

Research article

Habitat loss shapes the structure and species roles in tropical plant–frugivore networks

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Oikos

2022: e09399

doi: [10.1111/oik.09399](https://doi.org/10.1111/oik.09399)

Subject Editor: Anna Traveset

Editor-in-Chief: Dries Bonte

Accepted 8 November 2022

Habitat loss is a global threat to biodiversity with pervasive effects on species and populations. These impacts may generate cascading effects on ecological processes propagating across ecological networks. Thus, understanding how habitat loss affects ecological networks is fundamental for conservation. We used a database of 25 plant–frugivore networks distributed across the whole Brazilian Atlantic Forest to understand how landscape-scale habitat loss shapes network structure, robustness, species role and traits related to seed dispersal. We compared whether these network properties have linear or non-linear relationships and used centrality metrics and indirect effects to evaluate if habitat loss change the role of species in plant–frugivore networks. We found linear and non-linear relationships with negative effects of habitat loss on the network structure. As a consequence of shifts in species richness and number of links, the number of interactions and the proportion of possible interactions observed (connectance) were negatively associated with habitat loss. In contrast, nestedness increased with habitat loss. Network robustness, mean bill width and mean seed size were not significantly related to habitat loss. In addition to changes in interaction patterns at network level, habitat loss also favors changes in interaction among species, shifting the species playing central roles in network organization or contributing to indirect effects in the networks. In forested landscapes, obligate frugivores are the main central species in the network, and the ones potentially contributing to indirect effects, while in deforested landscapes these roles are fulfilled by occasional frugivores. Thus, our results emphasize the widespread effect of habitat loss on plant–frugivore systems, adding evidence that its pervasive effects on biodiversity also proliferate on mutualistic interactions with negative consequences for seed dispersal that potentially go beyond the direct pairs of interacting species.

Keywords: Atlantic Forest, birds, deforestation, forest cover, mutualistic networks, plant–animal interactions

Introduction

Habitat loss is one of the main threats to biodiversity, with pervasive effects on species, populations and ecosystem services (Newbold et al. 2015, Barnes et al. 2017). In the tropical region, species have been impacted by human actions in unprecedented ways in the last decades (Barlow et al. 2018). These consequences are not limited to the direct loss caused by human activities. Rather, biodiversity loss might trigger cascading effects disrupting key ecological processes such as seed dispersal (Mommott et al. 2004, Valiente-Banuet and Verdú 2013).

Evidence of the negative effects of habitat loss on biodiversity has been shown for several clades, such as mammals (Pardini et al. 2010, Arroyo-Rodríguez et al. 2016, Muylaert et al. 2016), birds (Martensen et al. 2012, Morante-Filho et al. 2015) and plants (Rocha-Santos et al. 2017). However, species can exhibit divergent responses to disturbance, as certain generalist or disturbance-tolerant species can thrive in human-modified landscapes (Filgueiras et al. 2021). For instance, among birds, generalist species such as, *Campyostoma obsoletum* and *Elaenia flavogaster* increase their occupancy in deforested landscapes, whereas forest-dependent species, such as, *Ceratopipra rubrocapilla* and *Dixiphia pipra* thrive in forested landscapes (Morante-Filho et al. 2021). Also, sensitivity to deforestation in bird species is known to be shaped by ecological traits (Owens and Bennet 2000, Purvis et al. 2000), such as body size (Gaston and Blackburn 1995).

Habitat loss can lead to non-linear declines in biodiversity (Pardini et al. 2010, Martensen et al. 2012, Morante-Filho et al. 2015, Muylaert et al. 2016). In a seminal review, Andrén (1994) showed that in deforested landscapes, patch size decrease and isolation increase. Consequently, studies showed non-linear relationship between forest loss and biodiversity metrics due to the combined effects of habitat loss and fragmentation (Swift and Hannon 2010), with a threshold below which species richness and abundance of particular groups might decline or increase (Pardini et al. 2010, Morante-Filho et al. 2015, Muylaert et al. 2016).

Biodiversity loss also manifests as the loss of ecological interactions, which can precede species loss (Valiente-Banuet and Verdú 2013, McConkey and O'Farril 2016). For instance, the disruption of ecological interactions can reshape the organization and function of ecosystems (Paine 1966, Estes et al. 2011). Ecological interactions form networks upon which the ecosystem depends on (Valiente-Banuet et al. 2015). Thus, the anthropogenic disruption of ecological interactions (Valiente-Banuet and Verdú 2013) may lead to cascading effects that propagate across the ecosystems. Understanding how habitat loss affects the structure and robustness of ecological networks is crucial to identifying thresholds below which the loss of interactions cannot be reversed and the ecosystem collapses (Valiente-Banuet and Verdú 2013, McConkey and O'Farril 2015, Heleno et al. 2020). Previous work using patch-scale approaches provided insights on the relationship between habitat loss and the structure of frugivory networks

(de Assis Bomfim et al. 2018, Emer et al. 2020), and a next step is to explore how human activities may shift patterns at broader spatial scales (Guimarães 2020). Indeed, ecological patterns are always associated with particular scales (Levin 1992) and, therefore, we need to access the spatial scale at which patterns are more clearly predicted by explanatory variables (Jackson and Fahrig 2015). There is an urgent need to assess landscape-scale effects of habitat loss on ecological networks because biodiversity responses to anthropogenic drivers might vary across spatial scales (Fahrig et al. 2019).

