

ECOGRAPHY

Research

Local extinctions of obligate frugivores and patch size reduction disrupt the structure of seed dispersal networks

Jamille de Assis Bomfim, Paulo R. Guimarães Jr, Carlos A. Peres, Gustavo Carvalho and Eliana Cazetta

J. de Assis Bomfim (jamilleassis@hotmail.com) and E. Cazetta (http://orcid.org/0000-0002-2209-2554), Laboratório de Ecologia Aplicada à Conservação, Univ. Estadual de Santa Cruz, Ilhéus, Bahia, Brazil, and Programa de Pós-Graduação em Ecologia e Conservação da Biodiversidade, Univ. Estadual de Santa Cruz, Ilhéus, BA, Brazil. – P. R. Guimarães Jr (http://orcid.org/0000-0001-9161-8305), Depto de Ecologia, Inst. de Biociências, Univ. de São Paulo, São Paulo, Brazil. – C. A. Peres, Center for Ecology, Evolution and Conservation, School of Environmental Sciences, Univ. of East Anglia, Norwich, UK. – G. Carvalho, Depto de Botânica, Univ. Estadual Paulista, Rio Claro, São Paulo, Brazil.

Ecography

41: 1–11, 2018

doi: 10.1111/ecog.03592

Subject Editor: W. Daniel Kissling

Editor-in-Chief:

Jens-Christian Svenning

Accepted 12 February 2018

A central problem in ecology is to understand how human impacts affect plant–animal interactions that lead to effective seed dispersal services for plant communities. Seed dispersal services are the outcome of plant–frugivore interactions that often form local networks of interacting species. Recent work has shown that some frugivorous bird species are more critical to network organization than others. Here, we explore how patch size and the potential local extinctions of obligate frugivorous birds affect the reorganization of seed dispersal networks. We examined the structure of 20 empirical seed dispersal networks documented across tropical avian assemblages occupying widely variable habitat patch sizes, a surrogate of the amount of remaining habitat. Networks within small forest patches consistently supported both lower plant and bird species richness. Forest patch size was positively associated with nestedness, indicating that reductions in patch size disrupted the nested organization of seed dispersal networks. Obligate frugivores, especially large-bodied species, were almost entirely absent from small forest patches. Analysis at the species level showed that obligate frugivores formed the core of interacting species, connecting species within a given seed dispersal network. Our combined results revealed that patch size reduction erodes frugivorous bird diversity, thereby affecting the integrity of seed dispersal networks. We highlight the importance of conserving large forest patches to maintain tropical forest functionality.

Keywords: mutualistic networks, frugivory, patch size

Introduction

The theory of island biogeography (MacArthur and Wilson 1967) was extrapolated to terrestrial habitat patches (Levins 1970) and since then studies evaluating species richness as a function of patch size proliferated in the literature. This straightforward model predicts an increase in species richness with area, the species–area relationship (SAR),



and is considered one of the few ironclad laws in ecology (Scheiner 2003). However, the extinction of species interactions may precede the demographic extinction of species (Säterberg et al. 2013) and it would be reasonable to expect that the species–area relationship would also hold true for the interaction–area relationship (IAR) (*sensu* Sugiura 2010).

Understanding how species and their interactions are affected by anthropogenic changes including the reduction of natural habitats is crucial to the conservation of ecosystem functions and services (Valiente-Banuet et al. 2015). The pervasive effects of missing animal–plant interactions are strongly associated with the disruption of ecosystem services provided by these ecological interactions (Magrath et al. 2014). Seed dispersal by animals comprises one of the key ecosystem services that may be disrupted by habitat loss and fragmentation (Hagen et al. 2012). Yet, it remains unclear how animal-mediated seed dispersal systems are disassembled by losses of seed dispersers induced by habitat loss and other anthropogenic threats.

Studies in both temperate and tropical ecosystems have reported that some features of seed dispersal systems can be highly resilient in human modified landscapes (Garcia and Martinez 2012, Markl et al. 2012). In contrast, habitat loss – the reduction in the size of natural habitat patches – is one of the main landscape consequences of human land use, negatively affecting seed removal rates (Cordeiro and Howe 2003) and the overall number of interactions between frugivorous bird and fruiting plant species (McConkey et al. 2012). Yet the pathways through which seed dispersal systems respond to habitat loss vary according to habitat disturbance type, taxonomic group, and ecological guilds (Ewers and Didham 2006, Fontúrbel et al. 2015). Large-bodied frugivorous birds, which are able to consume a wider spectrum of fruits (Jordano 2000) and exhibit high dispersal capacity (Lees and Peres 2009), may be sensitive to small patch sizes depending on patch isolation, availability of food resources and local hunting pressure (Peres 2001, Ewers and Didham 2006, Lehouck et al. 2009), and large-seeded plant species, which rely heavily on large-bodied seed vectors, can show steep population declines or local extinctions in small fragments (Kitamura et al. 2002, Wotton and Kelly 2011). Because birds disperse seeds of many tropical plant families (Fleming and Kress 2011), an important step in maintaining forest functionality is to understand how habitat loss and fragmentation erode the organization of ecological interactions between plants and their avian seed dispersal agents.

At the community level, ecological interactions between fruiting plants and vertebrate seed dispersers are arranged as networks. The organization of these interactions can therefore be described in terms of network structural patterns (Bascompte and Jordano 2007). In this context, network structural changes may provide information on how the organization of seed dispersal interactions changes when confronted with anthropogenic stressors (Trojelsgaard et al. 2013, Schleuning et al. 2014a). It is possible to explore different structural patterns of seed dispersal systems and the effects of habitat loss on each of these network patterns.

In addition to species richness and total number of interactions, the way interactions are apportioned among potential partners may affect how seed dispersal systems can respond to anthropogenic perturbations (Vidal et al. 2013, 2014, Sebastián-González et al. 2015). In this sense, nestedness amounts to a central property of seed dispersal networks.

In nested mutualistic networks, species with fewer interactions interact with a narrow subset of partners of other species linked to a larger number of interactions (Bascompte et al. 2003). Nestedness implies that species can play different roles in the network structure (Saavedra et al. 2011), and a few, highly connected species contribute most to network organization (Olesen et al. 2007, Sazima et al. 2010). For example, birds that consume fruits as a main component of their diet interact with a wider range of plant species (Schleuning et al. 2011, Sebastián-González 2017), and occupy a more central role in networks (Mello et al. 2011, 2015) compared to opportunistic frugivores that only consume fruits sporadically. Thus, highly dedicated frugivorous birds account for the largest number of interactions, are indirectly connected with many other species, and render the networks more cohesive, all of which may affect both ecological and evolutionary dynamics (Guimarães Jr et al. 2011, Allesina and Tang 2012, Mello et al. 2015). Consequently, designing conservation programs that uphold full complements of ecological interactions relies on identifying those central species within each network (Lewinsohn and Cagnolo 2012).

