

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/338871397>

Urbanization homogenizes the interactions of plant–frugivore bird networks

Article in *Urban Ecosystems* · June 2020

DOI: 10.1007/s11252-020-00927-1

CITATIONS

61

READS

1,669

10 authors, including:



Israel Schneiberg

Federal University of Paraná

2 PUBLICATIONS 84 CITATIONS

[SEE PROFILE](#)



Mariano Devoto

University of Buenos Aires

60 PUBLICATIONS 1,749 CITATIONS

[SEE PROFILE](#)



Vinicius Marcilio-Silva

North Dakota State University

26 PUBLICATIONS 2,042 CITATIONS

[SEE PROFILE](#)



Milton Cezar Ribeiro

São Paulo State University

356 PUBLICATIONS 11,270 CITATIONS

[SEE PROFILE](#)

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/338871397>

Urbanization homogenizes the interactions of plant–frugivore bird networks

Article in *Urban Ecosystems* · January 2020

DOI: 10.1007/s11252-020-00927-1

CITATIONS

0

READS

207

10 authors, including:



Israel Schneiberg

Universidade Federal do Paraná

1 PUBLICATION 0 CITATIONS

[SEE PROFILE](#)



Danilo Boscolo

University of São Paulo

53 PUBLICATIONS 741 CITATIONS

[SEE PROFILE](#)



Mariano Devoto

Universidad de Buenos Aires

39 PUBLICATIONS 849 CITATIONS

[SEE PROFILE](#)



Vinicius Marcilio-Silva

Colégio Militar de Curitiba

11 PUBLICATIONS 93 CITATIONS

[SEE PROFILE](#)

Some of the authors of this publication are also working on these related projects:



Landscape Detectives [View project](#)



LS Apps - Tools for assessing landscape connectivity and exploring their effects on biodiversity [View project](#)



Urbanization homogenizes the interactions of plant-frugivore bird networks

Israel Schneiberg^{1,2} • Danilo Boscolo³ • Mariano Devoto⁴ • Vinicius Marcilio-Silva^{1,5} • Cilmar Antônio Dalmaso⁶ • John Wesley Ribeiro⁷ • Milton Cezar Ribeiro⁷ • André de Camargo Guaraldo¹ • Bernardo Brandão Niebuhr⁷ • Isabela Galarda Varassin^{1,2}

© Springer Science+Business Media, LLC, part of Springer Nature 2020

Abstract

Anthropogenic activities are the main cause of habitat loss and fragmentation, which directly affects biodiversity. Disruption in landscape connectivity among populations may affect complex interactions between species and ecosystem functions, such as pollination and seed dispersal, and ultimately result in secondary extinctions. Urbanization, one of the most intense forms of landscapes changes, has been reported to negatively affect bird and plant diversity. Still, little is known about the effects of urban landscapes on interaction networks. We investigated the relationship between urban landscape structure and plant-frugivore networks at different spatial scales. Coupling interaction data from urban areas and a model selection approach, we evaluated which landscape factors best explained the variation in urban networks properties. Our results indicate that urbanization decreases bird richness, mainly through the loss of habitat specialist species, which results in networks being composed mainly of birds well adapted to urban dwelling. We found that interaction evenness, a measure of homogeneity of interaction distribution between species, increases with urbanization. This is due to the strong dominance that generalist birds had in network composition because they foraged on all available fruits, including exotic plants. The ensuing homogenization of interactions can reduce the resilience of networks and affect the efficiency of ecosystems functions. Thus, urbanization plans should consider the proportion and distribution of green areas within cities, coupling human and ecosystem wellbeing.

Keywords Landscape ecology · Mutualistic network · Urban environmental

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s11252-020-00927-1>) contains supplementary material, which is available to authorized users.

