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Fragmented tropical forests lose mutualistic plant–animal interactions

Emma-Liina Marjakangas[1] | Nerea Abrego[1,2] | Vidar Grøtan[1] | Renato A. F. de Lima[3] |
Carolina Bello[4] | Ricardo S. Bovendorp[4] | Laurence Culot[5] | Érica Hasui[6] |
Fernando Lima[4,7] | Renata Lara Muylaert[4] | Bernardo Brandão Niebuhr[4] |
Alexandre A. Oliveira[3] | Lucas Augusto Pereira[5] | Paulo I. Prado[3] |
Richard D. Stevens[8,9] | Maurício Humberto Vancine[4] | Milton Cezar Ribeiro[4] |
Mauro Galetti[4,10] | Otso Ovaskainen[1,11]

[1]Centre for Biodiversity Dynamics, Norwegian University of Science and Technology, Trondheim, Norway

[2]Department of Agricultural Sciences, University of Helsinki, Helsinki, Finland

[3]Departamento de Ecologia, Instituto de Biociências, Universidade de São Paulo, São Paulo, Brazil

[4]Departamento de Ecologia, Instituto de Biociências, Universidade Estadual Paulista (UNESP), Rio Claro, Brazil

[5]Departamento de Zoologia e Centro de Aquicultura, Instituto de Biociências, Universidade Estadual Paulista (UNESP), Rio Claro, Brazil

[6]Instituto de Ciências da Natureza, Universidade Federal de Alfenas, Alfenas, Brazil

[7]IPÊ – Instituto de Pesquisas Ecológicas, Nazaré Paulista, Brazil

[8]Department of Natural Resources Management, Texas Tech University, Lubbock, TX, USA

[9]Museum of Texas Tech University, Lubbock, TX, USA

[10]Department of Biology, University of Miami, Miami, FL, USA

[11]Faculty of Biological and Environmental Sciences, University of Helsinki, Finland

Correspondence
Emma-Liina Marjakangas, Centre for Biodiversity Dynamics, Norwegian University of Science and Technology, Realfagbygget E1-137, Høgskoleringen 5,

Abstract

Aim: Forest fragmentation is among the principal causes of global biodiversity loss, yet how it affects mutualistic interactions between plants and animals at large spatial scale is poorly understood. In particular, tropical forest regeneration depends on animal-mediated seed dispersal, but the seed-dispersing animals face rapid decline due to forest fragmentation and defaunation. Here, we assess how fragmentation influences the pairwise interactions between 407 seed disperser and 1,424 tree species in a highly fragmented biodiversity hotspot.

Location: Atlantic Forest, South America.

Methods: We predicted interaction networks in 912 sites covering the entire biome by combining verified interaction data with co-occurrence probabilities obtained from a spatially explicit joint species distribution model. We identified keystone seed dispersers by computing a species-specific keystone index and by selecting those species belonging to the top 5% quantile.

Results: We show that forest fragmentation affects seed dispersal interactions negatively, and the decreased area of functionally connected forest, rather than increased edge effects, is the main driver behind the loss of interactions. Both the seed disperser availability for the local tree communities and in particular the proportion of interactions provided by keystone seed dispersers decline with increasing degree of fragmentation. Importantly, just 21 keystone species provided >40% of all interactions. The numbers of interactions provided by keystone and non-keystone species, however, were equally negatively affected by fragmentation, suggesting that seed dispersal interactions may not be rewired under strong fragmentation effects.

Conclusions: We highlight the importance of understanding the fragmentation-induced compositional shifts in seed disperser communities as they may lead to lagged

N-7491 Trondheim, Norway.
Email: emma-liina.marjakangas@ntnu.no

and multiplicative effects on tree communities. Our results illustrate the utility of model-based prediction of interaction networks as well as model-based identification of keystone species as a tool for prioritizing conservation efforts. Similar modelling approaches could be applied to other threatened ecosystems and interaction types globally.

KEYWORDS

Atlantic Forest, co-occurrence, ecological network, fragmentation, frugivory, Hierarchical Modelling of Species Communities, joint species distribution model, keystone species, seed dispersal, zoochory

1 | INTRODUCTION

Deforestation is among the principal causes of global biodiversity loss (Haddad et al., 2015). Alarmingly, deforestation rates are higher in biodiversity-rich areas, such as the tropics (Hansen et al., 2013). Forest loss, edge effects and reduced connectivity among remaining forest patches (for simplicity, hereafter together referred to as forest fragmentation) directly affect biodiversity (Fahrig, 2003, 2017; Pfeifer et al., 2017), for example by driving populations beyond their extinction thresholds (Hanski, 1999). Indirectly, forest fragmentation can reduce biodiversity by disrupting species interactions (Fortuna & Bascompte, 2006; Valiente-Banuet et al., 2015). Mutualistic interaction networks, such as seed dispersal networks, are fundamental in maintaining ecosystem functioning and thus their disruption can lead to profound cascade effects on important ecosystem services (Bello et al., 2015; Schleuning, Fründ, & García, 2015). Therefore, determining how forest fragmentation influences mutualistic interaction networks should be a central goal in biodiversity conservation (Tylianakis, Laliberté, Nielsen, & Bascompte, 2010).

The integrity of species interaction networks contributes to the stability of ecological communities (Okuyama & Holland, 2008). Yet, the species richness in the landscape alone does not explain the type and number of interactions: not all species are equally important in maintaining community stability (Dáttilo et al., 2016; Emer et al., 2018; Hagen et al., 2012). Interaction networks are more sensitive to the loss of those species that interact with many other species (Morris, 2010). In particular, the so-called keystone species, defined as those "whose impact is disproportionally large relative to their abundance" (Power et al., 1996), are tightly connected to other species and considered critical for the structure of communities. Importantly, keystone species have been found to ensure the resilience of communities in fragmented landscapes (Peterson, Allen, & Holling, 1997). Thus, detecting and focusing conservation efforts on keystone species may be a useful strategy for preserving ecosystem functioning.

In forest ecosystems, frugivorous animals, particularly birds and large mammals, are the most important seed dispersers (Fleming

& Kress, 2013; Sebastián-González, 2017), but they face rapid decline due to forest fragmentation and defaunation (de Assis Bomfim, Guimarães, Peres, Carvalho, & Cazetta, 2018; Galetti et al., 2013; Nagy-Reis et al., 2017). Large mammals can disperse a magnitude of large seeds over long distances (Vidal, Pires, & Guimarães, 2013), whereas small- and medium-sized birds are limited to small seeds due to trait matching (Bender et al., 2018), but tend to be more abundant and thus interact more frequently and with a higher number of plant species. In general, landscapes with large, continuous forest fragments hold more animal and plant species as well as interaction links between taxa than their more fragmented counterparts (Hanski, Zurita, Bellocq, & Rybicki, 2013). Forest fragmentation may disrupt seed dispersal networks, which in turn may profoundly alter patterns of plant reproduction, such as seed size and spatial aggregation of seedlings (Galetti et al., 2013; Kurten, 2013). Species-specific responses to habitat fragmentation, on the other hand, depend on life-history traits (Hagen et al., 2012; Henle, Davies, Kleyer, Margules, & Settele, 2004). Small, abundant and generalist animals are more likely to be tolerant of fragmentation than large, rare specialists (Beca et al., 2017; Henle et al., 2004). Parallel to animals, the most negatively affected tree species are rare specialists that are animal-pollinated and produce few large seeds (Cramer, Mesquita, & Bruce Williamson, 2007; Kolb & Diekmann, 2005; Markl et al., 2012).