Here, we explore to what extent habitat patch size affects species interactions (*i.e.* the interaction–area relationship) and consequently seed dispersal network organization, emphasizing the role of obligate frugivorous species. We compiled a dataset of 20 empirical seed dispersal networks between plants and birds in tropical forest environments, and used forest patch size as a proxy of habitat loss. First, we investigated the influence of patch size on network organization, focusing on changes in network cohesion. In this analysis, we included temperature and precipitation in our models to control for confounding effects of climate. Second, we assessed to what extent forest patch size affected the role of primarily frugivorous species in the structure of networks. Because previous studies reported the importance of large-bodied frugivores as dispersal vectors of large-seeded plants, we quantified to what degree large-bodied frugivores are affected by patch size, and whether they are prevalent among obligate frugivorous birds. Specifically, we tested three sets of predictions related to how patch size affects the reorganization of seed dispersal networks in small habitat patches. First, we predicted a decline in both plant and bird species richness, particularly large-bodied species, and the overall number of interactions that effectively operate in small patches. Second, we expected networks from small patches to be simplified in their organization, leading to networks that are both less nested and less cohesive. Third, we expected that obligate frugivores will have a disproportionately greater contribution to the overall organization and cohesion of networks in large forest patches, in contrast with networks in small patches which should be dominated by more occasional frugivores.

Collectively, our results support the notion that forest patch size reduction erodes the local diversity of obligate frugivores, thereby degrading the structure and overall complexity of seed dispersal networks.

Methods

Dataset

Our dataset includes seed dispersal networks compiled using two main sources. First, we searched studies describing interacting assemblages of tropical fruiting plants and frugivorous birds using Web of Science, Scopus, Science Direct, and Google Scholar based on the keywords ‘mutualistic network’, ‘frugivor*’, ‘seed dispersal’, ‘bird’ and ‘diet’. Second, we used four fruit–frugivore interaction networks available from two network databases: Interaction Web Database (<www.nceas.ucsb.edu/interactionweb/>) and Web of Life (<www.web-of-life.es/>). We selected only studies that provided both the interaction networks and level of sampling effort at the community level, through either direct plant observations (such as focal observations of fruiting plants and feeding bouts) or fecal samples collected from mist-netted birds. We searched for site-specific patch size information at the time of each study available in each article, on the web, or upon direct request to authors. We recorded 52 networks but after applying these criteria, we selected 20 binary networks distributed throughout the Neotropics, Africa and south-east Asia (Fig. 1; Supplementary material Appendix 1 Table A1). When networks recorded all interactions regardless of the pattern of fruit handling by frugivores (e.g. whole fruit

consumption, pulp thieves), we assumed that all bird species were potential seed dispersers as a first approximation. Since the number of species and interactions, and certain network metrics may be affected by sampling effort (Nielsen and Bascompte 2007), we tested the effects of study duration (in months) on network metrics prior to the analyses. We log₁₀-transformed patch size to account for large data gaps along the scale of all recorded patch sizes.

Frugivory classification and body mass

We used the bird dietary classification proposed by Kissling et al. (2009) in which the diet of a given species is classified into nine categories of food items (fruits, fish, nectar, vertebrates, terrestrial invertebrates, aquatic invertebrates, plant material, carrion, and seeds). This classification defines frugivorous birds as those species that consume fruits as their main dietary item and that do not consume more than three categories of food items. We refer to these species that rely heavily on fruits as ‘obligate frugivores’, whereas birds that consume fruits only sporadically as ‘occasional frugivores’. This classification also includes some Psittacidae species (parrots and parakeets), as obligate frugivores. Psittacids are typically considered as seed predators, but they can also act as seed dispersal agents (Tella et al. 2015, Blanco et al. 2016) and therefore we opted to maintain these species in the analyses. However, in the dataset we compiled, psittacids accounted for only 1.73% of all interactions and were present in only nine networks. To evaluate the influence of patch size on large-bodied birds, we compiled body mass data from Dunning (2007).

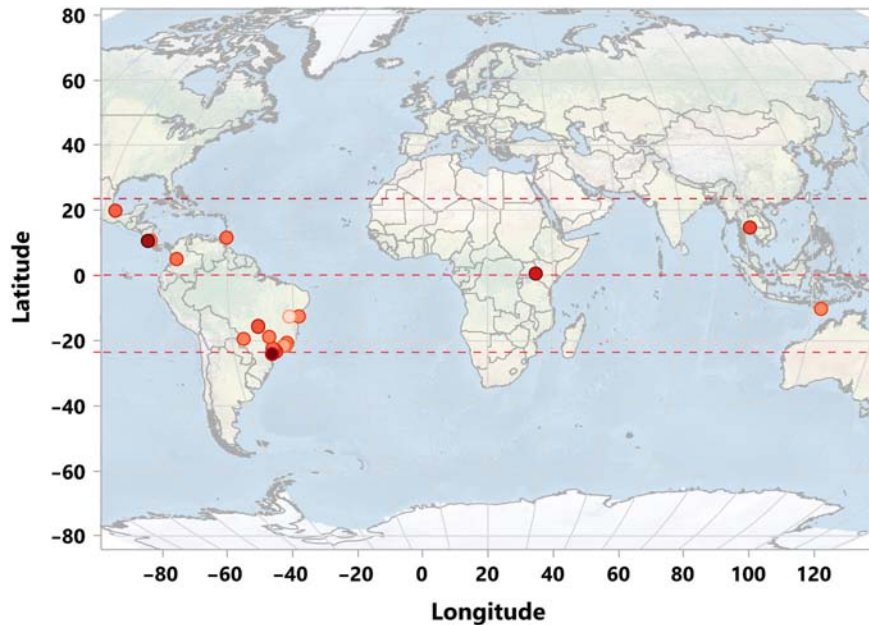


Figure 1. Geographic distribution of all 20 plant–frugivore seed dispersal networks that were quantitatively assessed in this study. All sites are restricted to forest fragments within neotropical (17 sites) and paleotropical landscapes (3 sites). Circles are colour-coded from light to dark red according to an increase in the total number of observed interactions (on a log₁₀ scale).