✉ Israel Schneiberg
israelschneiberg@gmail.com

Danilo Boscolo
danilo.boscolo@usp.br

Mariano Devoto
mdevoto@agro.uba.ar

Vinicius Marcilio-Silva
viniciuschms@gmail.com

Cilmar Antônio Dalmaso
cilmard@gmail.com

John Wesley Ribeiro
jw.ribeiro.rc@gmail.com

Milton Cezar Ribeiro
miltinho.astronauta@gmail.com

André de Camargo Guaraldo
ac@guaraldo.bio.br

Bernardo Brandão Niebuhr
bernardo_brandaum@yahoo.com.br

Isabela Galarda Varassin
isagalarda@gmail.com

Extended author information available on the last page of the article

Introduction

Anthropogenic activities affect ecosystems across the world, causing habitat loss and fragmentation which results in biodiversity loss (Vitousek et al. 1997; Newbold et al. 2015). One of the main results of these activities is the conversion of natural areas to human-modified landscapes, such as urban and agricultural areas. The response of each species to the loss of natural areas may vary according to its niche requirements (Ferraz et al. 2007) and dispersal ability (Martin et al. 2016). Local factors such as patch size and patch quality may affect species persistence in a given area (Hodgson et al. 2011; Beninde et al. 2015), while landscape elements such as the environment between natural areas or the presence of ecological corridors may constrain or enhance species movement through the landscape (Fahrig 2003; Niebuhr et al. 2015; Fletcher et al. 2018). These changes in both landscape configuration and composition have several consequences for the presence and abundance of species (Tscharntke et al. 2002; Haddad et al. 2015). Not only is the persistence of species put at risk through landscape changes, the interaction between species may also be disrupted (Hagen et al. 2012; Valiente-Banuet et al. 2014; Emer et al. 2018), which affects ecological processes at multiple spatial scales (Cushman and McGarigal 2004; McConkey et al. 2012; Galetti et al. 2013).

Urbanization is one of the most aggressive and rapidly expanding forms of landscape change (McKinney 2002; McPhearson et al. 2016; Zhao et al. 2016). The process of urbanization is characterized by an intense transformation of the landscape's biophysical structure (Alberti 2008; McPhearson et al. 2016), resulting in a reduction and fragmentation of natural areas (Liu et al. 2016). These changes in landscapes affect the movement of species (Pena et al. 2017) and decrease biotic diversity (Marzluff and Ewing 2001). This includes birds, which are well studied in urban environments because they are easy to see and perform important ecosystem services such as pollination and seed dispersal (Beissinger and Osborne 1982; Bregman et al. 2014). There is a consensus that urbanization leads to a decrease in species richness in urban areas (Crooks et al. 2004; Garaffa et al. 2009; Meffert and Dziok 2013) and to an increase in the density of some well-adapted species (Marzluff and Ewing 2001). This may lead to biotic homogenization in urban areas (McKinney 2006; Garaffa et al. 2009; Vallejos et al. 2016). It can be thus expected that ecosystem services provided by birds (e.g. seed dispersal) in urban forest patches will be greatly impacted due to a reduction of more sensible species, such as obligate frugivorous and habitat specialists species (Bregman et al. 2014; Mello et al. 2015). Despite this, the impacts of urbanization on species interactions and ecological processes have seldom been the focus of the ecological literature.

Biodiversity patterns and ecological processes arise from interactions between the elements of ecosystems (Norris 2012). Therefore, the persistence of a species may depend on the presence of other species with which it interacts and on the possibility of encounters between them (Fortuna and Bascompte 2006; Tylianakis and Morris 2017). In this context, the approach of interaction networks allows the description of interactions between multiple species (Blüthgen 2010), as well as the comparison of interaction patterns among communities (Blüthgen et al. 2006). It is thus possible to predict the anthropogenic effects on interactions loss (Tylianakis et al. 2007; Valiente-Banuet et al. 2014), in addition to providing valuable information for the conservation of mutualistic interactions and ecological processes (Tylianakis et al. 2010; Devoto et al. 2012; Ribeiro da Silva et al. 2015).

Given the fast-paced landscape changes and urban growth worldwide (Seto et al. 2012), there is a growing need for assessments of the effects of anthropogenic activities on the properties of interactions networks, particularly in urban and altered landscapes (Geslin et al. 2013; Ferreira et al. 2013; Rodewald et al. 2014). Here we investigated the impacts of changes on the structure of plant-frugivore networks across a gradient of local and landscape level anthropogenic changes (i.e. habitat loss and fragmentation) of Atlantic Forest remnants in urban landscapes. This is especially informative given that the Brazilian Atlantic Forest is one of the world's biodiversity hotspots, which shelters more than 120 million people in urban areas (Pinto et al. 2014). We expected urban landscapes to shape network properties in many ways. First, we expected a decrease in bird richness and an increase in bird diet breadth with increasing urbanization, which results in a network dominated by generalist species, i.e. species with many partners and with overlapping interactions. Second, due to a decrease in bird richness, mainly caused by the loss of habitat specialist species, i.e. forest specialist species, we expected a network dominated by abundant species that can move across heterogeneous landscapes. We thus expected a decrease in complementary specialization (H_2') and weighted nestedness ($WNODF$) and an increase interaction evenness (IE) (Fig. 1). Understanding interactions in this context may have important consequences for urban landscape planning and the conservation of species and ecosystem services in cities and urbanized ecosystems.