Theory predicts that response of ecological systems to perturbation will depend on network structure (Silva et al. 2007). In frugivory networks, nestedness is a common pattern, in which the interactions of specialists are a subset of the interactions performed by generalist species (Bascompte et al. 2003). Nested networks confer functional redundancy and the possibility of alternative routes against disturbance (Bascompte and Jordano 2007). Studies have shown both positive and negative responses of nestedness patterns to disturbances (Laurindo et al. 2019, Vidal et al. 2019, Morrison et al. 2020). The uncertainty of how network patterns respond to habitat loss extends to estimates of the robustness of ecological networks to extinctions (Fortuna and Bascompte 2006, Evans et al. 2013, Vidal et al. 2019). Network robustness measures the system's tolerance to secondary extinctions (Dunne et al. 2002, Mommott et al. 2004). Interestingly, more intensely degraded landscapes may have more connected networks (Morrison et al. 2020), leading to higher robustness. Also, network structure responds non-linearly to habitat loss, with a sudden decay at a certain level of habitat destruction (Fortuna and Bascompte 2006, Fortuna et al. 2013, Vidal et al. 2019). Habitat loss can also shape the role species play in the network, e.g. central species, connecting different parts of the networks. In this sense, we still do not know if, by changing the central species in ecological networks, habitat loss may generate far-reaching effects to ecological assemblages, as those generated by indirect effects, i.e. effects that propagates across species that do not directly interact with each other. Specifically, we still need empirical datasets to analyze how landscape-scale forest loss affects such networks and if its effects translate into changes in the traits related to seed dispersal (Galetti et al. 2013) as a consequence of the extinction and replacement of frugivorous birds in relation to forest loss (Morante-Filho et al. 2018).

Here, we use an empirical database of 25 avian frugivory networks encompassing the Brazilian Atlantic Forest, to evaluate how forest loss affects these networks. Specifically, we assessed how habitat loss shapes network structure, robustness, traits related to seed dispersal (bill width and seed diameter) and the role of different bird species in mutualistic networks. We hypothesized that non-linear relationships, based on Andrén's threshold (Andrén 1994), best describe the relationship between interactions and habitat loss due to the sensitivity of birds (Martensen et al. 2012, Morante-Filho et al. 2015) and plants (Rigueira et al. 2013, Lima and Mariano-Neto 2014) to the extinction threshold (Swift and Hannon 2010). We expected that this non-linear trend could be extended to

the network structure and robustness, as suggested by empirical and simulated studies (Fortuna and Bascompte 2006, Evans et al. 2013, Fortuna et al. 2013, Vidal et al. 2019). Additionally, we predicted that forest loss would have negative effects on the network structure and robustness, shaping the role of bird species in mutualistic networks. These changes are expected because obligate and occasional frugivore species composition change with habitat loss (Morante-Filho et al. 2018) and functional roles of frugivores, e.g. the patterns of interaction of species within networks, vary across species in seed dispersal networks (Mello et al. 2015, Dehling et al. 2021). Finally, we also expected that this replacement of species due to habitat loss will negatively affect the traits related to seed dispersal, such as bill width (Galetti et al. 2013).

Methods

We gathered information from published studies on frugivory networks in the Brazilian Atlantic Forest. This biodiversity hotspot has suffered from intense deforestation, and currently less than 30% of its forest still remains (Rezende et al. 2018, Galetti et al. 2021). The Atlantic Forest is considered a hotspot of biodiversity in the world due to the high diversity, levels of endemism and the presence of threatened species (Myers et al. 2000). In the Atlantic Rainforest, seed dispersal by animals is mainly performed by a diverse assemblage of bird species, especially in areas in which large mammals died out due to multiple forms of human impact. In this paper, we have focused in the seed dispersal by birds.

Data on plant–bird networks were obtained in the largest published database on interactions available for the Brazilian Atlantic Forest (Fig. 1), the ATLANTIC FRUGIVORY (Bello et al. 2017). This database compiled more than 8000 frugivory interactions from 331 vertebrates and 788 plant species recorded in 166 studies. From the database we selected only network studies focusing on birds. Our dataset includes only community-level studies (i.e. those that recorded the interactions between bird and plant assemblages in a forest fragment, using different methodologies such as focal observations, feeding bouts, etc.). Thus, we excluded from the database studies focusing on plant or animal populations. We completed the data searching for additional studies on plant–bird interactions in the Web of Science and Scopus using the following search terms: ('ecological network*' OR 'mutualistic network*' OR 'frugivor*') AND ('bird*') AND ('Atlantic Forest') in TOPIC. From this search, we included only network studies that have the coordinates of the sampling fragment and provided the matrix of interactions. Our final database is composed of 25 qualitative plant–bird frugivory networks from different forest fragments, 12 from the ATLANTIC FRUGIVORY and 13 from the literature search (Fig. 1, Supporting information).

Descriptors of network structure

To describe each network, we calculated the number of bird and plant species and the total number of interactions. We

also calculated the following descriptors of network structure: connectance (proportion of realized interactions in relation to all possible interactions, Gardner and Ashby 1970, Jordano 1987); the average number of links per species (sum of links divided by the number of species); the level of nestedness (a pattern where the interactions performed by specialist species are a subset of those of generalist species, Almeida-Neto et al. 2008). We selected those metrics because they are commonly used in network studies and describe the diversity of species and interactions in the entire network, providing insights into the structure and dynamics of ecological networks (Dehling 2018, Guimarães 2020). All network metric were calculated using the function *networklevel* in the package *bipartite* (Dorman et al. 2009). Nestedness was calculated using the 'Nestedness metric based on overlap and decreasing fill' (NODF) index (Almeida-Neto et al. 2008). We used null models to test if nestedness shows patterns that are higher than expected by both species richness and the variation in the number of links across species. We used the Patefield algorithm that randomizes the distribution of links between species while maintaining the number of links per species (Dormann et al. 2009). We created 1000 null models for each site and used Z-scores to test if the observed value of the network differs significantly from the theoretical benchmark provided by the null model. Z-scores were calculated as:

$$Z = \frac{O - E}{\sigma}$$

where O =observed value; E =average value for the ensemble of null model networks and σ =standard deviation of the ensemble of null model networks.