Forest fragmentation affects frugivory and seed dispersal through various processes, including habitat loss (García & Chacoff, 2007; Valdivia & Simonetti, 2007), fragment isolation and edge effects (Magrach, Laurance, Larrinaga, & Santamaria, 2014), and changes in within-habitat quality (Lehouck, Spanhove, Colson, et al., 2009). The effects of forest loss and fragmentation on biodiversity are often difficult to disentangle without appropriate sampling design as they can occur in synergy (Fahrig, 2003). However, together these processes may cause frugivore population declines or extinctions (Cordeiro & Howe, 2003), and changes in the frugivore community composition (Santos & Tellería, 1994) or in the capacity of functional complementarity among frugivores (Lehouck, Spanhove, Demeter, Groot, & Lens, 2009). The fragmentation mechanisms affecting seed dispersal interactions have mainly been studied locally

(but see Fontúrbel et al., 2015; Magrach et al., 2014; Markl et al., 2012), focusing on patterns of community composition and species richness of frugivores (e.g., García & Martínez, 2012). Furthermore, direct observations on seed disperser interactions are usually reported for few taxonomic groups, and at small temporal and geographical scales. Since the available data on species interactions limit research spatially and taxonomically, community modelling approaches can be used to approximate interaction patterns at large spatial scales (Ovaskainen et al., 2017; Zurell, Pollock, & Thuiller, 2018).

Here, we test the hypothesis that increasing fragmentation in the landscape negatively impacts seed dispersal interactions, namely the number of interactions, connectance and nestedness of networks, and the proportion of interactions provided by keystone seed dispersers. We expect negative effects on seed dispersal interactions due to loss of seed dispersers in the landscape. However, we also expect some of these negative effects to be counteracted or diluted by seed disperser replacement, that is network rewiring. We compiled data on the occurrences of 407 animal and 1,424 tree species occurring within the Atlantic Forest of South America, a highly fragmented biodiversity hotspot (Ribeiro, Metzger, Martensen, Ponzoni, & Hirota, 2009). We combined species assemblage and network modelling to evaluate the effects of forest fragmentation on seed dispersal. More specifically, we predicted species occurrences using a spatially explicit joint species distribution model (Ovaskainen et al., 2017) and inferred interactions from co-occurrences by utilizing verified interaction data (Bello et al., 2017).

2 | METHODS

2.1 | Data on species communities and environmental covariates

The Atlantic Forest biome provides an excellent model system for studying the effects of forest loss as it presents a full gradient of fragmentation due to the historic land use (Ribeiro et al., 2009). We used the most spatially and taxonomically comprehensive community databases available for the Atlantic Forest in Brazil (the ATLANTIC series data papers: https://github.com/LEEClab/Atlantic_series, and the Neotropical Tree Communities database (TreeCo version 2.0): http://labtrop.ib.usp.br/doku.php?xml:id=projetos:treeco:start). Altogether, we compiled data on 1,831 species occurring in 1,953 sampling sites, totalling nearly 59,000 species occurrence records (Figure 1). The data were collected between years 1990 and 2017, during which the geographical coordinates are of required accuracy (Bovendorp et al., 2017; Culot et al., 2018; Hasui et al., 2018; Lima et al., 2017; de Lima et al., 2015; Muylaert et al., 2017). A list of the filtered tree data sources is found in Appendix S1, Table S1.1. Surveys were selected based on the reported information on the sampling design making sure that sampling was conducted within the Atlantic Forest biome limits sensu Ribeiro et al. (2009) and that there was sufficiently detailed information on the sampling site as well as the

sampling design. For each of the major taxonomic group (bats, birds, large mammals, primates, small mammals, and trees), we compiled data on (a) the occurrences of species in the surveys; (b) species' life-history traits; (c) taxonomic relationships among the species; and (d) environmental covariates associated with each sampling site, in addition to geographic coordinates (Table 1).

2.1.1 | Species occurrences

We used presence–absence data of 407 seed disperser and 1,424 tree species to produce occurrence matrices. As our focus was on seed dispersal networks, we included only animals identified to species-level and reported as frugivores (≥10% of the diet consists of fruits) in the EltonTraits database (Wilman et al., 2014). Furthermore, we included those tree species that were identified as zoochoric (Almeida-Neto, Campassi, Galetti, Jordano, & Oliveira-Filho, 2008; Bello et al., 2017) and had ≥5 occurrences in the original data. We considered as trees those tree and palm species that are reported to grow ≥4 m high. For the full list of all included species, see Table S2.1. The four mammal data sets overlapped partially in a sense that one species from the bat data, six species from the primate data and three species from the small mammal data also occurred in the large mammal data. We included these overlapping species in the joint species distribution models of both data sets with the aim of testing the robustness of the predicted occurrence probabilities for data collected on the same species by different methods.

2.1.2 | Species traits

Seed disperser life-history trait data were first obtained from the EltonTraits database (Wilman et al., 2014), and missing values were then completed using various data sources (Table S3.1). The included seed disperser life-history traits were body mass, degrees of frugivory and omnivory, endemism in the Atlantic Forest, foraging strata, and commonness. In rare cases of missing data ($n = 2$), the trait value of a close relative was used. For tree species, we included seed size, wood density, maximum height and commonness. The life-history traits of trees were obtained from the TreeCo database and completed with genus-level averages in cases of missing values (35% of species with data available on all four traits), except for the maximum heights of the species for which we only used the species-level data (Díaz et al., 2015).