Material and methods

We recorded plant-frugivore interactions in seven forest patches embedded in the urban matrix of the city of Curitiba (25°45'S, 49°25'W), Paraná, in Southern Brazil, with a population reaching two million inhabitants (IBGE 2018) (Fig. 2,

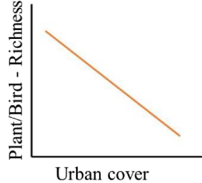
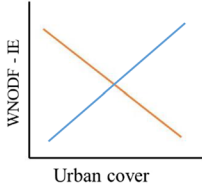
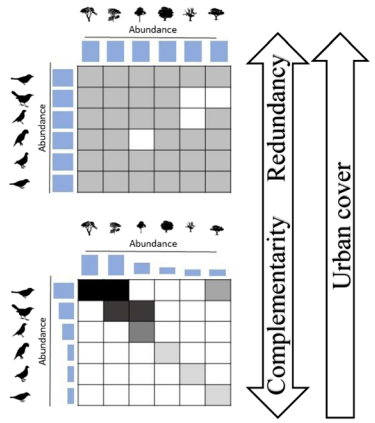
Hypothesis	Description	Expected Results
H1	Plant/Bird richness decrease within forest patches in landscapes with higher urban cover.	
H2	The lack of habitat/diet specialists in more urbanized area contributes to a decrease in nestedness (<i>WNODF</i>) – red line. Also, some species interact in higher frequencies than others, the dominance of generalist species in landscapes with higher urban cover leads to networks with high interaction evenness (<i>IE</i>) – blue line.	
H3	Complementary specialization (H_2') in urban landscapes is mainly affected by species abundance. Landscapes with higher urban cover are home to species with similar abundances. These species exhibit overlap in interactions (low H_2'). On the other hand, landscapes with higher forest cover show differences in frequencies of interactions. This pattern is influenced by the difference in species abundance, which results in low overlap of interactions (high H_2').	

Fig. 1 Representation of three hypotheses, with their respective description and expected results

Supplementary material Appendix 1 Fig. A1). The sampled patches were remnants of *Araucaria* Forest (i.e. mixed ombrophilous forest), within the Brazilian Atlantic Forest biome, and varied in size, quality (see below), and surrounding forest cover (Fig. 2). Our selection criteria were: (a) forest patches fragments larger than 3.3 ha and (b) safe places (i.e. places where the observer was not at risk due to the presence of robbers or other dangerous situations). According to these criteria, we could select seven sampling units. The city of Curitiba is dominated by an urban matrix (61% of the area) that limits the movement of many of the native bird species (Tremblay and St. Clair 2011; Concepción et al. 2015), but also includes forest (19%) and non-forest natural areas 18% (i.e. grasslands, shrublands) (Supplementary material Appendix 1, Fig. A1). The altitude varies between 910 and 979 m, and the climate is subtropical humid, with no dry season and hot summers (Peel et al. 2007). We sampled vegetation structure variables and the frequency of plant-frugivore interactions for each forest patch. Using in situ information, remote sensing, and mapping tools, we calculated patch quality and the structural and functional metrics of the landscape, as well as plant-frugivore network metrics.

Patch quality

Within each forest patch, we sampled trees in three plots of 10×20 m. Within these plots, we sampled shrubs in a plot of 5×5 m. We registered all trees with diameter at breast height > 4.5 cm and all shrubs higher than 1.30 m. We distributed the plots in 40 m distance from each other along a transect of 180 m, located at the center of each forest.

We measured the plant height (PH) and the diameter at breast height (DBH) for trees, and the basal diameter (BD) for shrubs for each plant inside the plots. Plant height was measured using a laser rangefinder, model Bosch GLM 40.

We developed an environmental quality index (Q) to consolidate different aspects of the environmental quality of each forest patch into a single metric (see Supplementary material Appendix 1, Text A1). This index considered 10 parameters related to different aspects of environmental quality, such as species richness, tree density, evolutionary distinction (Supplementary material Appendix 1, Table A1), and ranged from 0 to 1, indicating locations with low to high relative quality, respectively.