Network structure

We first described the structure of the 20 study networks using the following eight network-level descriptors: 1) plant species richness, 2) bird species richness, 3) species richness of obligate frugivorous birds, 4) number of recorded interactions, 5) connectance, 6) degree variance, 7) nestedness, and 8) average path length. The first three descriptors (species richness of plants, species richness of bird species, and the species richness of obligate frugivores) comprise the most basic description of fruit–frugivore assemblages. The total number of interactions allows us to explore the level to which the assemblage is connected. We explored if the proportion of possible interactions that were observed in the networks is also related to forest patch size. To do so, we computed the connectance, C , defined as $C = I/AP$, in which I is the sum of all observed interactions, A and P are the bird and plant species richness, respectively, and AP is the maximum number of possible interactions in a given seed dispersal network (Jordano 1987). Degree variance characterizes how variable is the number of interactions per species. Because the mean number of interactions per species is often small, high variance implies that some species interact more than others and are likely to be structurally more important (Jordano et al. 2003).

Nestedness allows us to characterize if the interaction network patterns is characterized by a core of highly connected species and asymmetrical interactions between specialists and generalists (Bascompte et al. 2003). We estimated nestedness using the NODF metric (Almeida-Neto et al. 2008) using the ANINHADO software (Guimarães and Guimarães 2006). We tested if the observed nestedness of real networks was higher than expected by the theoretical benchmark given by the basic attributes of seed dispersal assemblages (richness, number of interactions, and degree variance) using a null model approach. We generated 1000 random networks using the null model 2 proposed by Bascompte et al. (2003), in which the probability that an interaction between an animal i

and a plant j will occur, P_{ij} , is defined as $P_{ij} = 0.5 \left(\frac{k_i}{P} + \frac{k_j}{A} \right)$,

i.e. this is based on the mean number of interactions of each bird and plant species (Bascompte et al. 2003). To compare nestedness estimates among networks, we standardized this metric using the z-score, $Z\text{-NODF} = (N - \bar{N}_{nm}) / \sigma_{nm}$, in which N is the NODF-value for the empirical network, \bar{N}_{nm} is the mean NODF-value for the null model network, and σ_{nm} is the standard deviation of the NODF-values of the null model network. These z-scores allow us to compare nestedness values after controlling for species richness, connectance, and variance in the number of interactions.

Average path length is the average of the shortest distances between all species in a network (Watts and Strogatz 1998), and describes how close species are in a network in terms of number of direct and indirect interactions. Low average path length values indicate that the network is very cohesive (Albert et al. 2000). The average path length is

defined as: $\langle \ell \rangle = \sum_i^N \sum_j^N \ell_{ij} / N(N-1)$, in which i and j

are any two species, N is the total species richness, and ℓ_{ij} is the length of the shortest path linking species i and j , measured in number of interactions. For example, an interacting pair of plant and animal species has $\ell_{ij} = 1$, whereas two plants that share the same seed disperser have $\ell_{ij} = 2$. We wrote a MATLAB script to compute the average path length using matrix multiplication, which is available upon request.

We performed multiple linear regressions between all network descriptors against forest patch size and climatic variables to examine the effects of these variables on seed dispersal networks. We extracted the temperature ($^{\circ}\text{C} \times 10$) and precipitation (mm) values from the WorldClim Database (Hijmans et al. 2005). For these analyses, we used the mean annual temperature and precipitation for the 1960–1990 period. Because species richness has a strong influence on the total number of interactions (Bascompte et al. 2003, Dormann et al. 2007), we also included this variable in the models. Species richness, number of interactions, and patch size were log-transformed ($\log_{10} x$) prior to the analyses. We used the function ‘avPlots’ from the ‘car’ package (Fox and Weisberg 2011) in R platform (R Core Team), to represent the relationship between patch size and the richness and interaction pattern of the networks through a partial regression plot. We also tested for the influence of spatial autocorrelation on the species richness of plants, birds and all species combined, and the richness of obligate frugivorous birds using semivariograms and Moran’s index to evaluate the autocorrelation using the model residuals of each variable (Dormann et al. 2007). However, no variable exhibited spatial dependency (Supplementary material Appendix 1 Table A2). The autocorrelation analyses were carried out in R software (R Core Team) using geoR (Ribeiro Jr and Diggle 2001), and ape (Paradis et al. 2004) packages.

Species-level analyses

We performed analyses at the species level to assess the contribution of obligate frugivores to network structure. We first measured the contribution of obligate frugivores to the average path length (APL) of the network. APL is the mean distance, in number of interactions, between the species and all other species in the network. We then tested whether obligate frugivores have a higher degree (k) and higher betweenness centrality (BC) than occasional frugivores. Species with higher BC values are those that mediate the shortest path connecting other species in the network (Costa et al. 2007). We computed the BC metric of each species within the two-mode seed dispersal network, using a MATLAB script, which is also available upon request.

We used analysis of covariance (ANCOVA) to examine the relationships between degree of frugivory (obligate vs occasional frugivores) and species contribution to the network structure (BC, k , contribution to average path length per species) across the entire patch size gradient. We also

used ANCOVA to assess whether the mean body mass of obligate and occasional frugivores was related to patch size, and whether this relationship differed between the two frugivore guilds. The degree of frugivory was the categorical variable and patch size the covariate. The degree k and BC were \log_{10} -transformed and body mass was Box–Cox transformed ('bcPower' from 'car' package) prior to the analyses, with optimal lambda value ($\lambda = -0.26$) identified through the 'powerTransform' function from the 'car' package. For all analyses at the species level, we used the mean values of each response variable for each site. When an ANCOVA interaction term was significant, and consequently the slopes were not identical, we performed linear regressions to assess the relationships between the variables.

All statistical analyses were performed within the R platform (R Core Team).

Data deposition

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.k25rq40>> (de Assis Bomfim et al. 2018).

Results

Seed dispersal networks analyzed here varied widely in their species richness, connectivity, and structural patterns. We recorded 696 plant species (mean \pm SD = 38.3 ± 47.6 plant species per network; range = 10–179), 454 bird species (mean \pm SD = 35.1 ± 21.7 bird species per network; range = 7–86), and 3870 interactions (mean \pm SD = 193.5 ± 236.1 ; range = 22–989) across all 20 binary networks evaluated. Network connectance varied between 0.06 and 0.36 (mean \pm SD = 0.19 ± 0.09). Variation in species richness, connectivity, and network structure could not be attributed

to sampling effort, since the duration of each study did not affect the number of species observed, the number of interactions, or the structural network metrics (Supplementary material Appendix 1 Table A3). Moreover, sampling effort was unrelated to the patch size gradient (Supplementary material Appendix 1 Table A3). In general, networks were more nested than expected from the null model, regardless of forest patch size, except for three networks (14.3% of networks) that were not significantly nested.