2.1.3 | Taxonomic relationships

Due to the lack of comprehensive quantitative phylogenies, we derived the phylogenetic correlation matrices from the taxonomic trees that included the levels of orders, families, genera and species (except for bats: subfamilies, genera and species; and for primates families, genera and species), and that assumed equal branch lengths
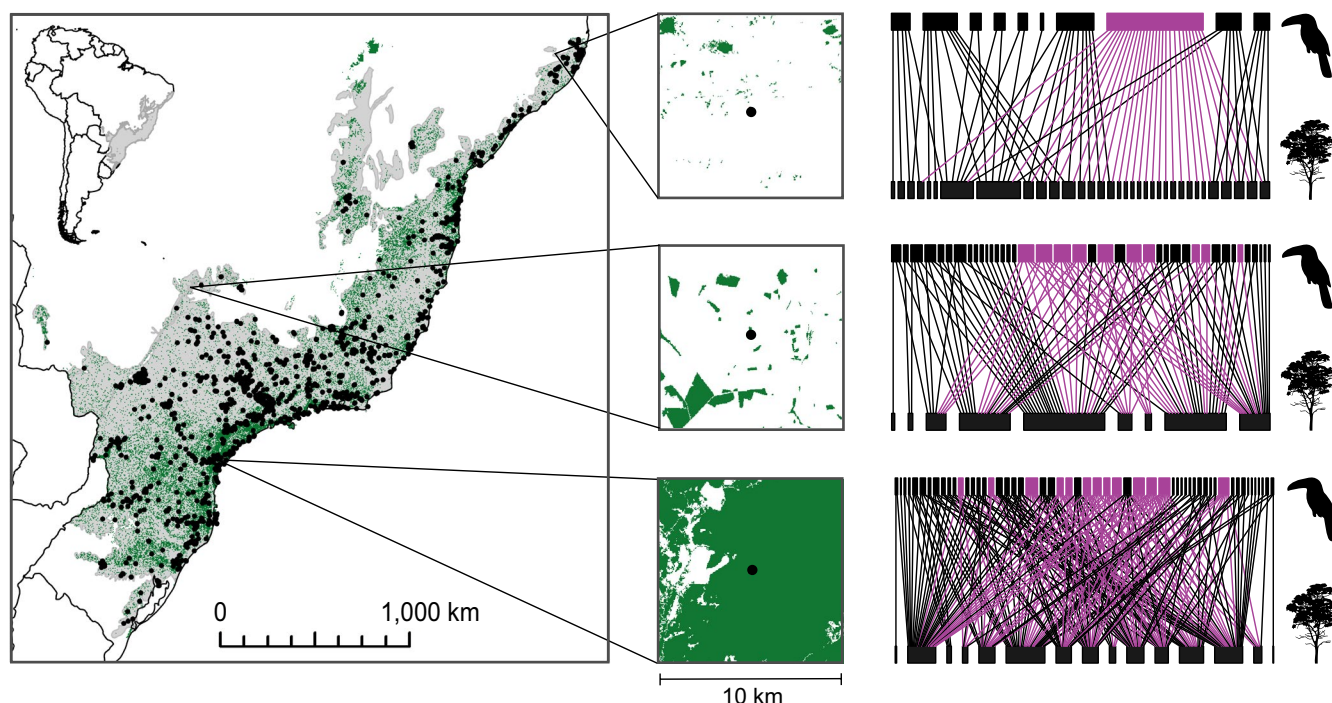
FIGURE 1 The study design and schematic illustration of the key results. In the left-most panel, the black dots represent the sampling sites (*N* = 1,953) from which occurrence data on seed dispersers and trees were acquired. The grey colour delineates the original extent of the Atlantic Forest biome, and green colour shows remaining forest fragments. The three locations highlighted in the middle panel have been selected to represent a gradient in forest fragmentation, with decreasing degree of fragmentation from top to bottom. The right-most panel shows predicted interaction networks as bipartite graphs, where the upper and lower boxes correspond, respectively, to the seed dispersers and trees, and purple colour indicates keystone seed dispersers and their respective interactions. For illustrative purposes, species are ordered to minimize the overlap of the shown interactions

for the levels. Due to computational limitations, we did not include taxonomic correlations in the bird and tree models.

2.1.4 | Environmental covariates

Environmental covariates were obtained from a variety of sources based on the reported geographical coordinates of sampling sites (Fick & Hijmans, 2017; Hijmans, Cameron, Parra, Jones, & Jarvis, 2005; Ribeiro et al., 2009; Soares-Filho et al., 2013; M. C. Ribeiro, personal communication). These covariates were selected among a larger set of potential environmental covariates based on preliminary analyses that aimed at identifying a set of uncorrelated covariates (for the full correlation matrix of the selected covariates, see Table S4.1). We computed the selected environmental covariates at landscape scale to best account for their effects on occurrences of species with varying sets of traits, such as species-specific range size. As fragmentation-related variables, we included ratio of forest core to forest edge within 10-km window, area of functionally connected forest, and distance to nearest road (data obtained between 2013 and 2015). We set 120 m as the threshold value for considering separate forest fragments to be part of "a functionally connected forest patch" to allow meaningful comparisons between species with very different gap crossing capabilities (e.g., Lees &

Peres, 2009). This value does not match perfectly the movement of some smaller or resident species, but we assume that it provides a useful proxy for average matrix crossing capability of all species. We note that the impacts of forest loss and fragmentation cannot be discerned without an appropriate sampling design, and therefore, our fragmentation-related variables may represent synergistic effects of both forest loss and fragmentation. Size of the focal forest fragment was not included in the analyses due to its strong correlation with area of functionally connected forest (Spearman correlation coefficient = 0.78). In addition to the fragmentation-related variables that were of our focal interest, we included climatic, topographic and land use variables to control for their influence on variation in species occurrences. We used Albers Equal Area Conic projection with SAD69 Datum in all spatial analyses.

2.2 | Joint species distribution modelling of each taxonomic group

To synthesize data on species occurrences, environmental covariates, spatial context, species traits and taxonomic relationships within a single modelling framework, we applied Hierarchical Modelling of Species Communities (HMSC; Ovaskainen et al., 2017). HMSC is a joint species distribution model, and it thus models the

TABLE 1 Description of data compiled on (A) species occurrence data, (B) species life-history traits, (C) taxonomic levels used to build the taxonomic correlations and (D) data on environmental covariates

(A) Species occurrences

Taxonomic group	$N_{species}$	N_{sites}	Sampling method(s)	Total effort (occurrence records)
Bats	48	186	Mist nets	1,753
Birds	251	456	Mist nets, point counts	11,674
Large mammals	36	133	Camera traps	930
Primates	22	325	Transect lines, camera traps, visualizations, vocalizations, surveys	558
Small mammals	60	275	Live traps, pitfall traps	1,369
Trees	1,424	578	Plots	42,666

(B) Life-history traits

Trait	Description	Bats	Birds	L. mammals	Primates	S. mammals	Trees
Commonness	Total number of occurrences in database.	x	x	x	x	x	x
Body mass	Body mass (log10 g).	x	x	x	x	x	
Frugivory	Proportion of fruits in diet (%).	x	x	x	x	x	
Omnivory	Proportion of total number of food sources listed as dietary categories in source data (%).	x	x	x	x	x	
Foraging strata	In case of mammals, main foraging stratum of the species. Levels: ground, scansorial, arboreal, aerial. In case of birds, proportion of time spent in each foraging stratum (%). Levels: water, ground, understory, midheight, canopy, aerial.	x	x	x	x	x	
Endemism	Endemic to Atlantic forest. Levels: endemic, non-endemic.	x	x	x	x	x	x
Wood density	Wood density (g/cm^3).						x
Seed size	Seed length (cm).						x
Height	Maximum growth height (m).						x

