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Seed-dispersal networks in tropical forest fragments: area effects, remnant species, and interaction diversity

Carine Emer^{1*}, Pedro Jordano², Marco A. Pizo³, Milton C. Ribeiro¹, Fernanda R. da Silva⁴ and Mauro Galetti^{1,5}

¹Departamento de Ecologia, Instituto de Biociências, Universidade Estadual Paulista (UNESP), CP 199, 13506-900, Rio Claro SP, Brazil

²Integrative Ecology Group, Estación Biológica de Doñana (EBD-CSIC), Consejo Superior de Investigaciones Científicas, Avenida Americo Vespucio 26, E – 41092, Sevilla, Spain

³Departamento de Zoologia, Universidade Estadual Paulista (UNESP), CP 199, 13506-900, Rio Claro SP, Brazil

⁴Instituto de Biologia, Universidade de Campinas (UNICAMP), R. Monteiro Lobato, 255 - Cidade Universitária, 13083-862, Campinas SP, Brazil

⁵ Department of Biology, University of Miami, Coral Gables, FL, USA.

*corresponding author: c.emer09@gmail.com

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25 **ABSTRACT**

26 Seed dispersal interactions involve key ecological processes in tropical forests that help to maintain
 27 ecosystem functioning. Yet this functionality may be threatened by increasing habitat loss, defaunation
 28 and fragmentation. However, generalist species, and their interactions, can benefit from the habitat
 29 change caused by human disturbance while more specialized interactions mostly disappear. Therefore
 30 changes in the structure of the local, within fragment, networks can be expected. Here we investigated
 31 how the structure of seed-dispersal networks changes along a gradient of increasing habitat
 32 fragmentation. We analysed 16 bird seed-dispersal assemblages from forest fragments of a
 33 biodiversity-rich ecosystem. We found significant species-, interaction- and network-area relationships,
 34 yet the later was determined by the number of species remaining in each community. The number of
 35 frugivorous bird and plant species, their interactions, and the number of links per species decreases as
 36 area is lost in the fragmented landscape. In contrast, network nestedness has a negative relationship
 37 with fragment area, suggesting an increasing generalization of the network structure in the gradient of
 38 fragmentation. Network specialization was not significantly affected by area, indicating that some
 39 network properties may be invariant to disturbance. Still, the local extinction of partner species,
 40 paralleled by a loss of interactions and specialist-specialist bird-plant seed dispersal associations
 41 suggests the functional homogenization of the system as area is lost. Our study provides empirical
 42 evidence for network-area relationships driven by the presence/absence of remnant species and the
 43 interactions they perform.

44

45

46 **RESUMO**

47 Interações de dispersão de sementes formam um processo ecológico chave em florestas tropicais onde
 48 colaboram na manutenção do funcionamento do ecossistema. Porém, esta funcionalidade pode estar

ameaçada pelo aumento na perda e fragmentação do habitat. Enquanto espécies generalistas e suas interações podem se beneficiar da mudança de habitat causada por distúrbios antrópicos, interações envolvendo espécies mais especialistas são, na maioria, eliminadas. Desta forma, mudanças nas redes locais, dentro de fragmentos florestais, são esperadas. Neste trabalho nós investigamos como a estrutura de redes de dispersão de sementes mudam em um gradiente de fragmentação do habitat. Nós analisamos 16 comunidades de dispersão de sementes espacialmente explícitas e distribuídas em fragmentos florestais de um ecossistema rico em biodiversidade. Nós encontramos relações significativas entre a área do fragmento e espécies, interações e estrutura das redes, sendo que o último foi determinado pelo número de espécies remanescentes em cada comunidade. O número de espécies de aves frugívoras e plantas e as interações entre eles, bem como o número de links por espécie diminuíram significativamente conforme a área dos fragmentos é perdida. Por outro lado, o aninhamento da rede mostrou uma relação negativa com a área do fragmento, sugerindo um aumento da generalização da estrutura das redes com a fragmentação do habitat. No entanto, o grau de especialização das redes não foi afetado pela área, indicando que algumas propriedades de rede podem ser resistentes à perturbação. Sendo assim, a extinção local de espécies parceiras, conjuntamente com a perda das interações e associações planta-dispersor mais especializadas, sugere uma homogeneização do sistema conforme a área do fragmento é perdida. Nosso estudo fornece evidências empíricas para as relações rede-área, sendo estas direcionadas pela presença e/ou ausência das espécies remanescentes bem como das interações que estas realizam.