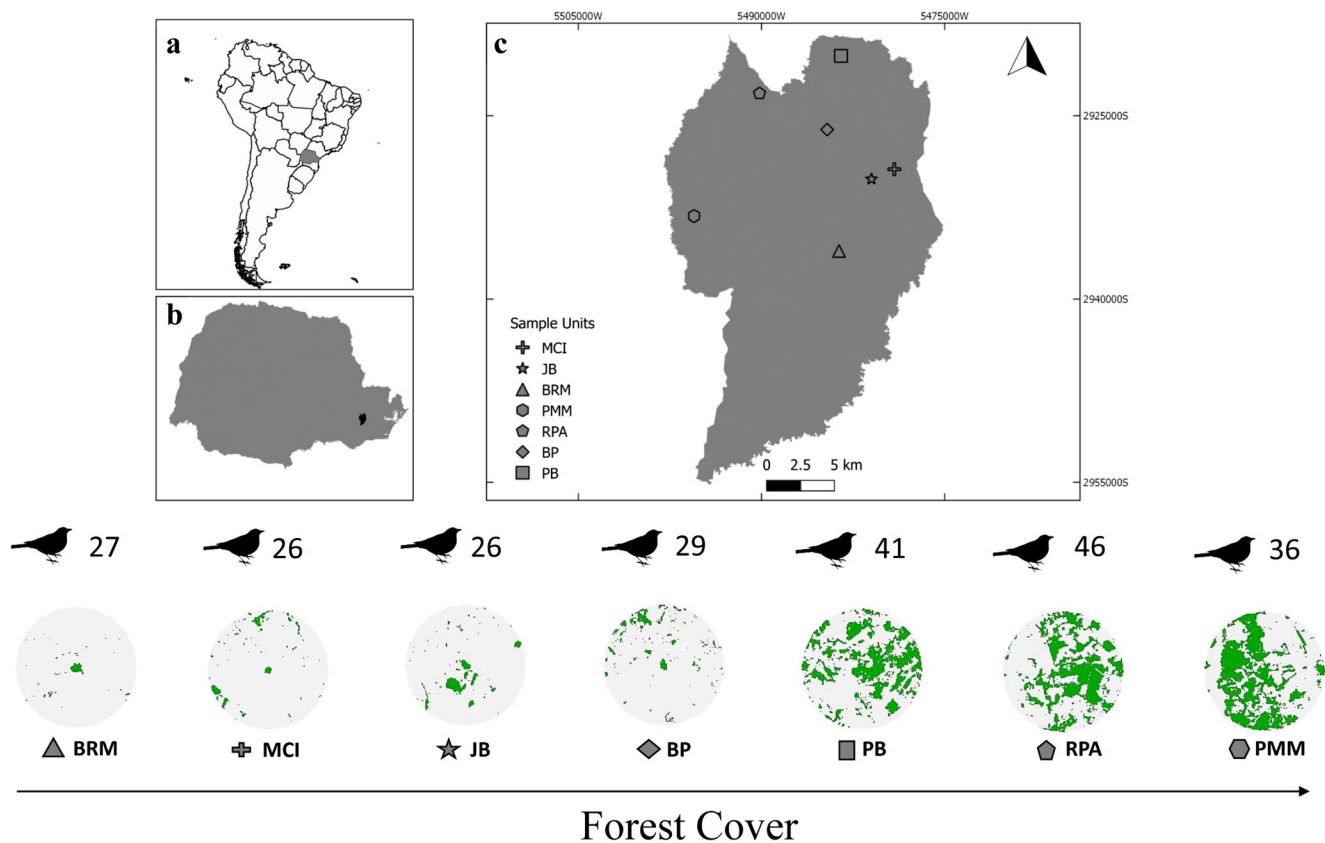


Fig. 2 Location of the sampled forest patches at Curitiba, southern Brazil (a to c). **a** represents South America. **b** Paraná state and Curitiba city (black area). **c** Sampled forest patches highlighted (symbols) within

Curitiba urban area. Forest cover around each forest patch, located in its center, in a 2000 m radii landscape; the number of total bird richness is shown above of each landscape

Bird records and interaction sampling

To investigate whether there were changes in bird species along a gradient of urbanization, we recorded all bird species (i.e. total bird richness) at each forest patch (i.e. even those not interacting with fruits). We performed bird sampling using the point count method, a traditional and commonly technique used to assess forest species (Sutherland et al. 2004). To this end, we recorded two 15-min points in the center of the forest patch, one at the beginning and the other at the end of interaction records. Besides that, we added to our species list any new species heard or seen during the interaction records.