We assumed that robustness can be described by simple coextinction dynamics in which if all partners of a given species die out the species also dies out. We then calculated network robustness, which measures the area under the secondary extinction curve – the curve describing the number of remaining plant species after the sequential removal of animal species – after simulating bird extinction assuming a random extinction process (Memmott et al. 2004). Simulations were performed through 100 randomizations using the functions *second.extinct* and *robustness* in package *bipartite* (Dorman et al. 2009).

We then turned our attention to descriptors of roles of bird species in network structure. For each bird species, we calculated betweenness centrality, which assesses the importance of each species in connecting different parts of the network (Dáttilo and Rico-Gray 2018). Species may also be important by creating pathways that indirectly connect species, allowing the propagation of indirect effects (Guimarães et al. 2017).

To compute the potential for indirect effects associated with a given bird species, we assumed a model in which indirect effects are stochastic perturbations that propagates across interacting species in the network (see Pires et al. 2020 for a similar approach for coextinction cascades). Potential indirect effects were calculated considering that stochastic

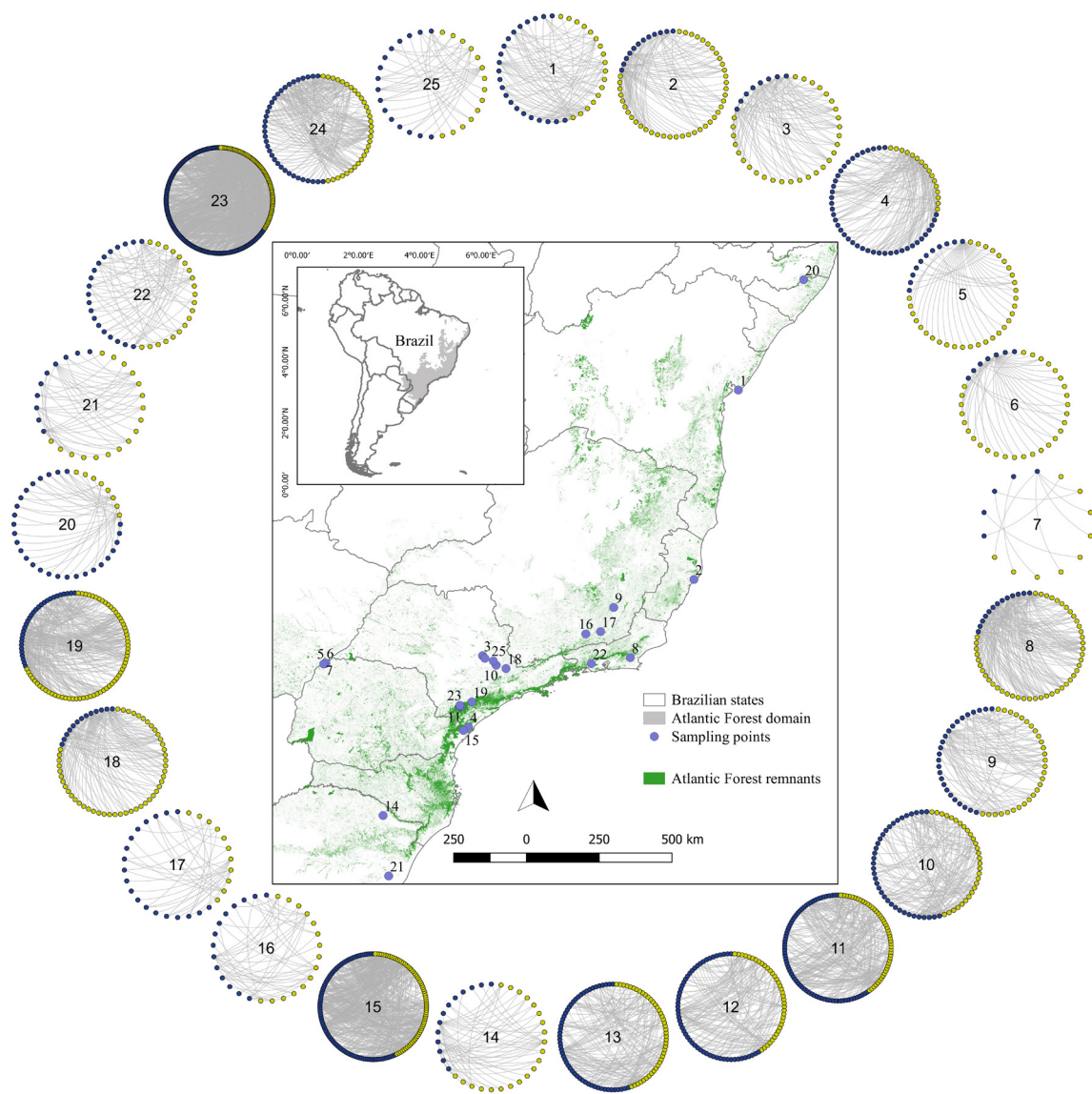


Figure 1. Location of the 25 forest fragments highlighting the structure of the plant–bird frugivore interaction networks in the Brazilian Atlantic Forest. In each network blue dots represent plant species, yellow dots bird species and the gray lines the interaction among them. Figure based on Emer et al. (2019).

perturbations propagate through links connecting interacting species (see Pires et al. 2020 for a similar approach). Specifically, we assumed that an effect propagates from a given species i to its partner j with probability λ . Similarly, with the same probability λ , an effect propagates from species j to its partner k . Thus, with probability λ^2 , the effect propagates from i to k through j . We compute the potential of a species to propagate indirect effects in a network with S species, T_{out} , as $T = V(I - W)^{-1}$ (Pires et al. 2020), in which T is a $S \times 1$ row vector in which each element describes the T_{out} of each species in the network, V is an all-ones, $S \times 1$ row vector, I is an $S \times S$ identity matrix, W is a $S \times S$ row stochastic matrix in which each element is $w_{ij} = 1/k_i$ if there is an interaction between i and j and zero otherwise and k_i is the number of species interacting with species i . The values of

λ are bounded between 0 and 1 and the higher the value, the stronger is the impact of indirect pathways on the T_{out} . We set $\lambda = 0.95$, since our aim is characterizing the potential for indirect pathways and, consequently, the potential of indirect effects. Note that T_{out} is an application of Katz centrality (Katz 1953) for row stochastic matrices.