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Keywords: frugivory; species interactions; human disturbance; defaunation; forest fragmentation; network-area relationship; Atlantic Forest.

72

73 INTRODUCTION

74 THE ON-GOING, FAST-PACED DEFORESTATION HAS CREATED FRAGMENTED FORESTS POSING INCREASING
75 challenges to the conservation of species interactions and ecological processes (Janzen 1974, Bruna et
76 al. 2005, McConkey et al. 2016, Tylianakis & Morris 2017). Even though fragmentation is well
77 documented to affect species persistence and the connectivity among forest patches (da Silva &
78 Tabarelli 2000, Rybicki & Hanski 2013, Hagen et al. 2012), the remnant fragments are also proven to
79 hold an important fraction of biodiversity (Barlow et al. 2007, Sekercioğlu et al. 2007, Bongers et al.
80 2015). The pool of species and interactions persisting in forest fragments is formed by a non-random
81 subset of smaller-sized species while the whole spectrum of sizes found at the landscape level can only
82 occur in large, more pristine areas (Morante-Filho et al. 2015, Emer et al. 2018). Such local
83 assemblages configure local networks of interacting partner species whose structure may be affected by
84 the constraints imposed by fragment area (Aizen et al. 2012, Emer et al. 2013, Bomfim et al. 2018)
85 while resilience to habitat loss may occur in specific systems (e.g., Passmore et al. 2012). A recent
86 theoretical framework has proposed different mechanisms by which network-area relationships may
87 emerge, such as the constraints imposed by species-area relationships, the selection towards generalist
88 species and the dispersal limitation in smaller spatial scales (Galiana et al. 2018). Yet, whether network
89 structure is robust enough to be maintained across fragmented forests, or whether it changes as habitat
90 area is lost is still an open question to be tested with empirical data.

91 Ecological networks are the outcomes from associations among interacting species (Jordano et
92 al. 2003, Lewinshon & Prado 2006). Mutualistic associations between animal and plants are a
93 fundamental process to maintain forest dynamics (Herrera & Pellmyr 2002, Dennis et al. 2007). Seed
94 dispersal by birds, in which both interacting species benefit by using resource from one another, are
95 ubiquitous in tropical forests in which up to 90 percent of the plant species rely on birds to be

effectively dispersed (Howe & Smallwood 1982, Jordano 1995). Such associations between tropical frugivorous birds and the plants they feed upon can form complex and diverse seed-dispersal networks, characterized by a large number of species and interactions (Bascompte & Jordano 2007, Schleuning et al. 2014, Dügger et al. 2018). Disruptions in the functionality of this system can be inferred by the emergence of ecological patterns depicted from the correct interpretation of the structural properties of the networks (Bascompte & Jordano, 2007, Memmott 2009, Howe 2016). For instance, changes in the mean number of interactions (links) per species may indicate a reduction on the number of partners available to interact with in smaller areas, in which generalist species are favoured (Morante-Filho et al. 2016, Galiana et al. 2018). Likewise, increases in nestedness, a pervasive pattern in mutualistic networks that suggests the presence of highly generalist species interacting with both generalist and specialist ones, may suggest the loss of specialist interactions in disturbed communities (Aizen et al. 2012, Bomfim et al. 2018). Similarly, a reduction of network specialization, estimated by the H2' index based on Shannon diversity, would suggest the community is losing diversity of interactions among species, with the prevalence of more generalist species.