(Continues)

TABLE 1 (Continued)

(C) Taxonomic levels

Class	Bats	Birds	Large mammals	Primates	Small mammals	Trees
Order	–	15	7	–	2	29
Family	–	36	19	4	4	97
Subfamily	4	–	–	–	–	–
Genus	25	145	31	7	30	328
Species	48	251	36	22	60	1,424

(D) Environmental covariates

Covariate	Description	Category	Reference
Core-edge ratio	Each 60 m × 60 m forest pixel was classified to belong to edge (respectively, core) if the distance to nearest forest edge was at most (respectively, at least) 120 m from the nearest edge. We computed the core-edge ratio as the ratio between the percentage of core and edge forest within a square window of side length 10,000 m, centred on the sampling site.	Fragmentation	M.C. Ribeiro, personal communication
Area of functionally connected forest	Area of functionally connected forest (ha), that is forest that could be reached from the sampling site without crossing gaps larger than 120 m. Sampling sites up to 120 m from the forest edge obtain the value as if located inside the fragment. Log10 transformed, at 30 m resolution.	Fragmentation	M. C. Ribeiro, personal communication
Distance to road	Euclidean distance to nearest road (m), at 30 m resolution.	Fragmentation	M. C. Ribeiro, personal communication
Matrix composition	The proportion of different matrix types within 10,200 m diameter of the sampling site (%), at 500 m resolution. Levels: water, urban, pasture, savanna, annual agriculture, perennial agriculture.	Land use	Soares-Filho et al. (2013)
Temperature seasonality	Temperature seasonality measured by standard deviation, at 982 m resolution.	Climate	Fick and Hijmans (2017)
Precipitation	Mean annual precipitation (mm), at 982 m resolution.	Climate	Fick and Hijmans (2017)
Precipitation seasonality	Precipitation seasonality measured by coefficient of variation, at 982 m resolution.	Climate	Fick and Hijmans (2017)
Altitude	Height above sea level (m), at 982 m resolution.	Topography	Hijmans et al. (2005)
Declivity	Inclination of the surface in relation to the horizontal (%).	Topography	Hijmans et al. (2005)

Note: Each environmental covariate is classified as fragmentation-related, land use-related, climate-related or topography-related. There are no missing values for any of the environmental variables and traits mentioned in the table.

occurrences of all species simultaneously, allowing both species- and community-level predictions. Joint modelling allows including rare species in the analyses as information can be "borrowed" from more common species through shared traits and evolutionary history, as well as spatial configuration of species co-occurrences. In addition to modelling the species-specific responses to environmental covariates, HMSC examines how these responses are influenced by species traits and phylogenetic relatedness. Separately for each taxonomic group, we fitted a binomial model with probit link to the presence–absence data. In all models, we included spatially structured latent variables to account for spatial autocorrelation in the species occurrence data (Ovaskainen, Roy, Fox, & Anderson, 2016; Ovaskainen et al., 2017). We fitted the models in Bayesian inference framework using the Matlab implementation of HMSC provided by Ovaskainen et al. (2017) with default prior distributions (for Matlab code, see Appendix S5).

To evaluate the predictive power of the HMSC models, we applied a cross-validation procedure. Cross-validation is a useful tool to measure the predictive performance of a model without extensive and often unfeasible fieldwork. We partitioned the sites randomly into five sets, fitted the model using four of the five sets as training data and predicted the validation data on the remaining fifth set of sites. We repeated this analysis five times, thus generating an independent prediction for each site. We evaluated the predictive performances of the HMSC models by computing Tjur's R^2 (Tjur, 2009) and area under curve (AUC) using "PresenceAbsence" package in ʀ software version 3.5.0 (Freeman & Moisen, 2008) for the match between model prediction and the validation data.

Using HMSC, we examined the roles of the fragmentation-related covariates (core-edge ratio, area of functionally connected forest and distance to road) by partitioning the explained variation among the predictors, and by assessing how the responses to the environmental predictors were mediated by species traits.

2.3 | Generating predicted communities

To overcome the problem of low spatial overlap among survey locations across taxonomic groups, we used HMSC to generate predicted communities for the entire Atlantic Forest in Brazil. We created a regular grid of 40,000 sites spanning the Atlantic Forest limits in ᴀʀᴄɢɪs software (version 10.3). Then, we selected those 912 sites that overlapped with the Atlantic Forest remnants and used the fitted models to predict species communities of all taxonomic groups. These predictions utilize all information in the data, as they are based on the measured values of the environmental covariates in the grid cells (through the fixed effect part of the HMSC), as well as on the occurrences of the species in nearby sampling sites (through the spatially structured latent variable part, see Ovaskainen et al., 2016). By sampling the model parameters from the full joint posterior distribution, we accounted for parameter uncertainty while generating 500 replicates of predicted communities for each of the 912 prediction sites.

2.4 | Modelling interactions between seed dispersers and zoochoric trees

Two conditions need to be simultaneously satisfied to enable a particular animal species to act as a seed disperser for a particular plant species in a particular site. First, the animal species and the plant species need to have the potential for interaction, that is the animal uses the plant as a resource. Second, the animal and plant species need to co-occur at the particular site. We modelled these two components separately, so that the predicted probability of the two species interacting at a particular site is the probability that they potentially interact (which is independent of the site), multiplied by the probability that the two species co-occur at the particular site. We examined these associations between seed dispersers and trees based on the predicted communities. For each prediction site and each replicate of predicted community, we calculated the co-occurrence probability for each seed disperser-tree pair as the product of their species-specific occurrence probabilities. Similarly to Marjakangas et al. (2018), we used the ATLANTIC-FRUGIVORY database (Bello et al., 2017) to assign all seed disperser-tree pairs a semi-quantitative probability of potential for an interaction. The database presents occurrences of fruit consumption events, excluding pulp consumption and seed predation. We considered potential for an interaction to be very likely (probability 1) if it was recorded by more than one study in different locations and likely (probability .75) if it was recorded by one study in one location. Due to low taxonomic coverage of the interaction database (84% of seed disperser and 30% of tree species), we completed the data by considering potential for an interaction plausible (probability .5) if the seed disperser interacts with another tree species within the focal tree species' genus and unlikely (probability 0) if the seed disperser has no recorded interactions with any tree species within the focal tree species' genus. We set the probabilities of interactions recorded by only one study to be <1 to account for uncertainty in their spatial prevalence and to obtain conservative estimates on pairwise interactions in local communities. Finally, we calculated predicted site- and replicate-specific seed disperser-tree interaction probabilities as the product of their co-occurrence probabilities and their potential for interaction probabilities. Essentially, we assume an interaction if the two species co-occur in a site and have the potential to interact, the latter in the sense that they have been observed to interact at least in some location. To support this analytical approach, we tested for the phylogenetic signal of interaction partner sharing among plant species and found that plant species within a genus shared more interaction partners (on average 2.6 shared interaction partners) than plant species that belonged to different genera (on average 0.7 shared interaction partners; Appendix S6).