To assess the functional basis of the changes promoted by habitat loss on the role of species in plant–frugivore networks, we gathered information on two important traits related to the seed dispersal process, bill width and seed diameter. The bill width (from Bello et al. 2017 and Rodrigues et al. 2019) is an important trait that can trigger phenotypic evolutionary changes in the dispersed plants, such as evolution of decreased seed size (Galetti et al. 2013). Seed diameter limits which frugivore will be able to consume the fruit, and is related to seed

fitness (Stanton 1984, Silvertown 1989). We collected information on seed diameter from Bello et al. (2017) and from the Neotropical Tree Communities database (TreeCo ver. 4.0): <http://labtrop.ib.usp.br/doku.php?id=projetos:treeco:start>.

Landscape descriptors

To estimate forest cover, a proxy of habitat amount, we used land use and cover maps derived from classified Landsat satellite images with 30 m spatial resolution from the project MapBiomass ver. 5.0 (Souza et al. 2020). We calculated the percentage of forest cover (corresponding to natural forest formations) (Souza et al. 2020), within circular buffers with radius varying from 500 to 2000 m at 100 m intervals, to assess the scale of effect. We used these buffers to include the scale of effect previously found for birds in the Atlantic Forest (600 m, Morante-Filho et al. 2015) and the median between-patch dispersal found for frugivorous (Mueller et al. 2014). All maps were downloaded based on the year that each study started sampling the interactions. To calculate the percentage of forest cover in each radius we used the package *landscapemetrics* (Hesselbarth et al. 2019) in R ver. 3.5.3 (www.r-project.org).

Data analysis

To take into account the possible effects of sampling effort on network metrics, we constructed a generalized additive model, with Gaussian distribution for continuous and Poisson distribution for count variables, using sampling effort, provided by each study, as predictor and network metrics as response variables (Supporting information). Because some network metrics were related to sampling effort, we extracted the residuals of all models and used them as response variables (i.e. response corrected for sampling effort). We also tested the scale of effect, i.e. the spatial scale at which each response variable best responded to the predictor (Jackson and Fahrig 2015). To do this, we constructed models for each response variable in each radius segment and for different types of models (i.e. linear and non-linear). Afterwards, we compared the Akaike weights of these models to choose the appropriate scale of effect, corresponding to the model with the largest Akaike weight (Supporting information).

We compared five models to evaluate the effects of forest cover on each network structure metric: a null model, which represents the absence of relationship, a linear model, expected when the response variables increase linearly with increasing forest cover, and three non-linear models: quadratic, power law and piecewise (see the Supporting information for explanation about each model). Linear relationships imply constant increase or decrease of the response variable with the explanatory variable, whereas non-linear models imply a variable and often suddenly decay or increase.

We used the best scale of effect (Supporting information) and compared the different models based on their delta Akaike information criteria corrected for small sample size ($\Delta AICc$; Burnham and Anderson 2002) using the MuMIn package (Barton 2015). We selected as the most plausible the

simplest model between those with $\Delta AICc \leq 2$; when two models with $\Delta AICc \leq 2$ were equally simple (i.e. had the same number of parameters), we selected the one with the lowest $\Delta AICc$. When the null model was included in those with $\Delta AICc \leq 2$ we consider it as the best model. All models were checked for normality of the model residuals. We also checked for spatial auto correlation using Moran I ($p > 0.05$ for all models) in the best models prior to the comparisons using the function *Moran.I* from package *ape* (Paradis and Schliep 2019). All analyses were implemented in R ver. 3.5.3 (www.r-project.org) and the script and data are available at https://github.com/CesarEco/Publications/tree/main/Paper_mutualism.

To assess whether species roles in plant–frugivore networks change in relation to habitat loss, we first classified landscapes according to three levels of forest loss: 1) deforested (less than or equal to 30% of remaining forest cover); 2) intermediate (more than 30% and less than or equal to 60% forest cover); and 3) forested (more than 60% forest cover). We defined these levels of forest loss based on studies that suggest low levels as less than 30% of remaining habitat (Fahrig 2003) and intermediate levels between 30 and 60% of remaining habitat (Oliveira Filho and Metzger 2006). We then classified, for the whole network, each species as occasional frugivorous (i.e. those that consume less than 80% fruits in their diet) or obligate frugivorous (i.e. those that feed heavily on fruits and whose diet is constituted of more than 80% of fruits), following Wilman et al. (2014). Also, in each level of forest loss, we verified the percentage of the five species per fragment that are occasional or obligate frugivorous for central species (i.e. species with the highest value of betweenness centrality) and those contributing to indirect effects (i.e. species with the highest values of T_{out}).

Results

In the 25 plant–bird interaction networks, 469 plant and 215 bird species were recorded. The mean number of plant species was 32.0 ± 32.5 (mean \pm SD per network, ranging from 5 to 150), mean number of bird species was 31.7 ± 18.4 (ranging from 8 to 76) and the mean number of interactions per network was 147.2 ± 184.1 (ranging from 13 to 883). The most frequent plant species were *Casearia sylvestris* (recorded in 10 networks), *Guapira opposita* (9 networks) and *Trema micrantha* (8 networks). The most frequent bird species were *Turdus rufigiventris* (18 networks) and *Pitangus sulphuratus* (17 networks).