In addition to bird species composition, we sampled plant-frugivore interactions along a 180x10m transect located at the center of each forest patch. We sampled interactions from October 2015 to May 2016, which is the period of peak fruit production in *Araucaria* Forest (Marques et al. 2004). We choose one individual per fruiting plant species for focal observations. Frugivorous interactions with fruiting trees were recorded with binoculars (8 × 42) for 50 min per individual species, between 07:00 and 14:00 by one expert ornithologist (see Supplementary material Appendix 1, Table A2 for sampling effort). The differences in sampling effort between the sites (20 h – 67 h) resulted from the availability of fruit-

bearing species. We checked then for the difference in sampling effort with the help of sampling effort curves adapted for interaction networks (Chacoff et al. 2012). We used the accumulated number of interactions to construct the interaction frequency matrix for each forest patch. The dependence of birds on fruits was described based on the different proportions of fruits in their diets, following Wilman et al. (2014) (see Supplementary material Appendix 1, Table A3). We defined an interaction whenever a bird was observed consuming fruits at a given plant, from the time it started foraging on the fruits until it left the plant.

Network properties

We calculated interaction network metrics using weighted data (interaction frequency) since they are more robust to sampling bias (Blüthgen et al. 2006; Dormann et al. 2009a; Devoto et al. 2012). Some of the possible metrics to be used in interaction networks studies are especially important because of their ecological relevance and their sensitivity to environmental variations (Tylianakis et al. 2010; Devoto et al. 2012; Soares et al. 2017). We calculated interaction evenness (IE), weighted nestedness (WNODF) and complementary specialization (H_2'). All metrics were calculated using the