We used the predicted interaction probabilities to compute for each site the interaction link connectance (CON), defined as the proportion of seed disperser-tree pairs that interact out of all pairs that are present in the site, with value ranging between 0 and 1 (Jordano, 1987). Connectance of a network corresponds to the overall complexity the network (Dunne, Williams, & Martinez, 2002) and

reflects changes in the number of interaction links (realized interactions) and species richness (potential interactions). Furthermore, connectance is strongly related to other network properties (Delmas et al., 2019; Fortuna et al., 2010). In addition to connectance, we calculated network nestedness (NODF; Almeida-Neto, Guimarães, Guimarães, Loyota, & Ulrich, 2008) with 10 replicates of binary shuffles where matrix elements are shuffled randomly (Staniczenko, Kopp & Allesina, 2013). To allow computing binary nestedness scores, we sampled the co-occurrence and interaction probability matrices 20 times within each of the 912 prediction site and each of the 500 replicates of predicted communities to obtain binary interaction matrices. Then, we calculated the average of the 56 samples for each site and replicate. The network is highly nested when the species interacting with specialists are a subset of the species interacting with generalists (Almeida-Neto, Guimarães, et al., 2008). Nestedness is considered an important descriptor of network structure (Almeida-Neto, Guimarães, et al., 2008; Tylianakis et al., 2010), and NODF score in particular is a commonly used nestedness metric for bipartite networks. NODF scores vary between 0 (low nestedness) and 100 (high nestedness). We also computed for each site a measure of seed dispersal availability for the local tree community (SA), defined as the mean number of seed dispersal interactions over tree species.

To identify community-level keystone seed dispersers, we utilized two alternative methods. As a model-based approach, we computed for each seed disperser a keystone index, defined as the expected number of tree species with which it interacts, averaged over the sites where the seed disperser is predicted to occur (Eq. S7.1). Following the definition by Power et al. (1996), we identified as keystone species those seed dispersers that had a disproportionally large impact on the community in relation to their abundance, their keystone index value belonging to the top 5% quantile (Table S7.1). Due to the lack of abundance data for all seed disperser species, we use species' commonness as a proxy for their abundances. As a traditional approach, we selected 5% of the species as keystone seed dispersers based on species' contributions to interaction network structure, relative abundances and vulnerability, as these characteristics have been found important by previous studies (Table S7.2; Domínguez-García & Muñoz, 2015; Vidal et al., 2014). Finally, we computed for each site the proportion of interactions that were provided by the keystone seed dispersers identified by the model-based approach (KEY) and by the traditional approach. We chose these four interaction metrics (CON, SA, KEY, NODF) because they represent key characteristics of the seed dispersal network structure and can offer complementary information on fragmentation effects on the interactions that tropical trees heavily depend on (de Assis Bomfim et al., 2018; Delmas et al., 2019; Vidal et al., 2014).

To investigate how seed dispersal interactions depend on fragmentation, we derived for each prediction site values of core-edge ratio, area of functionally connected forest and distance to nearest road. We then examined how connectance (CON), nestedness (NODF), seed dispersal availability (SA) and proportion of interactions provided by keystone seed dispersers (KEY), co-varied with these three fragmentation covariates. To do so, we fitted for each pair of interaction metric (the response variable) and fragmentation-related covariate (the explanatory variable) 500 linear regressions, that is one for each posterior replicate of the predicted community. We computed the posterior probability for the association being positive (i.e., fragmentation reducing seed dispersal interactions; note that all our fragmentation-related covariates decrease with increased degree of fragmentation) as the fraction of positive slopes among the 500 slopes and quantified explanatory power as the mean R^2-value over the predictions. We note that these regression models do not account for possibly spatially autocorrelated residuals, and thus they should be considered to examine realized patterns of covariation between fragmentation and seed dispersal rather than causal links between these. Finally, species richness has been found to be an important driver of species interaction numbers (de Assis Bomfim et al., 2018). Thus, we assessed the relationships between the posterior means of interaction metrics and species richness in each prediction site with linear regressions.

In addition to overall analysis involving the entire Atlantic Forest biome, we conducted the above-described analyses separately for each of the seven biogeographical sub-regions of the biome (Figure S8.1; Ribeiro et al., 2009). This was done to examine the robustness of the results with respect to uneven sampling effort and other variation possibly not controlled for in our analyses. Furthermore, to account for possible bias, we repeated the analyses without completing the interaction matrix and instead used the original data on pairwise interactions in binary format as basis for post hoc calculations (Appendix S6).

3 | RESULTS

3.1 | Spatial and taxonomic variation in species occurrences

Using Tjur's R^2 as measure for predictive performance, the fitted models explained 19%–54% (and predicted 14%–36% based on the cross-validation) of the variation in species' occurrences across the Atlantic Forest (Table 2). Among the studied taxa, primates showed the most predictable patterns in their occurrences (explanatory R^2 = 54%), followed by large mammals (R^2 = 33%), birds (R^2 = 32%), bats (R^2 = 30%), small mammals (R^2 = 28%) and trees (R^2 = 19%). AUC as a measure for predictive performance yielded parallel, but slightly higher model performance estimates compared to those by Tjur's R^2 (Table 2). Some of the species were included in two models (see Section 2), and we found that their mean predicted occurrence probabilities did not differ notably between the two separate analyses (Table S9.1).

Overall, climate was the most important environmental predictor of species occurrences. Averaged over the taxonomic groups, the three climatic variables explained 26% of the total variation (Table 2). Land use around the sampling site explained 24% and fragmentation

TABLE 2 Summary of the results of taxon-specific joint species distribution models

Output parameter	Taxonomic group					
	Bats	Birds	Large mammals	Primates	Small mammals	Trees
Explanatory R^2	.30	.32	.33	.54	.28	.19
Predictive R^2	.16	.20	.14	.36	.17	.15
AUC	0.73	0.76	0.70	0.86	0.76	0.71
Phylogenetic signal ρ	0.95	—	0.49	0.06	0.59	—
Variation due to traits γ (%)	64	61	75	77	43	36
Variance partitioning						
Fragmentation (%)	13.7	6.7	16.5	10.5	16	2.6
Land use (%)	25.3	11.6	37.7	35.3	28	8.6
Topography (%)	13.5	8.6	8.1	6.5	10.1	7.9
Climate (%)	32.8	13	21.3	31.5	36.2	22
Spatial random effect	14	60	13	15	9.2	59

Note: The explanatory and predictive powers are based on model fit to the data used to parameterize the model (explanatory power) and independent validation data (predictive power). In addition, we calculated the area under the curve (AUC) for each model based on the cross-validated estimates. We obtained these values by partitioning the sites randomly into five sets, fitting the model using four of the five sets as training data and predicting the validation data on the remaining fifth set of sites. We repeated this analysis five times, thus generating an independent prediction for each site. The phylogenetic signal, ρ, measures how largely the species' responses to the environment are structured by their relatedness (based on the taxonomical correlations matrix), with 0 being the minimal and 1 the maximal value. The variable γ measures the proportion of the species' responses to the environmental covariates that can be attributed to the life-history traits included in the model. The mean posterior estimates of ρ and γ are presented. The percentages of explained variance attributed to fixed and random effects are shown as averages over species.