Thus, the winner species and their winner interactions able to thrive despite the disturbances imposed by habitat loss and fragmentation may be the ones defining the configuration of the local networks (Hobbs et al. 2006, Tabarelli et al. 2012, Vidal et al. 2014). For instance, diet generalist species are expected to be more resilient to habitat change due to their ability to feed on, and to be dispersed by, a wider range of interacting partners (Tabarelli et al. 2012, Morante-Filho et al. 2015). Likewise, generalist small-bodied bird species and plant species typical of secondary forest may form loose, generalists associations in fragmented landscapes (Emer et al. 2018), which may result in an increased generalization in seed dispersal networks. Furthermore, habitat fragmentation generates changes on biotic and abiotic conditions (Murcia 1995, Laurance et al. 2007) such as increases in

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temperature and light conditions that may favour the competitive ability of some plant species over the others (Laurance et al. 2010, Sfair et al. 2016). Associated to the negative effects of habitat reduction lays defaunation, a pervasive phenomenon characterized by the local or functional extinction of a given species, generally towards the larger body mass ones and often related to the reduction of habitat area (Dirzo et al., 2014, Young et al. 2016). Thus, interactions performed by large-bodied species dispersing large-seeded plants are expected to be absent in smaller areas (Pérez-Mendez et al. 2016, Emer et al. 2018) therefore affecting the local, within-fragment network structure.

Here we aim to understand how the reduction of habitat through landscape fragmentation affects the structure of tropical seed-dispersal networks. We gathered data of avian-seed dispersal interactions located in 16 fragments of the Atlantic Forest, a highly diverse and threaten tropical biome (Ribeiro et al. 2009). Our first prediction is that the number of species present in each fragment will follow a species-area relationship (MacArthur & Wilson 1967, Rybicki & Hanski 2013), i.e., the number of species reduces according to the loss of habitat area. Secondly, because smaller area fragments are disturbed habitats inhabited mostly by generalist species (Morante-Filho et al. 2016, Emer et al. 2018) able to cope with the biotic and abiotic changes promoted by edge-effects associated to other human-disturbance (Laurance et al. 2007), we expect a positive relationship between fragment area, the total number of bird-seed dispersal interactions and the mean number of links per species. Because the number of bird-seed dispersal interactions in forest fragments is selectively reduced towards generalist species (Morante-Filho et al. 2016, Emer et al. 2018), we expect that the remaining generalist interactions will lead to changes in network structure towards higher nestedness and lower specialization, with interaction links associated to a few dominant species.

METHODS

142 DATASET

143 We compiled 16 studies of avian plant-frugivore interactions sampled at the community level along the
 144 Atlantic Forest biome, a hotspot of biodiversity highly threaten by increasing human pressure (Ribeiro
 145 et al. 2009, Joly et al. 2014; Fig. 1, Table S1). The study areas varied from 0.66 to 42,000 ha, along a
 146 gradient of disturbance from semi-pristine Biological Reserves and State Parks to secondary forest
 147 fragments and restored private lands. The matrix surrounding the fragments is variable, including sugar
 148 cane fields, crop plantations, secondary forest, and urban areas. Overall the studies included here
 149 originally aimed to record bird-eating-fruit interactions and not necessarily effective seed dispersal;
 150 therefore we carefully checked every dataset and removed any interaction that would not characterize
 151 plant dispersal events, such as seed predation. In the particular case of parrots we excluded them from
 152 the analysis despite some rare evidences pointing to their role in effective seed dispersal of large nuts
 153 (Tella *et al.* 2016); in most cases we could not establish in the original papers whether the frequency of
 154 interactions involving parrots actually implied legitimate dispersal. We updated and standardized plant
 155 and bird species names using the taxize package (Chamberlain & Szocs, 2013) in R (R Development
 156 Core Team 2014).

157

158 NETWORK METRICS

159 For each community we built a correspondent seed-dispersal network as a bipartite graph represented
 160 by a weighted matrix A_{ij} in which the rows represent the i plant species and columns represent the j bird
 161 species. The elements a_{ij} indicate the frequency of interactions between the plant species i and
 162 frugivore bird species j . Changes in network structure were assessed by estimating the following non-
 163 correlated metrics ($r < 0.7$):
 164 (i) the number of bird species (A);

- 165 (ii) the number of plant species (P);
- 166 (iii) the number of interactions (I);
- 167 (iv) the mean number of links per species (L);
- 168 (v) weighted nestedness ($wNODF$), which estimates the presence of generalist species interacting with
- 169 more specialist ones, based on the NODF index (Almeida-Neto et al. 2008);
- 170 (vi) $H2'$ specialization ($H2'$), which estimates how strong species partition their interaction partners. It
- 171 measures the deviation of non-specialization in which values close to zero means low specialization of
- 172 the interacting species in the community while values close to one indicate high levels of specialization
- 173 (Blüthgen et al. 2006).

