ecological processes (Tambosi et al. 2014).

Areas with high functional connectivity between forest fragments are able to maintain higher phylogenetic diversity of frugivorous birds when compared to less connected or isolated forest patches (Fig. 3), thus suggesting that the connection between remnant areas of forests is important for maintaining key ecological processes such as seed dispersal. We know that birds, especially insectivorous and frugivorous ones, are among the most mobile vertebrates and consequently the most threatened by the fragmentation and isolation of tropical forests (Sekercioglu et al. 2002, Camargo et al. 2020). Landscapes with high functional connectivity allow such mobile organisms to seek resources in structurally dispersed forest fragments (Boscolo et al. 2008, Martensen et al. 2012). However, this also depends on the ability of species to cross the surrounding anthropogenic matrix, such as pastures, agriculture and *Eucalyptus* plantation (Andrade and Marini 2001, Da Silveira et al. 2016, Giubbina et al. 2018, Ramos et al. 2020). Management strategies that act upon fragment size, forest cover and functional connectivity are pivotal for mitigating the negative effects of habitat loss and fragmentation, thus allowing birds to use multiple functionally connected fragments (Martensen et al. 2008). Therefore, maintaining high levels

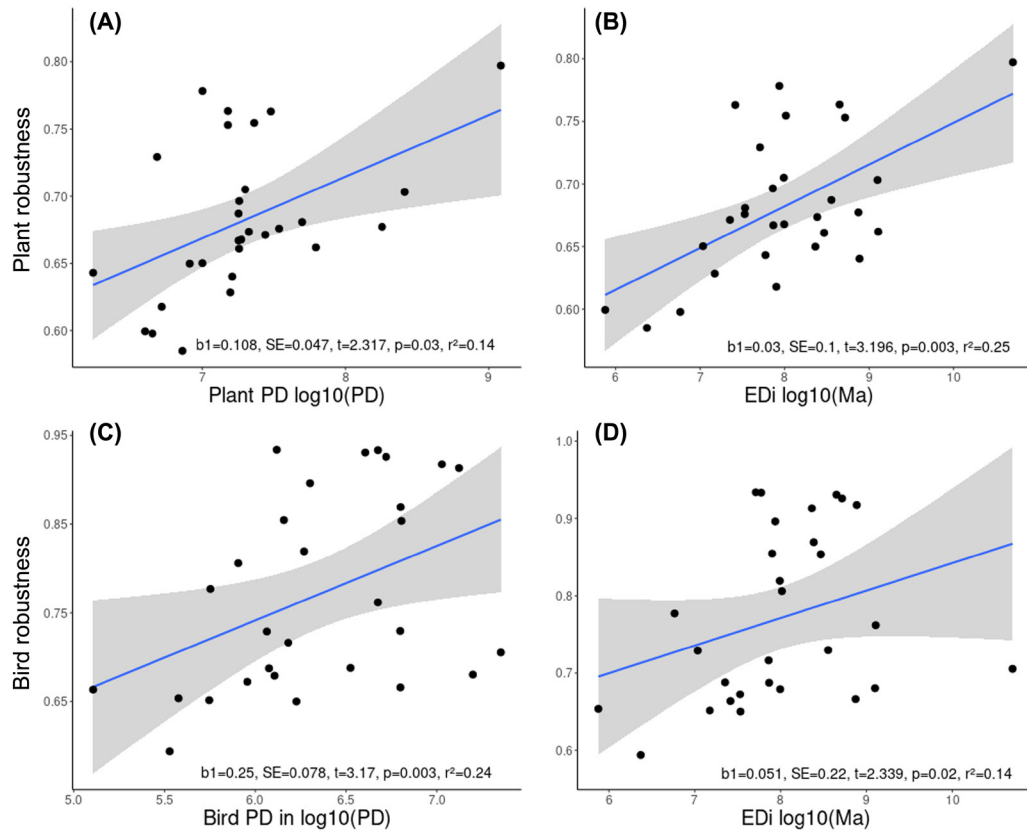


Figure 4. Linear regression showing that areas with greater evolutionary distinctiveness of interactions (EDi; A and C) and greater phylogenetic diversity (PD; B and D) have greater robustness in the interaction networks calculated by removing plants (A and B) and birds (C and D) in decreasing order of evolutionary distinctiveness (ED). The gray band represents the 95% confidence interval. EDi and PD were logged-transformed with base 10.

Table 1. Statistical summary of the linear models between plant robustness and EDi, bird robustness and EDi, plant robustness and PD, bird robustness and PD. The lines show robustness rewiring probability of zero, 25, 50 and 75%.

Rewiring	b	SE	t value	p-value	R ²
Plant robustness ~ log10(EDi)					
0.00%	0.034	0.01	3.196	0.003	0.25
25.00%	0.041	0.011	3.196	0.001	0.30
50.00%	0.047	0.012	3.94	0.001	0.34
75.00%	0.052	0.012	4.248	0	0.38
Bird robustness ~ log10(EDi)					
0.00%	0.051	0.022	2.339	0.027	0.14
25.00%	0.054	0.021	2.558	0.016	0.17
50.00%	0.055	0.019	2.797	0.01	0.19
75.00%	0.056	0.018	3.12	0.004	0.24
Plant robustness ~ plant phylogenetic diversity log10(PD)					
0.00%	0.108	0.047	2.317	0.03	0.14
25.00%	0.134	0.05	2.735	0.01	0.19
50.00%	0.167	0.051	3.241	0.003	0.25
75.00%	0.187	0.053	3.53	0.001	0.29
Bird robustness ~ bird phylogenetic diversity log10(PD)					
0.00%	0.25	0.078	3.172	0.003	0.24
25.00%	0.258	0.075	3.411	0.002	0.28
50.00%	0.258	0.075	3.411	0.002	0.29
75.00%	0.249	0.064	3.88	0	0.33