11% of the total variation. Fragmentation explained larger proportion of the total variation for seed dispersers than for trees (12.7% and 2.6%, respectively).

Averaged over the groups, traits explained 59.3% of the variation in species responses to environmental variables (Table 2). The influence of traits in explaining species responses was particularly high in the case of primates (77%) and low for trees (36%). Among the considered traits, commonness and endemism to Atlantic Forest had the strongest effects in explaining variation in species responses to environmental variables (Figure S10.1).

3.2 | Influence of fragmentation on interactions between seed dispersers and trees

Our results demonstrate that fragmented parts of the Atlantic Forest harbour much simpler interaction networks than its more continuous parts (Figure 1). We found that link connectance (CON), nestedness (NODF), seed dispersal availability (SA) and proportion of interactions provided by keystone seed dispersers (KEY) were influenced by the area of functionally connected forest, but not by core-to-edge ratio or distance to nearest road (Figure 2). Link connectance of interactions between seed dispersers and trees was generally higher in the southern parts of the Atlantic Forest and lower in the northern parts (Figure 3). When computed separately for each taxonomic group, connectance values were higher for primates (mean = 0.126, SD = 0.055) and birds (mean = 0.082, SD = 0.025), than for other seed disperser groups (mean value for bats = 0.028, for large mammals = 0.021, and

for small mammals = 0.003). The effect of fragmentation on network nestedness was small (Figure 2). Nestedness values did not exhibit very large overall variation, but the highest values were observed in coastal regions with largest proportions of remaining forest (Figure 3). Seed disperser availability varied between 1.3–8.8 seed disperser species per tree species, the highest values found in southern coastal areas (Figure 3). The model-based approach for identifying keystone seed dispersers pinpointed 21 species (Table S7.1), and on average across the biome, they provided 42% of all seed dispersal interactions. Numbers of interactions by both the keystone and the non-keystone species increased similarly with increasing area of functionally connected forest (Figure 4). One-third of the identified keystone and non-keystone seed dispersers are endemic to Atlantic Forest (38% and 32%, respectively). On average, the keystone seed dispersers had a higher proportion of fruits in their diet than the non-keystone seed dispersers (t = 2.65, p = .014, mean difference = 14.1%), but there was no difference in average body size between keystone and non-keystone species (t = 1.33, p = .20, mean difference = −230.6 g). Results based on the traditional approach for identifying keystone seed dispersers were parallel, albeit the selected species provided a smaller proportion of all seed dispersal interactions (17.3%) compared to those identified by the model-based approach (Table S7.3, Figures S7.1 and S7.2). Seven species were identified as keystone species by both selection methods (Tables S7.1 and S7.2).

Frugivore and tree species richness explained some of the variation in the interaction metrics calculated for the seed dispersal networks (Figure S11.1). In particular, tree species richness explained
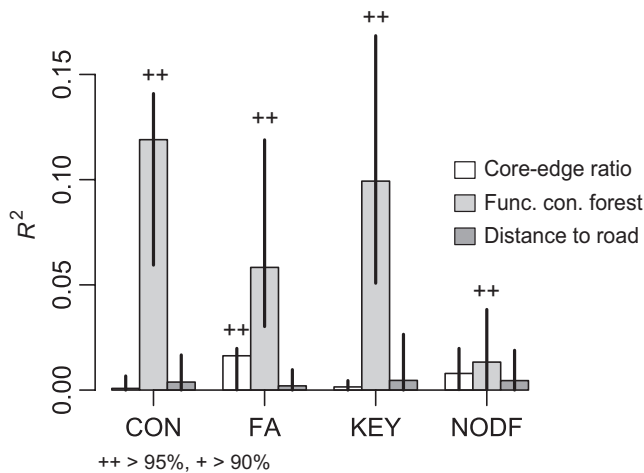
FIGURE 2 Effect of fragmentation-related covariates on metrics of seed dispersal interactions. Height of each bar represents the mean R^2-value over 500 linear regressions, where each interaction metric is considered as response variable and each fragmentation-related covariate as explanatory variable. The variation in R^2-values in indicated with vertical lines that illustrate the ranges of 95% of the observed values for each interaction metric-fragmentation covariate pair. The statistical support for fragmentation affecting seed dispersal interactions negatively is measured by posterior probability for the slope being positive (i.e., fragmentation reducing seed dispersal interactions; note that all our fragmentation-related covariates decrease with increased degree of fragmentation) and is indicated by the + or ++ symbols. CON, link connectance; NODF, nestedness; SA, seed dispersal availability; KEY, proportion of interactions provided by keystone seed dispersers according to the model-based approach

variation in connectance (R^2 = .26), nestedness (R^2 = .34) and seed dispersal availability (R^2 = .30). Frugivore or tree species richness did not contribute much to the variation in the proportion of interactions provided by keystone seed dispersers (R^2 = .05 and R^2 = .02, respectively).

The influence of fragmentation on the interaction metrics was qualitatively similar, but non-significant within each biogeographical sub-region, compared to the results obtained for the entire biome (Table S8.1). Furthermore, the results were parallel when using the known interactions data in binary format instead of semi-quantitative interaction probabilities (Figures S6.2–S6.4).

4 | DISCUSSION

Tree community composition, and thereby forest regeneration, is dependent on seed dispersal provided by frugivores (Asquith, Wright, & Clauss, 1997; Cramer et al., 2007). Consequently, several ecosystem functions and services may be at risk when the seed dispersal network is subjected to a fragmentation scenario. We demonstrated that forest loss and fragmentation affect seed dispersal interactions negatively: we found not only the overall connectance and seed dispersal availability, but also the proportion of interactions provided by keystone seed dispersers to decline with increasing degree of fragmentation. Probably due to complex patterns of nestedness along environmental