We then investigated the role of forest patch size and climatic variables on species richness and network connectivity. Forest patch size had a significant positive effect on both plant and bird species richness (Table 1; Fig. 2a, b), and richness of plants and birds combined (Table 1; Fig. 2c). Temperature did not influence any of our variables (Table 1) but precipitation had a significant effect on plant species richness (Table 1). The number of observed interactions in the networks was not influenced by patch size (Table 1; Fig. 2d), but was positively related to total species richness (Table 1). At the network level, patch size has a marked effect on nestedness. After controlling for the effects of species richness, connectance and degree variance, using Z-NODF values, networks were more nested in increasingly larger patches (Table 2; Fig. 3). In contrast, patch size did not affect overall connectance and other network structural patterns, such as the degree variance for plants and average path length (Table 2).

We then examined the effects of patch size on birds exhibiting different degrees of frugivory. Obligate frugivores were represented by 144 species (31.85% of total) that took part in 1845 interactions (47.67% of total), whereas occasional frugivores were represented by 310 species (68.28% of total) and 2025 interactions (52.32%). Occasional frugivores outnumbered obligate frugivores in all networks, and frugivore species richness increased with increasing patch size regardless of the degree of frugivory (Table 3; Fig. 4a).

Table 1. Summary of multiple linear regression models between patterns of species richness and number of interaction, and forest patch size and climatic variables, from 20 seed dispersal networks. All variables were \log_{10} transformed prior to the analyses. p-values in bold are significant at the $\alpha = 0.05$ level. Degrees of freedom (df) = 16 in multiple linear regression models for richness of all species and df = 15 for number of interactions.

Response variables	Predictor variables	β	SE	t	p
Plant richness	Patch size	0.15	0.06	2.39	0.03
	Temperature	−0.03	1.09	−0.03	0.98
	Precipitation	1.1	0.47	2.36	0.03
Bird richness	Patch size	0.15	0.06	2.6	0.02
	Temperature	−0.82	0.99	−0.83	0.42
	Precipitation	0.16	0.42	0.38	0.71
Total species richness	Patch size	0.15	0.05	2.92	0.01
	Temperature	−0.53	0.91	−0.58	0.57
	Precipitation	0.75	0.39	1.9	0.07
Richness of obligate frugivores	Patch size	0.21	0.06	3.28	0.005
	Temperature	−1.19	1.09	−1.09	0.3
	Precipitation	0.84	0.47	1.79	0.09
Number of interactions	Total richness	1.25	0.13	9.62	< 0.001
	Patch size	0.04	0.03	1.08	0.3
	Temperature	−0.52	0.48	−1.07	0.3
	Precipitation	0.15	0.23	0.68	0.51

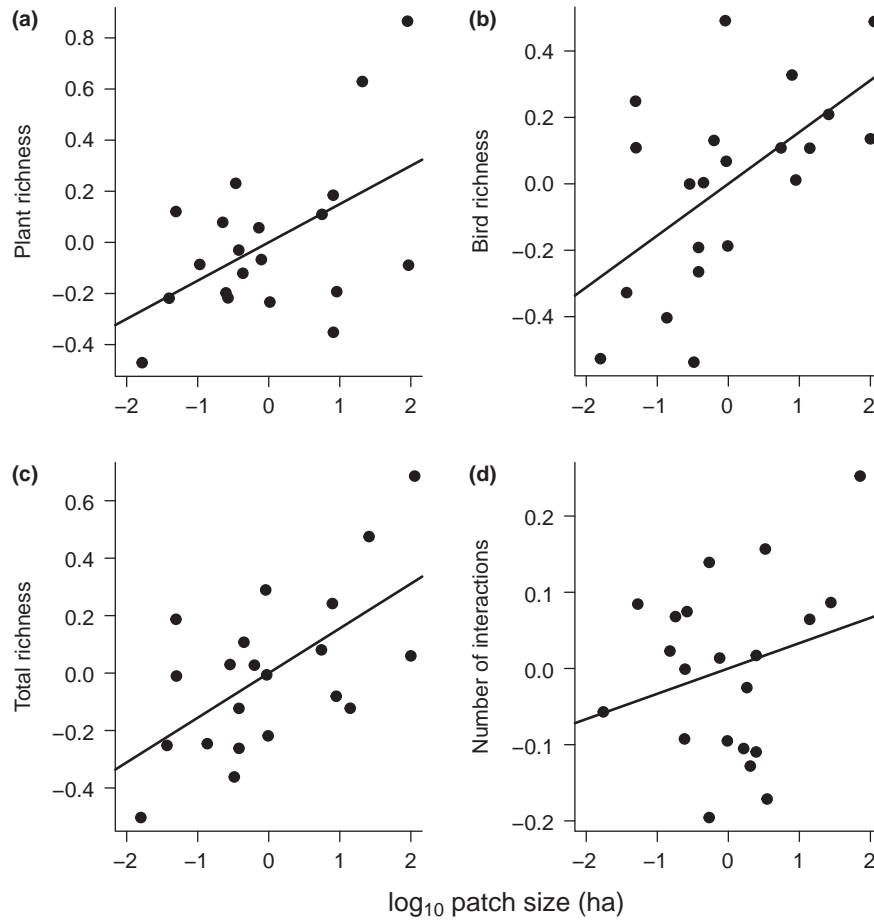


Figure 2. Partial regression plots showing the relationships between forest patch size and plant species richness (a), bird species richness (b), richness of plants and birds combined (c), and number of interactions (d) across 20 plant–frugivore mutualistic networks. All variables were log-transformed ($\log_{10} x$).

Obligate frugivores were typically more connected and more central within networks than occasional frugivores, playing a more pivotal role in network organization. Obligate frugivores often exhibited higher number of interactions partners (k) than occasional frugivores, regardless of patch size (Table 3). The mean level of centrality decays with patch size for both obligate and occasional frugivores. After controlling for the negative BC-patch size relationship, obligate frugivores were also more central than occasional

Table 2. Summary of linear relationships between the metrics of network structure and forest patch size. Degree variance of plants and birds were \log_{10} transformed prior to the analyses. Degree of freedom (df)=18 for all models.