The scale of effect varied among the response variables, but the 500 m radius was found to be the best scale for 12 out of 36 models (Supporting information). We observed a positive quadratic relationship ($y = \beta x^2 + \alpha$) between forest cover and both the number of plants ($\alpha = -0.14 \pm 0.06$, $\beta = 0.002 \pm 0.001$) and number of interactions ($\alpha = -0.14 \pm 0.13$, $\beta = 0.002 \pm 0.001$), indicating that species-rich systems with multiple interactions are observed in areas with higher amounts of forest cover, whereas at intermediate levels of forest cover, low number of plants and interactions are observed (Fig. 2). The number of bird species ($\beta = 0.04 \pm 0.01$) and

links per species ($\beta = 0.03 \pm 0.01$) increased with forest cover in a linear way (Fig. 2). In contrast, nestedness (NODF) decreased linearly with forest cover ($y = \beta x + \alpha$, $\beta = -0.01 \pm 0.04$, Fig. 2). Also, we observed a piecewise relationship between forest cover and connectance ($\beta = -0.02 \pm 0.006$) indicating an increase in connectance until ~90% of forest cover and a sudden decay in highly forested areas (Fig. 2). Finally, network robustness, mean bill width and seed diameter showed no significant relationship with habitat amount (Fig. 2, Supporting information).

Regarding the role of each species within networks, our results showed that obligate frugivores have greater indirect effects (one way ANOVA $p < 0.05$, $\beta = -13.79$), whereas occasional frugivores have higher betweenness centrality (one way ANOVA $p > 0.05$, $\beta = 0.03$, Fig. 3, Supporting information). Our analysis showed that increasing forest cover reorganizes the contribution of different species to network structure. In fact, increasing forest cover was associated with the percentage of occasional and obligate frugivorous species in the entire network and those species that occupy central positions and contributing to indirect effects (Fig. 4). Specifically, in

deforested landscapes, there is a high proportion of occasional frugivorous birds (90%), that assume a central role in these networks (i.e. high values of betweenness centrality, 90% of species) or contribute largely to indirect effects (i.e. high values of indirect effects, 88% of species). On the other hand, as forest cover increases, so does the proportion of species that are strictly dependent of fruits (28%), resulting in these species assuming central roles (43%) or contributing more to indirect effects in the networks (38%, Fig. 4).

Discussion

Here, we explored the relationship between habitat loss at the landscape scale and the structure and robustness of frugivory networks. The changes in frugivory networks associated with forest loss may be the direct outcome of habitat loss or an indirect consequence of forest loss such as increased hunting pressure associated with deforestation (Constantino 2016) or the demographic instability of small forest patches. By now and using an empirical data set, we showed for the first time that some responses to forest loss, when significant, were

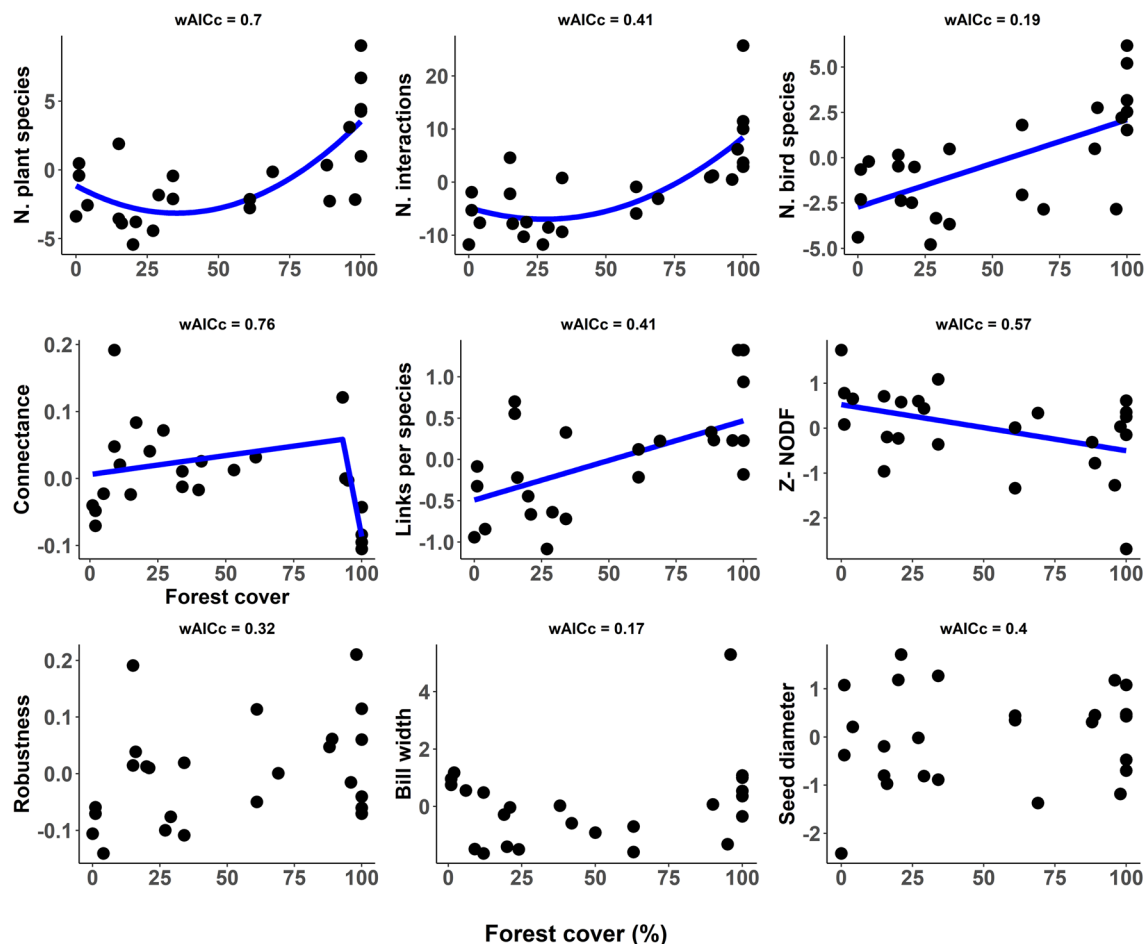


Figure 2. Effects of forest cover on plant–frugivore interaction network descriptors in the Brazilian Atlantic Forest. All metrics were first related to sampling effort and the residuals were used in the analyses. Blue lines represent the fitted values and are shown only when the null model was not included in $\Delta AICc \leq 2$. Negative values appear because we used residuals to correct for sampling effort.

