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## **Seed dispersal networks in tropical forest fragments: Area effects, remnant species, and interaction diversity** — [Source link](#)





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

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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

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

68

69

70 **Keywords:** frugivory; species interactions; human disturbance; defaunation; forest fragmentation;  
71 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

96 effectively dispersed (Howe & Smallwood 1982, Jordano 1995). Such associations between tropical  
97 frugivorous birds and the plants they feed upon can form complex and diverse seed-dispersal networks,  
98 characterized by a large number of species and interactions (Bascompte & Jordano 2007, Schleuning et  
99 al. 2014, Dügger et al. 2018). Disruptions in the functionality of this system can be inferred by the  
100 emergence of ecological patterns depicted from the correct interpretation of the structural properties of  
101 the networks (Bascompte & Jordano, 2007, Memmott 2009, Howe 2016). For instance, changes in the  
102 mean number of interactions (links) per species may indicate a reduction on the number of partners  
103 available to interact with in smaller areas, in which generalist species are favoured (Morante-Filho et  
104 al. 2016, Galiana et al. 2018). Likewise, increases in nestedness, a pervasive pattern in mutualistic  
105 networks that suggests the presence of highly generalist species interacting with both generalist and  
106 specialist ones, may suggest the loss of specialist interactions in disturbed communities (Aizen et al.  
107 2012, Bomfim et al. 2018). Similarly, a reduction of network specialization, estimated by the H2' index  
108 based on Shannon diversity, would suggest the community is losing diversity of interactions among  
109 species, with the prevalence of more generalist species.

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

119 temperature and light conditions that may favour the competitive ability of some plant species over the  
120 others (Laurance et al. 2010, Sfair et al. 2016). Associated to the negative effects of habitat reduction  
121 lays defaunation, a pervasive phenomenon characterized by the local or functional extinction of a given  
122 species, generally towards the larger body mass ones and often related to the reduction of habitat area  
123 (Dirzo et al., 2014, Young et al. 2016). Thus, interactions performed by large-bodied species dispersing  
124 large-seeded plants are expected to be absent in smaller areas (Pérez-Mendez et al. 2016, Emer et al.  
125 2018) therefore affecting the local, within-fragment network structure.

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

140

141 **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 ( $472.4 \pm 363.4$ ) was 16 times greater than the  
243 mean number of bird ( $32.3 \pm 17.9$ ) and plant species ( $30.7 \pm 42.6$ ) 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-richer 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

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

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

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

### 353 **DATA AVAILABILITY STATEMENT**

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

356

### 357 **LITERATURE CITED**

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561 **TABLES**

562

563 TABLE 1. Results of the Linear Regression Models after AICc model selection testing the effects

564 of fragment area on the structure of avian seed-dispersal networks. Area corresponds to the

565 logarithmic scale of hectares per fragment. Intensity corresponds to the average number of

566 interactions per species and was used as a fixed parameter to control for differences in sampling

567 effort among studies. Only models with delta AICc < 2 were selected as plausible explanations

568 for the observed patterns (see Table S1 for full model selection).  $wAICc$  gives an estimate of the

569 probability of that given model to be the best choice under the AICc criteria.  $r^2$  gives an

570 estimation of the variance explained by the optimal model while the coefficient  $t$  corresponds to

571 the importance of that parameter within the model ( $t > 2$  indicates the coefficient is significant

572 with > 95% confidence). ‘+’ indicates that the next presented variable is co-varying to explain the

573 changes on the corresponding network metric in the corresponding model.

574

575 TABLE 1.

<b>Network metric</b>	<b>Best model</b>	<b>wAICc</b>	<b>Est</b>	<b>SE</b>	<b><i>t</i></b>	<b><i>r</i><sup>2</sup></b>		
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 +		0.31	-0.02	0.02		-1.35	0.06
	Intensity		0.09	0.07	1.18			

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579 **FIGURE LEGENDS**

580

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

591

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

598

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600

## **SUPPLEMENTARY INFORMATION**

Content

Table S1-S4.

Fig. S1