	β	SE	t	r^2	p
ZNODF	1.57	0.66	2.37	0.24	0.03
Connectance	-0.02	0.02	-1.33	0.09	0.2
Degree variance of plants	0.14	0.11	1.32	0.09	0.2
Degree variance of birds	0.2	0.09	2.23	0.22	0.04
APL	0.03	0.07	0.37	0.008	0.71

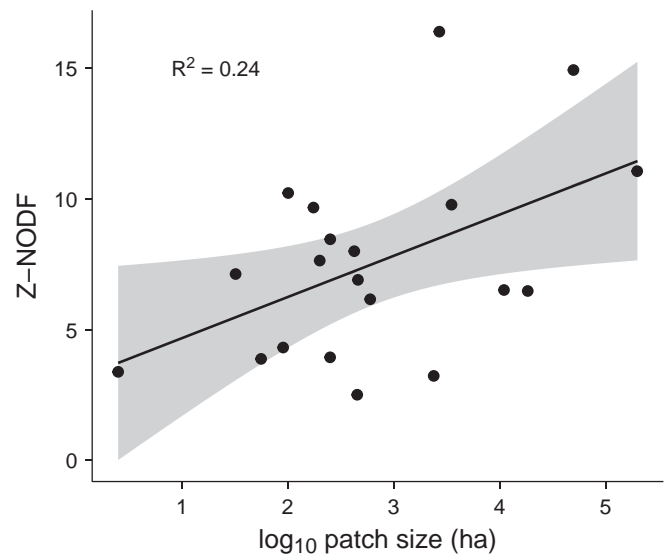


Figure 3. Effect of forest patch size on standardized nestedness (Z-NODF) of the 20 networks assessed in this study.

Table 3. Summary of the analysis of covariance (ANCOVA) on the species-level metrics, body mass, and bird species richness and forest patch size and degree of frugivory (both occasional and obligate frugivores). Degree, betweenness centrality and bird species richness were \log_{10} -transformed and body mass was Box-Cox transformed prior to the analyses. p-values in bold are significant at the $\alpha=0.05$ level.

		DF	MS	F	p
APL contribution	Patch size	1	0.16	0.88	0.35
	Frugivory degree	1	0.29	1.53	0.22
	Interaction term	1	0.34	0.18	0.67
	Error	36	0.19		
Degree (k)	Patch size	1	0.06	1.21	0.28
	Frugivory degree	1	0.37	7.23	0.01
	Interaction term	1	0.00	0.02	0.88
	Error	36	0.05		
Betweenness centrality (BC)	Patch size	1	1.3	7.88	0.008
	Frugivory degree	1	1.2	8.37	0.006
	Interaction term	1	0.03	0.21	0.65
	Error	36	0.14		
Body mass	Patch size	1	0.75	19.35	< 0.001
	Frugivory degree	1	0.25	6.56	0.01
	Interaction term	1	0.3	7.93	0.008
	Error	36	0.04		
Bird species richness	Patch size	1	1.3	12.05	0.001
	Frugivory degree	1	1.23	14.48	< 0.001
	Interaction term	1	0.02	0.19	0.66
	Error	36	0.08		

frugivores (Table 3; Fig. 4b). In contrast, species contributions to average path length did not differ between obligate and occasional frugivores nor along the patch size gradient (Table 3). Finally, patch size affected differences in body mass between obligate and occasional frugivores (Table 3). Obligate frugivores were larger than occasional frugivores (mean \pm SD = 159.09 ± 334.04 g; range = 9–3006 g; mean

\pm SD = 57.23 ± 100.17 g; range = 5–1391 g, respectively), and the interaction between body mass and patch size was significant (Table 3). Linear regression further indicated that obligate frugivores were on average larger in larger patches ($R^2=0.48$, $p < 0.001$, $df=18$), but this was not the case for occasional frugivores ($R^2=0.14$, $p=0.1$, $df=18$; Fig. 4c).

Discussion

Forest loss induced by land-use change affects mutualistic networks via at least two mechanisms by both reshaping the overall organization of networks (Fortuna and Bascompte 2006) and changing the relative importance of different functional groups in network organization (Pires et al. 2014). In this study, we explored both of these effects by examining how patch size covaries with changes in the network structure of avian plant–frugivore interaction systems, the so called interaction–area relationship (IAR). Our study provides three main contributions to our understanding of how interacting assemblages of plant and seed dispersers are affected by habitat loss, measured in terms of remaining forest patch size.

First, we showed that patch size affected both plant and bird species richness. The erosion of species richness was expected from the species–area relationship, which several studies have shown for both birds and plants (Hill and Curran 2003, Hill et al. 2011). A recent meta-analysis corroborated the detrimental impact of human disturbance on avian diversity and frugivore visitation rates (Fontúrbel et al. 2015). We also reported a positive IAR (Sugiura 2010), but we showed that only species richness explains the observed variation in the number of interactions. Due to the clear negative effect of patch size reduction on bird species richness, we can assume that there is an indirect effect of patch size on number of interactions. Nevertheless, we highlight the importance of

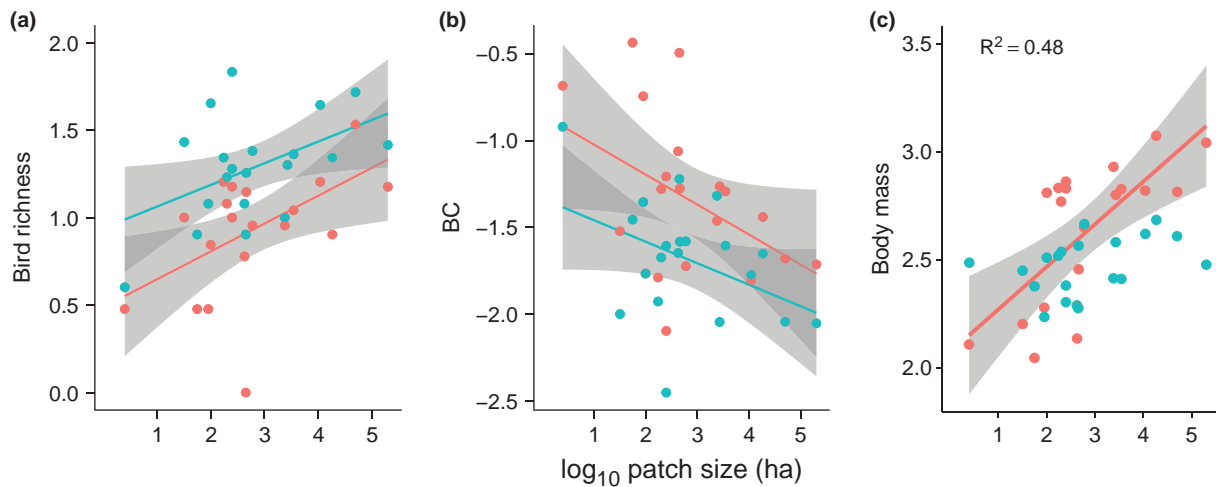


Figure 4. Relationships between forest patch size and either occasional or obligate bird species richness (a) and the betweenness centrality (BC, (b)) and body mass (c) of either obligate or occasional frugivorous birds across 20 forest sites where fruit–frugivore networks have been documented. Occasional and obligate frugivores are represented by blue and red solid circles (and linear fits), respectively. BC and bird species richness were \log_{10} -transformed and body mass (g) was Box-Cox transformed ($\lambda=-0.26$) prior to analyses.

assessing not only species loss, but also loss of interactions since many interactions may be lost even before species can be defined as demographically extirpated (Säterberg et al. 2013, Valiente-Banuet et al. 2015). Although climatic variables were identified as an important modulator of species richness patterns (Gentry 1988, Kissling et al. 2007), we did not find any effect of temperature on plant and bird species richness in the networks and precipitation influenced only plant richness.