174

175 LANDSCAPE METRICS

176 Landscape configuration can play an important role in determining species persistence in fragmented

177 landscapes (Ribeiro et al. 2009) and as such may influence NAR's as well. Therefore, for each studied

178 community we calculated the fragment area (ha), the functional connectivity, and the average isolation.

179 We used the same remnant forests map generated by Ribeiro et al. (2009) as input map for the

180 calculation of the landscape metrics. The maps had 50 m spatial resolution for Albers Equal Area

181 projection and South America Datum (SAD 69). Because some birds can successfully move among

182 fragments within a given distance (Pizo et al. 2011; Cornelli et al. 2017; Vélez et al. 2015), and some

183 interactions functionally persist throughout a fragmented landscape (Emer et al. 2018), we estimated

184 the functional connectivity as the amount of forest (ha) that any species can have access if it is able to

185 cross a 500 m matrix (Ribeiro et al., 2009). Average isolation was calculated by randomly choosing

186 1000 points in a 5 km buffer around the sampling coordinates and extracting the Euclidean mean

187 distance (in meters) to the nearest forest fragment.

188

189 DEFAUNATION

190 Likewise, for each studied community we estimated the intensity of defaunation relatively to the
191 regional pool of species expected for the Atlantic Forest biome. To do so, we calculated the difference
192 between the sum of all bird body masses at the regional landscape scale (considering all frugivore bird
193 species present in the Atlantic-Frugivory database [Bello et al 2017] as a proxy for the regional pool of
194 species) and the summed body masses of the birds that were recorded interacting with fruits in each
195 fragment. Defaunation is based only on the presence/absence of species in a given fragment.

196

197 STATISTICAL ANALYSES

198 To understand whether and how the structure of avian seed-dispersal networks is affected by habitat
199 change we used Linear Regressions and General Least Square (gls) models in the nlme package
200 (Pinheiro et al., 2016). Individual models were fit for each network metric therefore considering the
201 number of plant species, the number of bird species, the number of interactions, the mean number of
202 interactions per species, nestedness and H2' specialization as response variables. Network metrics were
203 logit-transformed to solve the issue of being bounded from zero to one, when needed (Warton & Hui,
204 2011). Because defaunation is negatively correlated with fragment area ($r = -0.89$) and the three
205 landscape metrics are highly correlated among them (Table S2), we parsimoniously chose area as the
206 variable representing changes in habitat configuration. Therefore, fragment area was fitted as the
207 independent variable along with two covariates: (i) sampling intensity, calculated as the root square of
208 the number of interactions divided by the root square of the network size (sum of plant species and bird
209 species), to control for differences in sampling effort among studies (following Schleuning et al. 2012),
210 and (ii) forest type, classified according to the vegetation structure of each community (Ombrofilous

211 Forest, Semideciduous Forest, Araucaria Forest, and restored forest) to control for possible effects of
 212 biotic and abiotic conditions intrinsic to each forest formation. Our spatially explicit models and model
 213 selection follows the protocols suggested in Zuur et al. (2009). We did not detect spatial correlation
 214 structure in our models after accounting for the geographic coordinates of each study site in the gls
 215 models, according to the Akaike Information Criterion (AICc). Therefore, we fit the full model to
 216 linear regressions with ‘Maximum Likelihood estimation’ while applying the ‘dredge’ function (Barton
 217 2013) to select for the best-fixed structure according to AICc. ‘Sampling intensity’ was used as a fixed
 218 parameter to test for the effects of area and forest type solely. Then, we used the Akaike weight of
 219 evidence (wAICc) to obtain the relative importance of the different models (Burnham and Anderson
 220 2002). Finally, we present the coefficients of each predictor and the variance explained by the optimal
 221 linear model. Lastly, we used two different but complementary null models to test for changes in the
 222 number of links per species, nestedness and H2’ specialization independently of network size by fitting
 223 standardized z-scores in the same model structure described above. Both null models constrained
 224 network size and were created using the ‘nullmodel’ function. First, we used ‘method = 1’ (Patefield
 225 algorithm) to randomize the distribution of links among species while maintaining the marginal totals
 226 constant, i.e., species have the same total number of interactions in the observed and randomized
 227 matrices, therefore maintaining their biological characteristic of being common or rare in the
 228 community (Dorman et al. 2009). Second, we used ‘method = 3’ (vaznull algorithm) to randomize the
 229 number of interactions among species without constraining marginal totals but maintaining
 230 connectance constant, i.e., species have the same number of qualitative interactions as in the observed
 231 matrix (Vázquez et al. 2007). Then, the mean and standard deviation of 100 iterations of each null
 232 model were contrasted against the observed values of links per species, nestedness and specialization;
 233 the resultant z-scores were used as the response variable in the statistical models. Network metrics and