gradients (Sebastián-González, Dalsgaard, Sandel, & Guimarães, 2015; Tylianakis et al., 2010), network nestedness was not strongly impacted by fragmentation, although the overall trend was parallel to the other interaction metrics. Importantly, we identified the area of functionally connected forest, rather than increased edge effects, to be the main driver behind the loss of seed dispersal interactions. This result is in line with the fact that individual species have been found to show varying responses to edge effects (Oliveira, Grillo, & Tabarelli, 2004; Ries, Fletcher, Battin, & Sisk, 2004), whereas the occurrence and persistence of most species generally depends positively on the area of available habitat (Bender, Contreras, & Fahrig, 1998). Furthermore, the Atlantic Forest is extremely fragmented with almost half of the forest cover within <100 m from the nearest edge (Ribeiro et al., 2009), thus most species that persist in the area are necessarily at least to some extent tolerant of edge effects (Beca et al., 2017). Furthermore, functional connectivity correlated with mean annual temperature and precipitation as well as with precipitation seasonality across the biome, suggesting that some of the fragmentation-induced effects on seed dispersal networks may be masked by the climatic effects in the model fitting. Yet, fragmentation and climate covariates were recorded at different spatial resolutions, thereby hampering the interpretation of their actual relationship. Moreover, fragmentation is a result of local and regional land use practices, leading to inevitable interplay of the factors. Hence, forest fragmentation may act in concert with climate and land use practices, and it should therefore be considered together with climate change and land use intensification when planning conservation and management actions. Finally, depending on the interaction measure in question, species richness of frugivores and trees were important factors in explaining variation in the seed dispersal interactions. Tree species richness was particularly important in explaining network nestedness that is generally known to be a sensitive metric to network size (Ulrich & Almeida-Neto, 2012). Nevertheless, species richness explained at most 34% of the variation and did not contribute much to the variation in the proportion of interactions provided by keystone seed dispersers. This indicates that the species composition must also contribute to the variation in the seed dispersal interactions.

Earlier studies have illustrated that individual interactions within networks can be gained or lost as a response to habitat alterations (de Assis Bomfim et al., 2018), even when changes in the species composition remain indistinguishable (Nielsen & Totland, 2014). Therefore, structural changes in the network, namely rewiring, could mitigate some direct and short-term effects of fragmentation on tree seed dispersal by the replacement of extinct interaction links. Our results, however, showed that the number of interactions provided both by keystone and non-keystone species was equally negatively affected by fragmentation, suggesting that the loss of interactions provided by keystone seed dispersers are not replaced by those provided by other species in the seed dispersal network. Donatti et al. (2011) found that keystone species replacement is unlikely to occur in highly fragmented landscapes because of network clustering and the nested nature of existing interactions. That is, interactions are more frequent within than among subsets of species (modules; Olesen, Bascompte, Dupont, & Jordano, 2007), and therefore, the number of functionally compensatory species
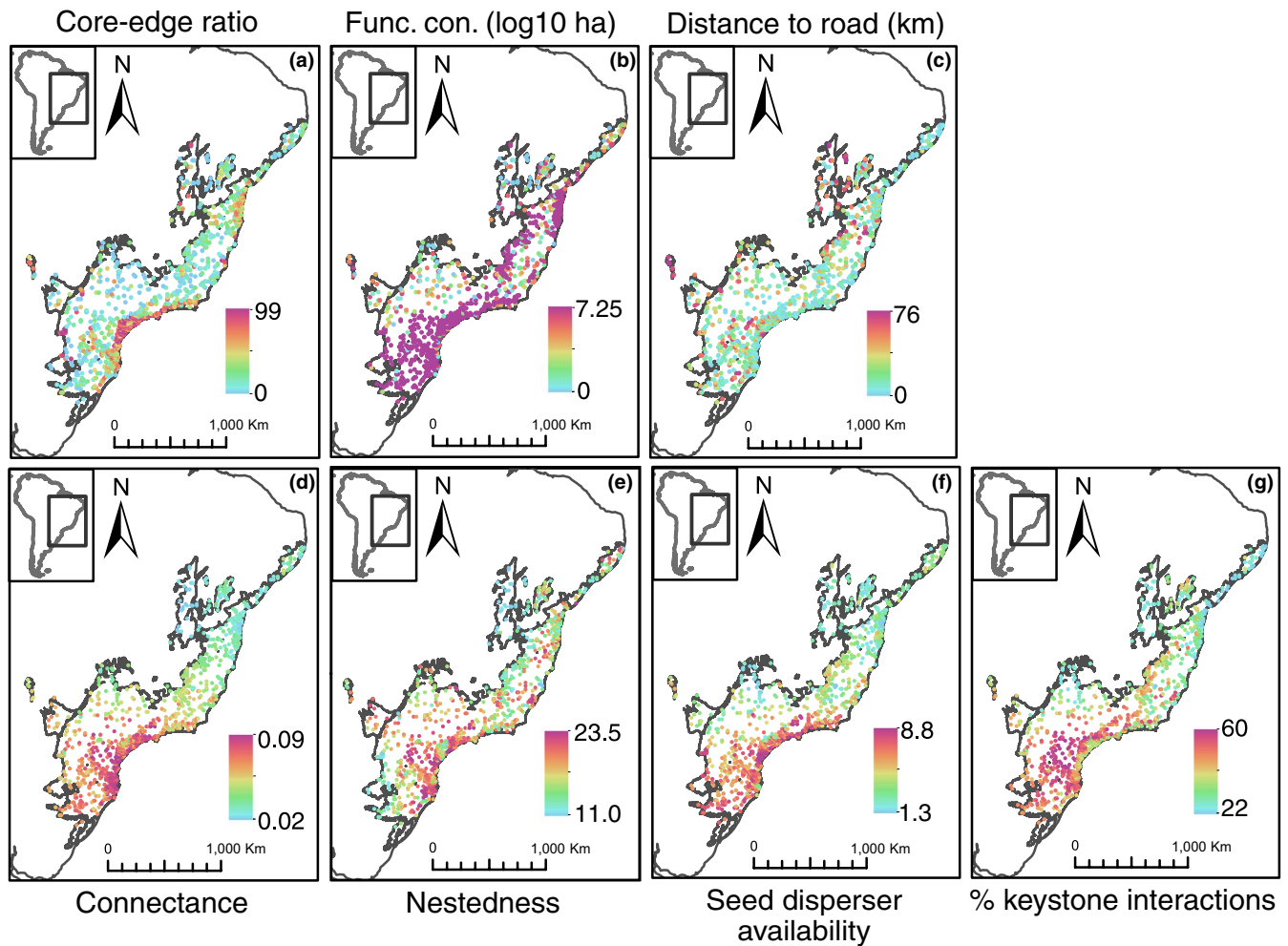
FIGURE 3 Spatial distribution of fragmentation-related variables and interaction metrics across the Brazilian Atlantic Forest. Panels (a–c) represent the fragmentation-relatedcovariates of core-to-edge ratio, area of functionally connected forest and distance to nearest road, respectively. Panels (d–g) represent the interaction metrics of connectance (CON), nestedness (NODF), seed dispersal availability (SA) and proportion of interactions provided by the keystone seed dispersers according to the model-based approach (KEY), respectively. The values of the variables in each prediction site are illustrated by a colour gradient

is limited to the species within each module. This in turn explains the extinct interactions in the local communities under strong fragmentation effects. The keystone seed dispersers that were identified with our model-based approach represent two ecologically distinct groups: old-growth forest habitat specialists and secondary forest diet generalists that are common throughout the Atlantic Forest. These two groups are unlikely to have mutually interchangeable compensation capacity for rewiring and should therefore be considered separately in conservation and management. On the other hand, Timóteo, Ramos, Vaughan, and Memmott (2016) revealed extensive structural plasticity through rewiring in a seed dispersal network following experimental removal of the dominant seed disperser. This indicates that when fruit resources are made available for other species, rewiring could be observed given the temporal extent of the study design. Nevertheless, sharing some sampling and prediction sites with Emer et al. (2018), our results align to support the view that the effects of losing community-level keystone species and related interactions can be detrimental for ecosystems, for which the conservation of keystone species is a viable solution.