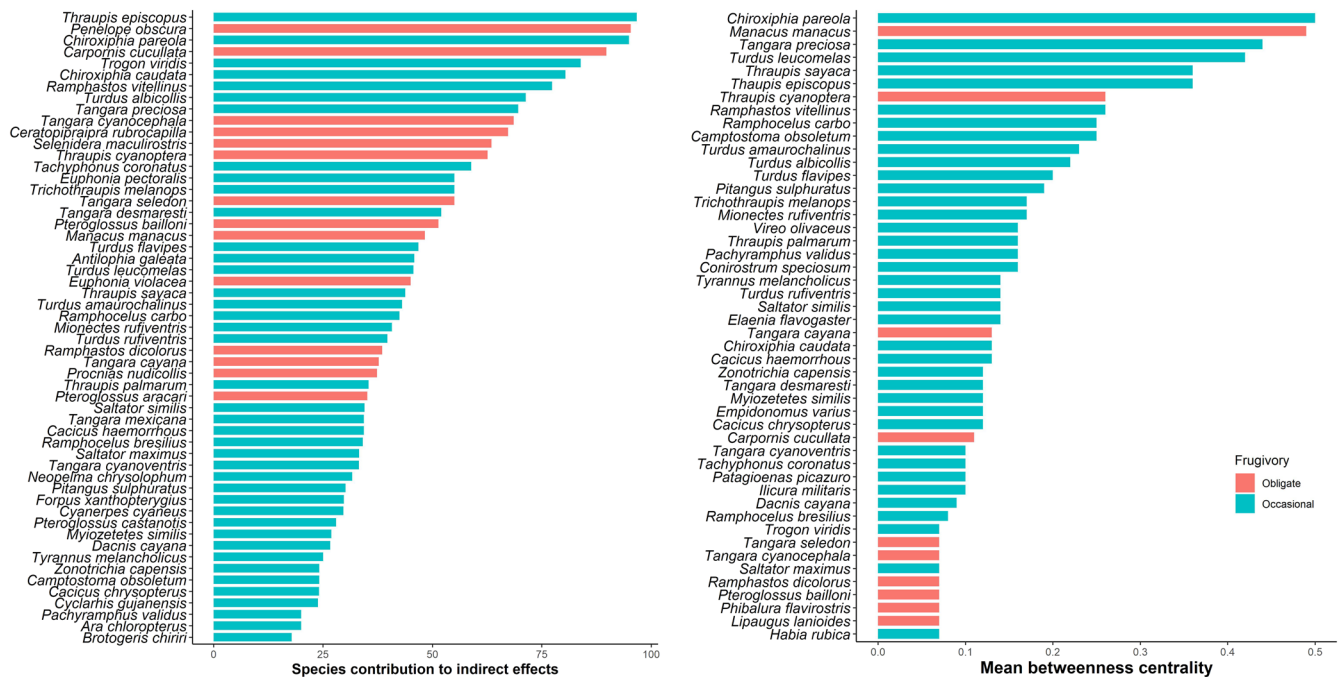


Figure 3. Mean values of contribution to indirect effects (T_{out}) and betweenness centrality of the species with the highest values of these metrics. Mean values were computed for the five species with highest values across all 25 mutualistic seed dispersal networks in the Brazilian Atlantic Forest.

linearly distributed (number of bird species, number of links per species and nestedness), and non-linear relationships were observed for number of plants, interactions and connectance. Forest loss was negatively associated with all network descriptors except for nestedness. Our results also showed that forest loss did not significantly affect the two functional traits evaluated (bill width and seed diameter) nor robustness. Moreover, our results highlight the potential role of habitat loss in reshaping the importance of different species in these mutualistic systems by changing the role of the species to the network organization along the deforestation gradient.

These results showed that the number of plant species, interactions and connectance decreased non-linearly as forest is lost at the landscape scale. These relationships point to a decrease in the number of plants and interactions at intermediate levels of habitat loss, as reported for fruit removal in the Atlantic Forest (Cazetta et al. 2019). When habitat is lost, a decrease in the total amount of habitat itself occurs, however, at intermediate levels of habitat loss, there is an increase in the number of fragments which result in more edges (Fahrig 2017), favoring pioneer plant species that proliferate (Santos et al. 2012), and few species dominate those landscapes, and consequently the number of interactions decrease. The loss of interactions can also be attributed to the loss of specialized frugivores such as toucans, trogons and cotingas that are absent or present in low densities at low habitat amount (i.e. below 60%) (Vidal et al. 2019). These specialized frugivores are known to consume more fruits and disperse seeds farther than less specialized species (Godínez-Alvarez et al. 2020). In deforested landscapes, generalist frugivorous birds, such as tanagers and thrushes, prevail

(Schupp et al. 2010). We also found that the connectance was particularly low for forested landscapes with > 90% of forest cover. This might be due to the increase in plant and bird species in more forested landscapes increasing the number of possible interactions while realized interactions are limited by selection and phenotypic constraints acting on the number of partners of any given species. However, given the small number of samples in highly forested regions, this result must be interpreted with caution.