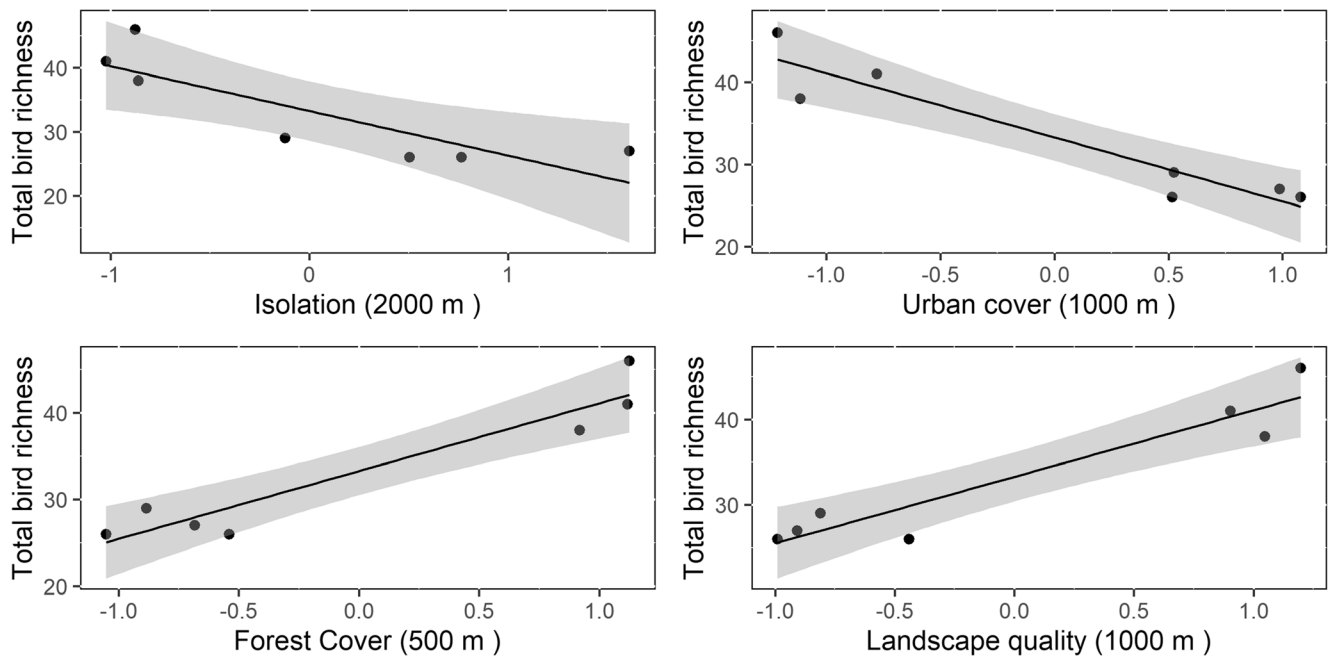


Fig. 3 Bird richness in urban landscapes at forest patches at Curitiba decreases with **a** the isolation between forest patches and **b** urban cover and increases with **c** forest cover and **d** landscape quality. The x-axis corresponds to the standardized values

bipartite package version 2.08 (Dormann et al. 2009) in the R 3.3.1.

Interaction evenness reflects homogeneity in the distribution of interactions across species in the network. Interaction evenness was calculated as the Shannon diversity of interactions divided by the natural logarithm of interaction richness (Blüthgen et al. 2006). Interaction evenness values range from 0, when there is a heterogeneous distribution of interactions (variation in interaction frequencies) to 1, when there is a perfectly homogeneous distribution (Sakai et al. 2016).

Weighted nestedness is a measure of interaction asymmetry that arises when less connected species are a subset of the core of highly connected species (Almeida-Neto and Ulrich 2011). Highly nested networks have been shown to be robust to disturbances because there is a core of generalist plants and animals to which all the species are connected (Bascompte and Jordano 2007; Burgos et al. 2007). Nestedness also reduces competition if there are enough shared interactions (Bastolla et al. 2009). Nestedness values range from 0 (non-nested network) to 100 (highly nested network).

Complementary specialization (H_2') measures interaction selectivity, defined as an interaction pattern that departs from what can be expected based on relative species abundances, and quantifies niche partitioning among them. This metric is useful in network comparisons because it is not affected by network size or sampling effort (Blüthgen et al. 2006). Complementary specialization values range from 0 (complementarity) to 1 (exclusiveness) for interactions.

Landscape metrics

We used a Landsat 8 image with 30 m resolution (bands green, red, and blue) collected on 11/11/2013 for mapping land use (Supplementary material Appendix 1, Fig. A1). Geometric grid corrections and supervised classification were performed through the QGIS software, version 2.16, using the Georeferenced and Semi-Automatic Classification Plugins. Land use classification considered seven classes: forest, urban areas, vegetation (e.g. grass, shrubs), bare ground, water, shadow, and clouds, using a maximum likelihood algorithm. We evaluated classification accuracy using a kappa index and error matrix. The overall accuracy of the classification was greater than 90% and the kappa coefficient was 0.86. The classification accuracy of each land class was over 85%.

We calculated five landscape structural metrics to investigate the relationship between landscape structure, plant and bird richness and the properties of the frugivory networks: number of fragments, forest cover and urban cover, landscape quality (i.e. sum of forest cover and vegetation cover) and isolation (i.e. mean distance to the nearest neighbor patch) (Supplementary material Appendix 1, Table A4). These metrics reflect landscape composition and configuration (Fahrig 2003; Boscolo and Metzger 2009), and are expected to affect the presence of plants and birds and the interactions between species (Hagen et al. 2012). Landscape structural metrics were calculated from the land use map using Fragstats 4.2. We calculated landscape metrics at three spatial extents (radius of 500 m, 1000 m and 2000 m around the central point of the sampled transects) in a multiple-scale approach.

Identification of the appropriate extent is important because landscape structure affects species and ecological processes at different spatial scales (Boscolo and Metzger 2011; Jackson and Fahrig 2015; Miguet et al. 2016). Previous studies have reported that these extents are considered sufficient to analyze the movement of birds from a landscape perspective (Hostetler and Holling 2000; Boscolo and Metzger 2009; Suarez-Rubio et al. 2013). The scales of effect between each landscape predictor and each response variable were assessed through the coefficient of determination of the univariate regression models relating each predictor-response pair (Miguet et al. 2016). This multiscale approach showed that the predictor variables affect different ecological response variables at different scales. The model selection analysis presented below therefore considered only the scales of effect for each pair of predictor-response variables. Because the range of absolute values of all landscape metrics varied, each metric was centered to zero and scaled by subtracting its mean value and dividing it by its standard deviation (see Data Analysis below).