Regardless of the comprehensive data used in this study, the uncertainty of the results poses limitations for several reasons. Firstly, we treat the data as a snapshot despite the underlying temporal aspect, which introduces additional noise to the obtained results. In particular, the data of rare species occurrences are still sparse, making it difficult to accurately predict their distributional ranges. There is also a temporal difference in collection of species occurrence and fragmentation data, further adding to the noise in the results. Secondly, robust quantification of fragmentation effects is especially difficult in the northern Atlantic Forest, where anthropogenic defaunation is more severe and sampling effort lower than in the southern parts (Canale, Peres, Guidorizzi, Gatto, & Kierulff, 2012). To test the robustness of the results with respect to these uncertainties, we computed interaction–fragmentation relationships for each biogeographical sub-region separately and found the patterns to be similar. Finally, the data on known interactions are biased towards well-studied species and areas, which we partly accounted for by completing the interaction data with genus-level generalizations (after generalization, we cover 84% of seed disperser and 80% of tree
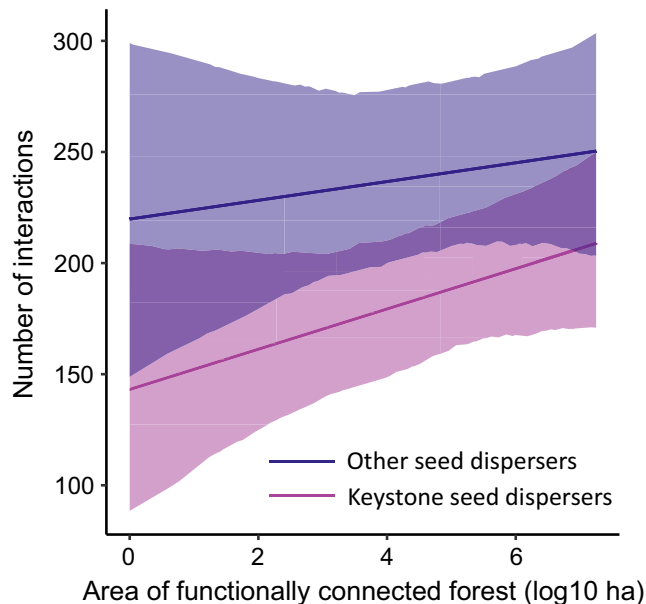
FIGURE 4 Relationship between the area of functionally connected forest and the number of seed dispersal interactions. The purple line and ribbon show the number of interactions provided by keystone species whereas the blue line and ribbon show the number of interactions provided by non-keystone species. Keystone seed dispersers were identified with the model-based approach. The lines (respectively, ribbons) show the 50% (respectively, 95%) quantiles of the slope of the linear regression between number of interactions and area of functionally connected forests

species). Moreover, spatial variation in pairwise interactions is not available. Thus, the interaction–fragmentation relationships are induced via shifts in species' occurrences, rather than in the direction or strength of their interactions. Since we accounted only for recorded interactions, our measure of seed disperser availability presents a conservative estimate, and consequently, the true numbers of interactions and interacting species are likely to be far larger. However, due to the large scale of the study area, some interactions may only be realized in parts of the study area, leading to overestimation of interactions in others (Fründ, Dormann, Holzschuh, & Tscharntke, 2013). In particular, functional traits related to mutualistic interactions tend to vary spatially among populations, leading to possible local deviances from the recorded interaction patterns (González-Varo & Traveset, 2016). In addition to the loss of species, forest fragmentation may have additional negative effects on seed dispersal interactions through changes in these functional traits, such as seed disperser foraging behaviour and plant phenology, which we did not consider in the present work. Therefore, we urge future research to improve the spatial and taxonomic extent of the interaction matrix by implementing trait matching models (Bartomeus et al., 2016; Sebastián-González, Pires, Donatti, & Dirzo, 2017), and by using DNA metabarcoding methods to directly observe the consumed plant species in the animal faeces (Hibert et al., 2013).

Generally, collection of ecological data is costly, which leads seed dispersal research, among other fields, to focus on well-studied bird taxa and small spatial scales (e.g., García, Martínez, Herrera, & Morales, 2013). Here, we used the best available data to approximate

structural changes in seed dispersal interactions at unprecedentedly large spatial scale and at the entire network level. Our results illustrate the utility of model-based prediction of interaction networks, as well as objective model-based identification of keystone species as a tool for prioritizing conservation efforts. Similar modelling approach could be applied to other threatened ecosystems and interaction types globally. To provide an even more synthesized view, we hope future work to include also other multi-layer networks relevant to plant recruitment beyond seed dispersal, such as seed predation and herbivory (García-Callejas, Molowny-Horas, & Araújo, 2018).

Understanding species interaction dynamics of biodiversity hotspots, such as the Atlantic Forest, under imminent anthropogenic threats is essential for reversing the global biodiversity loss. Since land use intensification and consequent forest fragmentation in the Atlantic Forest are recent in ecological and evolutionary timescales, it is likely that species communities have not had time to respond to the changes (Metzger et al., 2009, but see Galetti et al., 2013). Potentially, there is unpaid extinction debt in communities, and interaction networks might undergo fundamental transformations in the future (Metzger et al., 2009). In particular, this might be the case in the tree communities since their interaction partners are currently declining and thereby the future seedling recruitment could be left impaired. Therefore, compositional shifts in the seed disperser communities can serve as early warning signs for lagged and multiplicative fragmentation effects on the tree communities.

ORCID

Emma-Liina Marjakangas https://orcid.org/0000-0002-5245-3779
Maurício Humberto Vancine https://orcid.org/0000-0001-9650-7575

DATA AVAILABILITY STATEMENT

The data used in this paper are available through TreeCo database and ATLANTIC: Data papers from a biodiversity hotspot-series in Ecology.

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BIOSKETCH

Emma-Liina Marjakangas is broadly interested in species interaction dynamics in the tropics. Her current research focuses on species interaction and co-occurrence patterns along environmental gradients, combining large-scale data and newly developed joint species distribution models.

Author contributions: E.M., N.A. and O.O. conceived the idea; E.M., N.A., V.G., M.C.R., M.G. and O.O. designed the study; R.A.F.L., C.B., R.S.B., L.C., E.H., R.L.M., F.L., B.N., A.O., L.P., P.P., R.D.S., M.H.V., M.C.R. and M.G. compiled the data; E.M. conducted analyses; E.M., N.A. and O.O. wrote the first draft of the manuscript, and all authors contributed substantially to the final manuscript.

SUPPORTING INFORMATION

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