Second, the effect of habitat area on network organization goes well beyond the number of species persisting within a patch. The degree of nestedness was positively related to patch size. There is theoretical evidence that higher nestedness should favour robustness of mutualistic assemblages (Thébault and Fontaine 2010). If so, the widespread consequences of tropical forest loss, which often severely reduces patch size and increases isolation (Fahrig 2003), renders seed dispersal networks more vulnerable to perturbations. In contrast, degree variance for plants and average path length were unrelated to forest patch size, which suggests that some aspects of the network organization can persist in small fragments, perhaps because some aspects of network cohesion are maintained by bird and plant species that are insensitive to patch size reduction, like small-bodied habitat generalist birds that often thrive in degraded areas and can also act as important seed dispersers (Carlo and Morales 2016, Emer et al. 2018).

Third, patch size affected species richness and the role of both obligate and occasional frugivores on the network centrality of the seed dispersal assemblages. High diversity of fleshy fruits is an important determinant of habitat selection in frugivorous birds (Herrera 1985) and fruit availability is severely reduced in small patches, mainly due to losses of shade-tolerant species (Pessoa et al. 2017). Thus, small habitat remnants are unlikely to be able to harbour key fruiting plants to sustain the basic metabolic requirements of many obligate frugivorous. Several studies have highlighted the negative impacts of habitat loss to insectivores and forest specialist bird species (Ewers and Didham 2006, Bregman et al. 2014). Although, we have no information on food preferences and habitat use restrictions of the occasional frugivores evaluated here, it is possible that dietary and habitat specialization explain the decline in occasional frugivores in small fragments. Even though our results showed similar effects of patch size on obligate and occasional frugivores, we reinforce that previous works showed that obligate frugivores are involved in more interactions, and occupy more central network positions than occasional frugivores, indicating their key role in network organization (Mello et al. 2011, 2015, Sebastián-González 2017, but see Vidal et al. 2014). Our results also show that the central role of obligate frugivores fades away as forest patch size becomes ever smaller.

Phylogenetic relationships among species is an important determinant of interacting assemblages (Rezende et al. 2007) and may affect the role of obligate frugivores. For example, species that are important connectors of network modules

are more phylogenetically related (Schleuning et al. 2014b), and the number of interaction partners in tropical frugivore networks show high phylogenetic signal (Kissling and Schleuning 2015). However, a recent review using 23 seed dispersal networks around the world showed that degree of frugivory did not exhibit a phylogenetic signal and does not have a key role in network structure (Sebastián-González 2017). Therefore, we are confident that the role of obligate frugivores is not strongly mediated by phylogeny but by the functional differences between obligate and occasional frugivores (Jordano 2000).

Likewise, we found that large obligate frugivores, which were largely absent of small fragments, experience marked habitat area effects. Compared to small-bodied birds, many large-bodied avian frugivores are large-gaped and have greater capacity to consume larger amounts of fruits and disperse large-seeded species (Moermond and Denslow 1985, Jordano 2000). Medium and large birds also discard fewer seeds when handling fruits (Levey 1987), and can disperse ingested seeds farther away from parent plants as they can fly longer distances (Jordano et al. 2007). Even though large frugivores were more susceptible to reduction in patch size (Renjifo 1999), their wide dispersal capacity can ensure that even small habitat fragments continue to be visited depending on their degree of isolation and matrix quality (Hagen et al. 2012). We suggest that the absence of large-bodied birds in smaller fragments is mainly due to habitat loss and the covariate effects of isolation. In particular, the decline of large-bodied frugivores in small habitat patches suggest that the quality and amount of seed dispersal services are eroded (Kitamura et al. 2002), degrading most prospects for assisted regeneration of plant species in these areas (Cardoso da Silva and Tabarelli 2000, Galetti et al. 2013).

Some frugivore species can obviously persist in small forest fragments (Turner et al. 1996), thereby preserving some network structural properties depending on site protection and management (Sabatino et al. 2010, Herrera et al. 2011). However, habitat loss may reduce network tolerance against disturbance by reducing nestedness and decreasing obligate frugivore species diversity, which are critical in maintaining network cohesion. Because small fragments are more susceptible to other anthropogenic disturbances such as hunting, logging, and myriad edge effects we hypothesize that structural changes promoted by habitat loss have ecological and evolutionary implications for mutualistic networks.

To conclude our study provides strong evidence that forest patch size reduction is reshaping the overall organization of mutualistic networks. We showed the effects of patch size on species richness and highlighted the role of large-bodied obligate frugivorous birds that were preferentially affected. As a consequence, the persistence of plant species with certain functional attributes may be threatened, as indicated by previous studies in different anthropogenic landscapes (Magnago et al. 2014). We also show a nestedness reduction in smaller areas which indicate a decrease in seed dispersal redundancy (Bascompte and Jordano 2007). In smaller forest

patches, the dietary overlap between species is smaller and this may reduce the community resilience against anthropogenic disturbances (Rosenfeld 2002). Moreover, the cohesion of the seed dispersal networks in small fragments depended on few frugivore species, increasing the individual contribution of extant species in propping up the remaining parts of the network together, which in turn increases network susceptibility to collapse. Finally, the degree of frugivory and body mass are strongly related to the effectiveness of the seed dispersal service (Schupp et al. 2010), so our results highlight the importance of conservation strategies focusing on reduction of forest loss to maintain tropical forest functionality.

Acknowledgements – We thank Alessandro de Almeida Pereira for help with data compilation, and Marco A. Mello, Camilla Donatti, Marco A. Pizo, Mariana M. Vidal, Deborah Faria and Esther Sebastián-González for comments on an earlier version of the manuscript.

Funding – Funding provided from Fundação de Amparo à Pesquisa do Estado de São Paulo (2009/54422-8), JAB's PhD studentship was funded by the FAPESB (1492/2013) and CAPES, and CAPES grant (no. 004-2012) awarded to CAP. PRG was supported by CNPq and FAPESP (2017/08406-7). EC was funded by a CNPq fellowship (305812/2015-7). GC was supported by FAPESP (2015/14292-9).