In contrast, number of bird species, number of links per species and nestedness respond linearly to forest loss. In forested landscapes the number of frugivorous birds is high (Morante-Filho et al. 2018, Bonfim et al. 2021) possibly reflecting the increase in fruit availability and forest structure complexity (Morante-Filho et al. 2018). Our results showed that connectance increases as forest cover increases at the landscape scale. This is the result of the increase in the number of links per species in less disturbed landscapes, as previously shown for pollinators (Vanbergen et al. 2017) and frugivorous birds (Vidal et al. 2019). On the other hand, our results using empirical mutualistic networks show that increasing forest cover decreases nestedness. Indeed, some studies showed that disturbed areas are less nested (de Assis Bomfim et al. 2018, Traveset et al. 2018, Vidal et al. 2019), while the opposite pattern was observed by others, in which disturbed areas present higher nestedness (Menke et al. 2012, Vanbergen et al. 2017, Morrison et al. 2020). Our result is in line with those that point to a decrease in nestedness in forested landscapes. Nestedness may decrease due to reduction of niche overlap between species or because niche overlap expands, reducing the heterogeneity in the number of

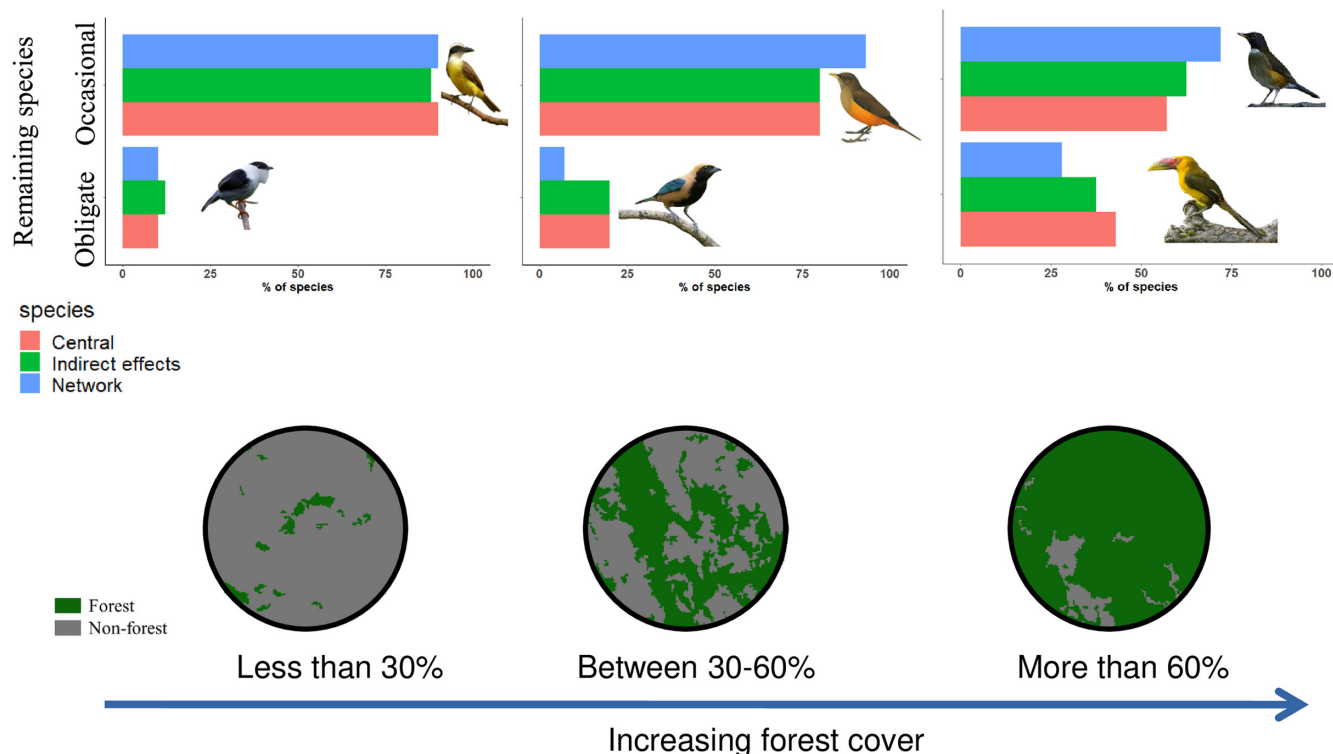


Figure 4. Percentage of obligate and occasional frugivorous species across networks and their role in network organization. Blue bars indicate the mean percentage of obligate and occasional frugivorous species in the entire network. The percentage of obligate frugivorous birds increases with forest cover. Similarly, when considered only the five species with the highest values of betweenness centrality (red bars) and indirect effects (green bars), the percentage of obligate frugivorous increases with forest cover. Bird pictures were downloaded from <https://wikiaves.com.br> after permission from authors. Examples of occasional species from left to right: *Pitangus sulphuratus*, *Turdus rufiventris* and *Turdus albicollis*. Examples of obligate frugivorous species: *Manacus manacus*, *Tangara cayana* and *Pteroglossus bailloni*.

interactions across species and, consequently, the structure of nested subsets (Almeida-Neto et al. 2007, 2008). We suggest that high overlap in fruit consumption could be observed in areas with low forest cover, where the number of frugivorous bird and plant species are low (Rocha-Santos et al. 2017, Morante-Filho et al. 2018), and species might share the same resource. This would be especially likely if species having other resources, as observed in the case of occasional frugivorous. Low overlap in fruit consumption is more likely to emerge in areas with high forest cover, in which the increase of plant species provides different resources and organisms can rely upon fruits as a major component of diet. The co-occurrence of multiple obligate frugivores may promote competition, which, in turn favor specialization in different resources, decreasing niche overlap and, consequently, nestedness.