234 null models were estimated in the bipartite package (Dormann et al., 2009). All analyses were run in R
235 (R Development Core Team, 2014).

236

237 RESULTS

238 Our dataset comprises 281 plant species (plus 54 plants identified and/or morphotyped at the genus or
239 family level) that interact with 175 frugivore bird species. We recorded a total of 7637 interactions and
240 2389 unique pairwise links, in which a bird species dispersed the seeds of a plant species in the studied
241 fragments of the Atlantic Forest.

242 The mean frequency of interactions per fragment (472.4 ± 363.4) was 16 times greater than the
243 mean number of bird (32.3 ± 17.9) and plant species (30.7 ± 42.6) recorded in each study site. The
244 most abundant interactions were those performed by generalist bird species dispersing secondary-forest
245 plant species, such as *Thraupis sayaca* dispersing seeds of *Cecropia pachystachya* (61 events of seed-
246 dispersal between three fragments; Fig S1). However, most of the events of seed-dispersal by frugivore
247 birds were rare given that 64% of the interactions occurred only once across the studied fragments (Fig.
248 S1).

249 We found significant species, interaction- and network-area relationships (Fig. 2, Table 1).
250 First, the number of bird and plant species decreased significantly with fragment area. Second, both the
251 number of bird seed-dispersal interactions and the mean number of links per species were negatively
252 affected by the reduction of fragment area. And finally, network nestedness showed a positive and
253 significant relationship with increasing fragmentation when controlling for sampling intensity while
254 specialization showed a tendency to decrease as area is lost, even though the variance explained by this
255 model was quite low. When network size was controlled for by the use of the null models, only
256 sampling intensity explained changes in the mean number of links per species, network nestedness and

257 H2' specialization (Table S3).

258

259

260 **DISCUSSION**

261 We found significant changes of network structure following the lost of habitat area in the fragments of
 262 the Atlantic Forest. The direction of these changes is driven by the non-random loss of frugivorous bird
 263 and plant species and the interactions they perform. Such changes derived from the lower number of
 264 links per species and the higher network nestedness observed in smaller area fragments, in which bird-
 265 seed dispersal interactions performed by small-sized generalist species are predominant (Emer et al.
 266 2018). Yet, the reduced community size in smaller areas led to the structural changes observed on the
 267 organization of seed-dispersal interactions, depicted by the influence of sampling intensity and the lack
 268 of significant effects when tested against proper null models. Nonetheless, network specialisation
 269 seems to be an invariant property of those communities given that it was not affected by habitat change
 270 or pairwise species losses.

271 Bird seed-dispersal networks of the Atlantic Forest are losing species and interactions as the
 272 landscape becomes more fragmented. Beyond the potential consequences for network stability (May
 273 1972, Valdovinos 2019) detected by the increasing nestedness and reduced number of links performed
 274 by the remnant species, those local communities are likely to be also losing important ecological
 275 functions. Species- and interaction-rich communities mostly hold higher functional diversity while
 276 the impoverished ones are likely to have gaps on ecosystem functionality (Isbell et al., 2011; Saavedra
 277 et al. 2014, Montoya et al., 2015). The impoverishment of plant species in forest remnants from the
 278 Northeast of the Atlantic Forest has led to a biotic homogenization across the fragmented landscape
 279 (Lobo et al. 2011). Likewise, the impoverishment of interactions found in this study and the persisting

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280 interactions performed by smaller-sized generalist species in the fragmented landscape (Emer et al.
281 2018) suggests that the Atlantic Forest is losing specific ecological functions, which may trigger
282 medium to long-term functional homogenization of interactions throughout the landscape (Olden et al.
283 2004, Laliberté & Tylianakis 2010). The changes on the number of links per species according to
284 habitat fragmentation may support our *a posteriori* hypothesis of functional homogenization potentially
285 driven by the persistence of a few, functionally-redundant sub-groups of interacting species that are
286 able to cope with the unstable conditions found in most forest fragments (Murcia 1995, Harper et al.
287 2005, Passmore et al. 2012).