References

- Albert, R. et al. 2000. Error and attack tolerance of complex networks. – *Nature* 406: 378–382.
- Allesina, S. and Tang, S. 2012. Stability criteria for complex ecosystems. – *Nature* 483: 205–208.
- Almeida-Neto, M. et al. 2008. A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. – *Oikos* 117: 1227–1239.
- Bascompte, J. and Jordano, P. 2007. Plant–animal mutualistic networks: the architecture of biodiversity. – *Annu. Rev. Ecol. Evol. Syst.* 38: 567–593.
- Bascompte, J. et al. 2003. The nested assembly of plant–animal mutualistic networks. – *Proc. Natl Acad. Sci. USA* 100: 9383–9387.
- Blanco, G. et al. 2016. Internal seed dispersal by parrots: an overview of a neglected mutualism. – *PeerJ* 4: e1688.
- Bregman, T. P. et al. 2014. Global patterns and predictors of bird species responses to forest fragmentation: implications for ecosystem function and conservation. – *Biol. Conserv.* 169: 372–383.
- Cardoso da Silva, J. M. and Tabarelli, M. 2000. Tree species impoverishment and the future flora of the Atlantic forest of northeast Brazil. – *Nature* 404: 72–74.
- Carlo, T. A. and Morales, J. M. 2016. Generalist birds promote tropical forest regeneration and increase plant diversity via rare-biased seed dispersal. – *Ecology* 97: 1819–1831.
- Cordeiro, N. J. and Howe, H. F. 2003. Forest fragmentation severs mutualism between seed dispersers and an endemic African tree. – *Proc. Natl Acad. Sci. USA* 100: 14052–14056.
- Costa, L. da F. et al. 2007. Characterization of complex networks: a survey of measurements. – *Adv. Phys.* 56: 167–242.
- de Assis Bomfim, J. et al. 2018. Data from: Local extinctions of obligate frugivores and patch size reduction disrupt the structure of seed dispersal networks. – Dryad Digital Repository, < <http://dx.doi.org/10.5061/dryad.k25rq40> >.
- Dormann, C. F. et al. 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. – *Ecography* 30: 609–628.
- Dunning, J. B. J. 2007. CRC Handbook of avian body masses. – CRC Press.
- Emer, C. et al. 2018. Seed-dispersal interactions in fragmented landscapes—a metanetwork approach. – *Ecol. Lett.* doi:10.1111/ele.12909
- Ewers, R. M. and Didham, R. K. 2006. Confounding factors in the detection of species responses to habitat fragmentation. – *Biol. Rev.* 81: 117–142.
- Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. – *Annu. Rev. Ecol. Evol. Syst.* 34: 487–515.
- Fleming, T. H. and Kress, W. J. 2011. A brief history of fruits and frugivores. – *Acta Oecol.* 37: 521–530.
- Fontúrbel, F. E. et al. 2015. Meta-analysis of anthropogenic habitat disturbance effects on animal-mediated seed dispersal. – *Global Change Biol.* 21: 3951–3960.
- Fortuna, M. A. and Bascompte, J. 2006. Habitat loss and the structure of plant–animal mutualistic networks. – *Ecol. Lett.* 9: 281–286.
- Fox, J. and Weisberg, S. 2011. An R companion to applied regression. – Sage Publications.
- Galetti, M. et al. 2013. Functional extinction of birds drives rapid evolutionary changes in seed size. – *Science* 340: 1086–1090.
- García, D. and Martínez, D. 2012. Species richness matters for the quality of ecosystem services: a test using seed dispersal by frugivorous birds. – *Proc. R. Soc. B* 279: 3106–3113.
- Gentry, A. H. 1988. Changes in plant community diversity and floristic composition on environmental and geographical gradients. – *Ann. Missouri Bot. Gard.* 75: 1.
- Guimarães, P. R. and Guimarães, P. 2006. Improving the analyses of nestedness for large sets of matrices. – *Environ. Model. Softw.* 21: 1512–1513.
- Guimarães Jr, P. R. et al. 2011. Evolution and coevolution in mutualistic networks. – *Ecol. Lett.* 14: 877–885.
- Hagen, M. et al. 2012. Biodiversity, species interactions and ecological networks in a fragmented world. – *Adv. Ecol. Res.* 46: 89–210.
- Herrera, C. M. 1985. Habitat-consumer interactions in frugivorous birds. – In: Cody, M. L. (ed.), *Habitat selection in birds*. Academic Press, pp. 341–365.
- Herrera, J. M. et al. 2011. Regional vs local effects of habitat loss and fragmentation on two plant–animal interactions. – *Ecography* 34: 606–615.
- Hijmans, R. J. et al. 2005. Very high resolution interpolated climate surfaces for global land areas. – *Int. J. Climatol.* 25: 1965–1978.
- Hill, J. K. et al. 2011. Ecological impacts of tropical forest fragmentation: how consistent are patterns in species richness and nestedness? – *Phil. Trans. R. Soc. B* 366: 3265–3276.
- Hill, J. L. and Curran, P. J. 2003. Area, shape and isolation of tropical forest fragments: effects on tree species diversity and implications for conservation. – *J. Biogeogr.* 30: 1391–1403.