We complemented the landscape structural metrics with a measure of landscape functional connectivity. We simulated Multiple Least Cost Corridors (MLCC) for each landscape that could be used by birds to move across space, using the package LSCorridors (Ribeiro et al. 2017). LSCorridors generate Multiple Least Cost Corridors (MLCC), which is a set of multiple corridors between pairs of locations of interest, with the possibility of adding stochastic variation in the landscape resistance to the movement of animals (Ribeiro et al. 2017). LSCorridors requires two maps: a resistance map and a source-target map. The resistance map may be created by assigning values of resistance to movement (or permeability) to each class in the land use map. In this way, pixels with low/high resistance values represent a higher/lower likelihood of animal movement within the landscape (Adriaensen et al. 2003). To estimate the resistance values, we used expert knowledge (i.e. direct consultation to experts) which is reported to contribute valuable information as well as to fill in gaps and uncertainties regarding habitat use and physiological requirements (Perera et al. 2012). Because our focus was on plant-frugivore networks, we focused on the ability of the landscapes to offer fruits as a *proxy* for landscape resistance. The average resistance values were thus assessed by directly consulting 13 ornithology specialists (see Acknowledgements), who scored each environment type in the land use map based on their ability to offer fruits, on a range from 1 (little probability of offering fruits) to 100 (a high probability of offering fruits). Other factors such as predation risk and disturbance may also affect resistance to movement, and different species may respond differently to these factors (Morales et al. 2010; Leblond et al. 2013; Doherty and Driscoll 2018). On this basis, we then considered that environments with more fruit resources were more prone to be

visited by birds so that the movement likelihood through these environments was higher and their resistance lower. Finally, we averaged the resistance value of the classes evaluated by the experts to create a final resistance surface map.

We generated 30 random spatial locations within forest patches (the source-target points) and simulated 100 corridors between each of them. We did not use the multiple-scale approach for simulating corridors because the large scale confers a wider range of movement and more accurate information over landscape permeability. All corridors were thus simulated within the 2000 m buffer. For more details, see Supplementary material Appendix 1 Text A2, Fig. A2. For each corridor, we recorded the Euclidean distance between the source and target locations and its functional cost, defined as the sum of the resistance of all pixels crossed by the corridor. We then calculated the functional connectivity index as:

$$CI = \frac{mED}{mFC} \quad (1)$$

The functional connectivity index (CI) results from the combination of the mean functional cost (mFC) and mean Euclidean distance (mED), averaged over all pairs of source-target points within a landscape.

Data analysis

Due to the complexity of the relationships between landscape structural and functional connectivity and patch quality, the predictor variables, and the properties of interaction networks, as well as plant/bird richness, the response variables, we compared the multiple competing hypotheses using a maximum likelihood model selection approach and a selection criterion corrected for small sample sizes (Akaike Information Criterion - AICc). We checked for multicollinearity between predictor variables using the Pearson correlation and removed variables with strong collinearity ($R > 0.7$) (Supplementary material Appendix 1, Table. A5). To select the spatial extent at which each landscape metric best predicted network properties, we performed univariate fits for each metric and extent, and selected the extent with the highest coefficient of determination (R^2) (Boscolo and Metzger 2009; Jackson and Fahrig 2015; Moreira et al. 2015). We modeled networks and plant and bird richness responses to explanatory factors using generalized linear models (GLM) with Gaussian (weight nestedness, interaction evenness and complementary specialization) or Poisson (plant and bird richness and network size) error distributions depending on the nature of the response variables (see Supplementary material Appendix 1, Table A6, for a complete list of models tested). The difference in the AICc value between a given model and the most parsimonious model ($\Delta AICc$) and the weight of evidence (w_i) was calculated for each model. Models with high (w_i) indicate a

Table 1 Generalized linear models testing the effects of landscape structure on network properties and plant/bird richness