288 The increasing nestedness of the bird-seed dispersal networks indicates that communities in
289 smaller area fragments predominantly include a core of generalist species that interact with a sub-group
290 of more specialist ones, while there is a lack, or at least a reduction of, specialist-specialist interactions.
291 In other words, the reduced species pool on smaller fragments are likely to promote their generalization
292 in terms of mutualistic partners while using whichever resource is available in these more disturbed
293 areas. Thus, it may indicate a community-level shift towards more generalist interactions as
294 fragmentation increases (Hobbs et al. 2006; Kiers et al 2010). Likewise, changes in the behaviour of
295 the species that persist in smaller fragments, or fluctuations in population dynamics, could also explain
296 the increasing network generalization (Awade et al. 2017; Cornelius et al. 2017). Furthermore, the
297 reduced community size in smaller areas apparently leads to some structural changes in the
298 organization of seed-dispersal interactions, as suggested by the influence of sampling intensity on
299 network nestedness when tested against proper null models.

300 In turn, network specialization was not significantly affected by habitat reduction. This suggests
301 that, despite negative effects of fragmentation on network size, the way remnant species interact in
302 terms of partners diversity is similar between small assemblages of bird and plant species in smaller

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303 areas, and large assemblages in larger areas. Considering that the minimum value of the H2' index
 304 indicates maximum niche overlap among interacting species (while the opposite indicates maximum
 305 niche divergence; Schleuning et al. 2012), our analysis reveals that niche partitioning of fruit food
 306 resources provided by the plants to the birds, or the seed dispersal service promoted by the birds to the
 307 plants, are not affected by the loss of area in smaller sized fragments. This suggests that network
 308 specialization in terms of niche partitioning is driven by different mechanisms other than habitat area
 309 (Schleuning et al. 2014, Mello et al. 2015). The presence of naturalized alien species in the system,
 310 mainly plants such as *Melia azedarach* and *Psidium guajava*, may numerically compensate the absence
 311 of some native ones, which are more sensitive to habitat change. Yet, their functionality as food
 312 resources for the bird community appears impoverished.

313 Tropical forest fragments are hyperdynamic systems facing population and community changes
 314 in response to primary effects of habitat loss followed by subsequent edge effects and stochastic events
 315 (Laurance et al. 2002, Laurance et al. 2010). Furthermore, the Atlantic Forest landscape holds very
 316 high levels of beta-diversity and turnover of birds, plants, and their interactions (Morante-Filho et al.
 317 2016, Farah et al. 2017, Emer et al. 2018), which could lead, at least partially, to the observed network-
 318 area relationships. Such community heterogeneities can be further influenced by other anthropogenic
 319 impacts such as hunting and logging, whose frequency and intensity of occurrence are context-
 320 dependent and vary among fragments (Joly et al. 2014, Galetti et al. 2016). Therefore, long-term effects
 321 of habitat fragmentation on network structure may go through different trajectories (Thompson 2005)
 322 but the impoverishment of the system is unlikely to change.

323 Finally, our findings have important implications for advancing the understanding of network-
 324 area relationships (NARs, *sensu* Galiana et al. 2018). While species-area relationships are one of the
 325 most pervasive rules in ecology (MacArthur & Wilson 1967, Lawton 1999), empirical data