- Jordano, P. 1987. Patterns of mutualistic interactions in pollination and seed dispersal: connectance, dependence asymmetries, and coevolution. – *Am. Nat.* 129: 657–677.
- Jordano, P. 2000. Fruits and frugivory. – In: Fenner, M. (ed.), *Seeds: the ecology of regeneration in plant communities*, 2nd ed. CABI Publ., pp. 125–166.
- Jordano, P. et al. 2003. Invariant properties in coevolutionary networks of plant–animal interactions. – *Ecol. Lett.* 6: 69–81.
- Jordano, P. et al. 2007. Differential contribution of frugivores to complex seed dispersal patterns. – *Proc. Natl Acad. Sci. USA* 104: 3278–3282.
- Kissling, W. D. and Schleuning, M. 2015. Multispecies interactions across trophic levels at macroscales: retrospective and future directions. – *Ecography* 38: 346–357.
- Kissling, W. D. et al. 2007. Food plant diversity as broad-scale determinant of avian frugivore richness. – *Proc. R. Soc. B* 274: 799–808.
- Kissling, W. D. et al. 2009. The global distribution of frugivory in birds. – *Global Ecol. Biogeogr.* 18: 150–162.
- Kitamura, S. et al. 2002. Interactions between fleshy fruits and frugivores in a tropical seasonal forest in Thailand. – *Oecologia* 133: 559–572.
- Lees, A. C. and Peres, C. A. 2009. Gap-crossing movements predict species occupancy in Amazonian forest fragments. – *Oikos* 118: 280–290.
- Lehouck, V. et al. 2009. Does landscape structure affect resource tracking by avian frugivores in a fragmented Afrotropical forest? – *Ecography* 32: 789–799.
- Levey, D. J. 1987. Seed size and fruit-handling techniques of avian frugivores. – *Am. Nat.* 129: 471.
- Levins, R. 1970. Extinction. – In: Gerstenhaber, M. (ed.), *Some mathematical problems in biology*. American Mathematical Society, pp. 77–107.
- Lewinsohn, T. M. and Cagnolo, L. 2012. Keystones in a tangled bank. – *Science* 335: 1449–1451.
- MacArthur, R. H. and Wilson, E. O. 1967. *The theory of island biogeography*. – Princeton Univ. Press.
- Magnago, L. F. S. et al. 2014. Functional attributes change but functional richness is unchanged after fragmentation of Brazilian Atlantic forests. – *J. Ecol.* 102: 475–485.
- Magrath, A. et al. 2014. Meta-analysis of the effects of forest fragmentation on interspecific interactions. – *Conserv. Biol.* 28: 1342–1348.
- Markl, J. S. et al. 2012. Meta-analysis of the effects of human disturbance on seed dispersal by animals. – *Conserv. Biol.* 26: 1072–1081.
- McConkey, K. R. et al. 2012. Seed dispersal in changing landscapes. – *Biol. Conserv.* 146: 1–13.
- Mello, M. A. R. et al. 2011. The missing part of seed dispersal networks: structure and robustness of bat–fruit interactions. – *PLoS One* 6: e17395.
- Mello, M. A. R. et al. 2015. Keystone species in seed dispersal networks are mainly determined by dietary specialization. – *Oikos* 124: 1031–1039.
- Moermond, T. C. and Denslow, J. S. 1985. Neotropical avian frugivores: patterns of behavior, morphology, and nutrition, with consequences for fruit selection. – *Ornithol. Monogr.* 36: 865–897.
- Nielsen, A. and Bascompte, J. 2007. Ecological networks, nestedness and sampling effort. – *J. Ecol.* 95: 1134–1141.
- Olesen, J. M. et al. 2007. The modularity of pollination networks. – *Proc. Natl Acad. Sci. USA* 104: 19891–19896.
- Paradis, E. et al. 2004. APE: analyses of phylogenetics and evolution in R language. – *Bioinformatics* 20: 289–290.
- Peres, C. A. 2001. Synergistic effects on amazonian forest vertebrates fragmentation. – *Conserv. Biol.* 15: 1490–1505.
- Pessoa, M. S. et al. 2017. Fruit biomass availability along a forest cover gradient. – *Biotropica* 49: 45–55.
- Pires, M. M. et al. 2014. Reconstructing past ecological networks: the reconfiguration of seed-dispersal interactions after megafaunal extinction. – *Oecologia* 175: 1247–1256.
- Renjifo, L. M. 1999. Composition changes in a subandean avifauna after long-term forest fragmentation. – *Conserv. Biol.* 13: 1124–1139.
- Rezende, E. L. et al. 2007. Non-random coextinctions in phylogenetically structured mutualistic networks. – *Nature* 448: 925–928.
- Ribeiro Jr, P. J. and Diggle, P. J. 2001. geoR: a package for geostatistical analysis. – *R-News* 1: 15–18.
- Rosenfeld, J. S. 2002. Functional redundancy in ecology and conservation. – *Oikos* 98: 156–162.
- Saavedra, S. et al. 2011. Strong contributors to network persistence are the most vulnerable to extinction. – *Nature* 478: 233–235.
- Sabatino, M. et al. 2010. Direct effects of habitat area on interaction diversity in pollination webs. – *Ecol. Appl.* 20: 1491–1497.
- Säterberg, T. et al. 2013. High frequency of functional extinctions in ecological networks. – *Nature* 499: 468–470.
- Sazima, C. et al. 2010. What makes a species central in a cleaning mutualism network? – *Oikos* 119: 1319–1325.
- Scheiner, S. M. 2003. Six types of species–area curves. – *Global Ecol. Biogeogr.* 12: 441–447.
- Schleuning, M. et al. 2011. Specialization and interaction strength in a tropical plant–frugivore network differ among forest strata. – *Ecology* 92: 26–36.
- Schleuning, M. et al. 2014a. At a loss for birds: insularity increases asymmetry in seed-dispersal networks. – *Global Ecol. Biogeogr.* 23: 385–394.
- Schleuning, M. et al. 2014b. Ecological, historical and evolutionary determinants of modularity in weighted seed-dispersal networks. – *Ecol. Lett.* 17: 454–463.
- Schupp, E. W. et al. 2010. Seed dispersal effectiveness revisited: a conceptual review. – *New Phytol.* 188: 333–353.
- Sebastián-González, E. 2017. Drivers of species role in avian seed-dispersal mutualistic networks. – *J. Anim. Ecol.* 38: 42–49.
- Sebastián-González, E. et al. 2015. Macroecological trends in nestedness and modularity of seed-dispersal networks: human impact matters. – *Global Ecol. Biogeogr.* 24: 293–303.
- Sugiura, S. 2010. Species interactions–area relationships: biological invasions and network structure in relation to island area. – *Proc. R. Soc. B* 277: 1807–1815.
- Tella, J. L. et al. 2015. Parrots as overlooked seed dispersers. – *Front. Ecol. Environ.* 13: 338–339.
- Thébault, E. and Fontaine, C. 2010. Stability of ecological communities and the architecture of mutualistic and trophic networks. – *Science* 329: 853–856.
- Trøjelsgaard, K. et al. 2013. Island biogeography of mutualistic interaction networks. – *J. Biogeogr.* 40: 2020–2031.

- Turner, I. M. et al. 1996. The conservation value of small, isolated fragments of lowland tropical rain forest. – *Trends Ecol. Evol.* 11: 330–333.
- Valiente-Banuet, A. et al. 2015. Beyond species loss: the extinction of ecological interactions in a changing world. – *Funct. Ecol.* 29: 299–307.
- Vidal, M. M. et al. 2013. Large vertebrates as the missing components of seed–dispersal networks. – *Biol. Conserv.* 163: 42–48.
- Vidal, M. M. et al. 2014. Frugivores at higher risk of extinction are the key elements of a mutualistic network. – *Ecology* 95: 3440–3447.
- Watts, D. J. and Strogatz, S. H. 1998. Collective dynamics of “small-world” networks. – *Nature* 393: 440–442.
- Wotton, D. M. and Kelly, D. 2011. Frugivore loss limits recruitment of large-seeded trees. – *Proc. R. Soc. B* 278: 3345–3354.

Supplementary material (Appendix ECOG-03592 at < www.ecography.org/appendix/ecog-03592 >). Appendix 1.