of functional landscape connectivity for frugivorous birds and high forest cover at landscape level are of utmost importance for guaranteeing high phylogenetic diversity of birds. However, plant phylogenetic diversity is mostly affected by forest cover, while functional connectivity was apparently not a reliable predictor of the phylogenetic diversity of interacting plant species, suggesting that seeds may not move among forest fragments as easily as birds. As a way to save energy during matrix crossing flight, frugivorous birds tend to rapidly discard seeds after ingestion, especially medium to large seeds that are quickly regurgitated (Moermond and Denslow 1985). Tanagers, which are among the most frequent seed dispersers in altered Atlantic Forest landscapes (Pizo 2007), do not even ingest such seeds, mashing fruits to discard the seeds beneath parent plants (Levey 1987). As a result, seeds may not always accompany frugivorous birds as they move among forest fragments. This is not good for secondary forest fragments but is especially harmful in restored forest that heavily depends on zoocoric seed dispersal. As demonstrated by others researchers, the forest reduction induce the downsizing of frugivores and seeds causing functional redundancy and loss of taxonomic, functional and phylogenetic biodiversity (Morante-Filho et al. 2015, Pérez-Méndez et al. 2015, McConkey and O’Farrill 2016, Emer et al. 2018). The recently shown decrease in the representativeness of large-seeded plants in the remaining Atlantic Forest fragments (Lima et al. 2020), and the high beta-diversity of the plant communities thriving in such forests (Vidal et al. 2019) may be partially explained by such constraints and lend support to our findings.

Areas with greater phylogenetic diversity of both plants and birds, as well as areas with more evolutionary distinct interactions, presented interaction networks with greater robustness. Some studies pointed out the role of species loss in the robustness of interaction networks involving parasite–host (Ives and Godfray 2006), herbivorous/predatory insects and plants (Haddad et al. 2009) and pollination (Memmott et al. 2004, Vásquez et al. 2009, Kaiser-Bunbury et al. 2010, Vieira et al. 2013). To our knowledge, however, Rezende et al. (2007) was the only to analyze the robustness of phylogenetically structured mutualistic networks. Indeed, studies have rarely shown how the loss of phylogenetic diversity (PD) and interactions between evolutionarily distinct species (EDi) lead to less robust networks and consequently more likely to collapse in response to anthropogenic changes. Our study shows the importance of maintaining large forest patches and clusters of functionally connected areas with ample phylogenetic diversity, which, in turn, can assure high levels of robustness to interaction networks. This agrees with previous studies showing that PD is linked to ecosystem functioning (Flynn et al. 2011, Srivastava et al. 2012) and promotes ecosystem stability (Cadotte et al. 2012), so that when species extinction occurs in areas with high phylogenetic diversity, the impact of such extinction is smaller due to the high diversity of interactions.

The possibility of extinction of plants and birds would theoretically lead to co-extinctions and, consequently, to the collapse of networks in these communities. However, the extinction of a species does not necessarily lead to the co-extinction of its interacting partners (Pires 2017). This is

because there is the possibility of interaction rewiring within complex networks, though often with unknown consequences for the effectiveness of the interaction (Gilljam et al. 2015). Therefore, we calculated robustness with different rewiring probabilities, to more realistically evaluate scenarios where plants and birds have the capacity to relocate their interactions following the extinctions of their partners (Kaiser-Bunbury et al. 2010, Schleuning et al. 2016). As expected, the increase of rewiring probability reflect in greater robustness because when a species goes extinct, the second extinction take time to occur thus increasing the probability nother of another partner taking place and avoiding extinction. Robustness calculated with high probability of rewiring is better predicted by PD and EDi (Table 1, Supporting information), indicating that in a more realistic scenario where different probabilities of rewiring are possible phylogenetic metrics can better reflect robustness.

In summary, we found that in addition to the well-established consequence of species extinction, deforestation causes the loss of evolutionary information embedded in the interactions between plants and their seed dispersers as already seen by Emer et al. (2019b). Consequently, the loss of evolutionary information can reflect negatively on the resilience of the seed dispersal interactions to anthropogenic disturbances. In critical environmental conditions, when forest cover and functional connectivity is exceedingly low, seed dispersal networks present low phylogenetic diversity and evolutionary distinction (Emer et al. 2019b), which may translate into low ecological resilience and low recovery capacity of ecosystems.

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Author contributions

Erison Carlos S. Monteiro: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Methodology (lead); Project administration (lead); Writing – original draft (lead). **Marco A. Pizo:** Conceptualization (equal); Data curation (equal); Investigation (supporting); Methodology (supporting); Project administration (equal); Supervision (lead); Writing – original draft (supporting); Writing – review and editing (equal). **Maurício Humberto Vancine:** Formal analysis (equal); Investigation (equal); Methodology (supporting); Writing – review and editing (equal). **Milton**

Ribeiro: Conceptualization (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Project administration (equal); Resources (equal); Supervision (supporting); Writing – review and editing (equal).

Data availability statement

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.ns1rn8psv>> (Monteiro et al. 2021).

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