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326 demonstrating whether or not interactions- and network-area follow the same rules are rare (but see
 327 Aizen et al. 2012, Passmore et al. 2012, Emer et al. 2013, Bomfim et al. 2018 for examples on
 328 mutualistic networks). Our results showed that, as expected, bird and plant species as well as their
 329 interactions, were strongly affected by fragment area. Likewise, the number of links per species and
 330 nestedness also changed with area but not network specialization. Yet, when the number of species in
 331 each community was considered using the null models, none of the network properties changed with
 332 area, only with sampling intensity. These findings suggest that area *per se* does affect network
 333 structure, but primarily mediates the presence/absence of remnant species in the fragments, as well as
 334 the interactions they perform. Furthermore, the lack of significant changes in network specialization
 335 independently of local species richness, contrasting with the richness-associated changes of the
 336 previous metrics, may suggest that the stability of complex system depends on the specific parameter
 337 and the system analysed (May 1972, Thébault & Fontaine 2010, Valdovinos et al. 2019). Specialization
 338 of the seed-dispersal interactions could be seen as an invariant property of the networks, at some extent
 339 robust to habitat loss. On the other hand, network size and the consequent number of interactions and
 340 nestedness seem to be more prone to collapse as disturbance increases with landscape fragmentation
 341 and reduced habitat area. Therefore, the loss of species and their interactions following habitat loss may
 342 be a good predictor of the directions of changes in network structure, providing guidance for an overall
 343 theory of NARs.

344

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352

DATA AVAILABILITY STATEMENT

Upon acceptance, the dataset used in this manuscript will be made available on the main author's GitHub repository (https://github.com/carineemer/network_area).

356

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TABLES

TABLE 1. Results of the Linear Regression Models after AICc model selection testing the effects of fragment area on the structure of avian seed-dispersal networks. Area corresponds to the logarithmic scale of hectares per fragment. Intensity corresponds to the average number of interactions per species and was used as a fixed parameter to control for differences in sampling effort among studies. Only models with $\Delta AICc < 2$ were selected as plausible explanations for the observed patterns (see Table S1 for full model selection). $wAICc$ gives an estimate of the probability of that given model to be the best choice under the AICc criteria. r^2 gives an estimation of the variance explained by the optimal model while the coefficient t corresponds to the importance of that parameter within the model ($t > 2$ indicates the coefficient is significant with $> 95\%$ confidence). ‘+’ indicates that the next presented variable is co-varying to explain the changes on the corresponding network metric in the corresponding model.

575 TABLE 1.

Network metric	Best model	$wAICc$	Est	SE	t	r^2
Number of bird species	Area +	0.75	0.08	0.03	2.39	0.29
	Intensity		0.17	0.14	1.28	
Number of plant species	Area +	0.84	0.14	0.05	2.66	0.28
	Intensity		-0.23	0.22	-1.05	
Number of interactions	Area +	0.96	0.12	0.03	3.45	0.72
	Intensity		0.70	0.14	4.98	
Number of links	Area +	0.86	0.15	0.05	3.25	0.41
	Intensity		0.19	0.19	1.03	
Nestedness	Area	0.72	-1.13	0.47	-2.43	0.50
	Intensity		6.74	1.89	3.56	
H2' specialization	Intensity	0.68	0.08	0.07	1.02	0.01
	Area +		-0.02	0.02	-1.35	
	Intensity		0.09	0.07	1.18	

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FIGURE LEGENDS

FIGURE 1. The structure of the 16 avian seed-dispersal networks and their location in the Atlantic Forest, SE Brazil. In each network, blue dots represent plant species, orange dots bird species, and the grey lines are the seed-dispersal interactions among them; the width of the grey lines correspond to the frequency of interactions in each area. Communities are numbered according to a decreasing order of fragment area (see Table S1 for details of each site): 1- Parque Estadual (PE) Intervales; 2- PE Carlos Botelho; 3- PE Ilha do Cardoso; 4- PE Poço das Antas; 5- PE Ilha Anchieta; 6- Minas Gerais fragment; 7- Estação Ecológica de Aracuri; 8- Mata Santa Genebra; 9- Itatiba fragment; 10- Rio Claro fragment; 11- restored area 15 years old; 12- restored area 25 years old; 13- restored area 57 years old; 14- São Paulo fragment; 15- restored area 8 years old; 16- Rio de Janeiro fragment.

FIGURE 2. The effects of fragment area on the structure of seed-dispersal networks of the Atlantic Forest. Each point corresponds to a single forest fragment. The gradient of colours correspond to the intensity of defaunation ('def') in each fragment, calculated as the difference between the total body mass of the frugivore birds expected for the Atlantic Forest (based on Bello et al. 2017) and the total body mass of bird frugivores recorded in each network. Defaunation and fragment area are highly correlated ($r = -0.89$).

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SUPPLEMENTARY INFORMATION

Content

Table S1-S4.

Fig. S1