Our results did not find significant effects of forest loss on network robustness, bill width or seed diameter. Robustness measures the system tolerance to secondary extinction (Memmott et al. 2004). Thus, our results imply that robustness to extinction is maintained even in deforested landscapes. Previous studies found that robustness can even increase in disturbed areas, for instance, forest edges (more disturbed) showed higher robustness than forest interior (Menke et al. 2012). In fact, increasing forest loss reduce the number of plant and bird species (Rocha-Santos et al. 2017,

Morante-Filho et al. 2018), however the remaining species in deforested landscapes are less specialized and possibly share resources, thus buffering the extinction of the plants foraged by them. Yet, for mean bill width and mean seed diameter our results could reflect the impoverishment of large-bodied species even in more forested landscapes which result in less consumption of seeds with large diameter by species with large bill width. Another possible explanation could be the replacement of large forest-dependent species by large frugivorous species that do not depend on forest and have large bill width (the correlation between body mass and bill width in our dataset was 0.88). For example, the large-bodied forest dependent species *Pipile jacutinga* (a ~ 1 kg cracid bird) is present only in areas with high forest cover, but this game bird species can be replaced by *Penelope superciliaris*, a large bodied species from the same family, that is present in less forested landscapes. Indeed, one mechanism that may explain the persistence of central frugivore clades is mutualistic networks against extinction dynamics, even at long temporal scales, is the replacement of extinct species by closely-related species (Burin et al. 2021).

Although functional traits of species did not change with forest cover, the role of different species did change. We showed that, as forest cover increases, there is a shift in species that play central roles in these mutualistic networks.

Whereas in less forested landscapes the species in the overall network and those playing central roles are mainly those that use fruits occasionally (90% for both the overall network and those playing central roles), in more forested landscapes these groups are replaced by obligate frugivores (28% for the whole network and 43% for species playing central roles). In fact, studies showed that, as habitat amount increases, there is a sort of compensatory dynamics at the landscape scale, with forest-dependent and obligate frugivores increasing in more forested landscapes, whereas the richness of species that do not depend on forest increases in less forested areas (Morante-Filho et al. 2018). This fact probably results from more plentiful resources for those that depend on them in more forested landscapes, whereas less forested ones offer different types of resources favoring species that do not depend exclusively on fruits. Indeed, as pointed by Vidal et al. (2019), in less forested landscapes (e.g. 30%) mainly thrushes and tanagers remain, whereas species that heavily depend on fruits such as cotingas and toucans occur mainly in areas with more than 60% of habitat at the landscape scale.

Previous studies have shown that obligate and occasional frugivorous species play complementary roles in seed dispersal (Dehling et al. 2021). However, our study contributes to the understanding of how the role of obligate and occasional frugivorous in plant–frugivore networks is reshaped by forest loss. Obligate frugivores have higher dispersal effectiveness than occasional frugivores (Schupp et al. 2010). Also, several obligate species are also large-bodied frugivores, responsible for consuming large number of fruits and dispersing seeds over larger distances (Godínez-Alvarez et al. 2020). Obligate frugivores also contribute more to indirect effects, thus the loss of these species can propagate extinction cascades for the whole network (Pires et al. 2020). Therefore, the loss of obligate frugivores has pervasive effects on mutualistic seed dispersal process, contributing not only with direct interactions, but supporting ecosystem integrity (through centrality) and potentially affecting indirectly multiple species in the network.

Conclusion

There is a solid body of research showing the negative effects of habitat loss on species richness (Foley et al. 2005, Newbold et al. 2015, Arroyo-Rodríguez et al. 2016, Muylaert et al. 2016, Barnes et al. 2017, Rocha-Santos et al. 2017, Morante-Filho et al. 2018). We extended these findings by unveiling an overlooked component of biodiversity, the loss of species interactions (Valiente-Banuet et al. 2015), as well as the non-linear nature of these relationships. As far as we know, this is the first empirical study to evaluate how landscape-scale habitat loss affects the structure and robustness of mutualistic networks and also to show the non-linear effects of habitat loss. These losses have consequences for network structure, such as reduction in mean number of interactions per species and connectance, which means that in less forested areas birds interact with fewer plant species, potentially reducing their long-term persistence. We also

showed a replacement of species when habitat is lost. The loss of obligate frugivores species can compromise seed dispersal reducing the number of seeds consumed and seed dispersal distance with potential cascading effects. We did not find effects of habitat loss on bill width and seed diameter, which can indicate that the defaunation of large seed dispersers is occurring even in forested landscapes or that bird species that do not strictly depend on forest compensate the loss of those forest-dependent species maintaining the mean value of bill width in deforested landscapes. Our findings add important information on how habitat loss shapes mutualistic network structure in tropical forest and how seed dispersal process can be impacted.

Acknowledgements – We are thankful to Renato Augusto Ferreira de Lima for sharing the data from TreeCo, an initiative financed by São Paulo Research Foundation (FAPESP) grant 2013/08722-5. We thanks to Leandro G. Cosmo for helping with Fig. 1. We also thank to Leonardo Casadei, Maria Jucá, Renério Almeida, Gabriel Mello and Dario Sanches, birdwatchers from WikiAves that shared photos for Fig. 4. We are grateful to Debora Rother, Pâmela Friedemann and Leandro G. Cosmo for helpful comments on the manuscript.

Funding – This study was financed in part by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) – Finance Code 001. PRG thanks CNPq (307134/2017-2), FAPESP (2018/14809-0) and the Royal Society, London (CHL/R1/180156) for financial support. EC thanks CNPq (306373/2018-1).

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Data availability statement

Data available from Dryad: <https://doi.org/10.5061/dryad.dbrv15f4w> (Bonfim et al. 2022).

Supporting information

The Supporting information associated with this article is available with the online version.

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