Response/predictor variable	ΔAICc	Weight (w_i)	Parameters	R^2	Estimate
a) Interaction Evenness					
Urban cover (500)	0	0.62	3	0.81	0.04
Landscape quality (1000)	3.11	0.13	3	0.66	−0.03
No effect model	3.83	0.09	2	—	—
b) WNODF					
No effect model	0	0.44	2	—	—
Number of forest patches (1000) + Forest cover (1000)	1.45	0.21	4	0.86	−0.83
Number of forest patches (1000) + Landscape quality (1000)	3.45	0.07	4	0.85	−8.78
					10.24
c) Complementarity Specialization (H_2')					
No effect model	0	0.72	2	—	—
Patch quality (local)	4.97	0.06	3	0.25	−1.740
Urban cover (500)	5.09	0.05	3	0.24	−0.002
d) Total Bird Richness					
Urban cover (1000)	0	0.26	3	0.91	−0.23
Landscape quality (1000)	0.03	0.26	3	0.90	0.23
Forest cover (500)	0.24	0.23	3	0.90	0.34
Isolation (2000)	1.76	0.10	3	0.76	−0.22
Functional connectivity (2000)	5.78	0.01	3	0.41	5.32
e) Total Plant Richness					
Functional connectivity (2000)	0	0.28	3	0.46	0.13
No effect model	1.12	0.16	2	—	—
Number of forest patches (2000)	1.14	0.16	3	0.36	7.26

The most parsimonious models, with $\Delta\text{AICc} < 2$, are shown in bold. The numbers in parenthesis indicate the best scale of effect for each variable

higher probability of presenting plausible explanations to the observed phenomena. Models with $\Delta\text{AICc} < 2$ were considered equally plausible. Model selection analyses were performed using the “AICcmodavg” package in R 3.3.1.

All code and data are available in the GitHub repository: https://github.com/LEEClab/ms_Schneiberg_etal_Urban_networks.

Results

We registered 73 bird species in all seven sampling units (Supplementary material Appendix 1, Table A7). Total bird richness was higher in landscapes with more forest cover within a 500 m extent ($\Delta\text{AICc} < 2$, $w_i = 0.24$) and landscape quality within 1000 m extent ($\Delta\text{AICc} < 2$, $w_i = 0.26$). Conversely, total bird richness decreased as the urban cover ($\Delta\text{AICc} < 2$, $w_i = 0.26$) and isolation increased ($\Delta\text{AICc} < 2$, $w_i = 0.11$), within 1000 m and 2000 m respectively (Figs. 2 and 3). The total plant richness was related to landscape structure across spatial scales, more specifically with functional connectivity within 2000 m and number of patches within

2000 m. However, no effect model was equally plausible, bringing uncertainty to these landscape factors (Table 1).

Overall, we recorded 313 interaction events between 21 bird species and 25 plant species. Three bird species were recorded in all networks and encompassed 70% of all interactions: *Turdus rufiventris* (135 interactions), *Thraupis sayaca* (60 interactions) and *Elaenia mesoleuca* (28 interactions) (Table 2). All the species recorded were facultative frugivores except *Procnias nudicollis*, a specialist species of obligate frugivores recorded at Parque Barreirinha (BP), a location that is among the landscapes with the highest proportion of forest cover. No plant species were recorded in all networks, however, *Ilex paraguariensis* (49 interactions) had the highest number of visits, followed by *Casearia decandra* (38 interactions), *Cabralea canjerana* (30 interactions), *Schinus terebinthifolia* (27 interactions), *Matayba elaeagnoides* (25 interactions), *Myrcia hatschbachii* (21 interactions) and *Eugenia uniflora* (20 interactions), which altogether represented 66% of the interactions. We found two exotic plant species, *Hovenia dulcis* and *Pittosporum undulatum*.

In general, the networks were small, nested and had few interactions (Fig. 4). The sampling effort curves of interactions showed that all networks were well sampled and

Table 2 List of plant and bird codes used in Fig. 4

Code	Plant	N° interactions	Code	Bird	N° interactions
T4	<i>Ilex paraguariensis</i>	49	B11	<i>Turdus rufiventris</i>	135
T2	<i>Casearia decandra</i>	38	B8	<i>Thraupis sayaca</i>	60
T1	<i>Cabralea canjerana</i>	30	B6	<i>Pitangus sulphuratus</i>	29
T22	<i>Schinus terebinthifolius</i>	27	B3	<i>Elaenia mesoleuca</i>	28
T5	<i>Matayba elaeagnoides</i>	25	B9	<i>Turdus flavipes</i>	18
T10	<i>Myrcia hatschbachii</i>	21	B4	<i>Pachyrhamphus castaneus</i>	8
T13	<i>Eugenia uniflora</i>	20	B1	<i>Cacicus haemorrhous</i>	5
T9	<i>Ficus luschnathiana</i>	19	B10	<i>Turdus leucomelas</i>	5
T3	<i>Casearia sylvestris</i>	15	B13	<i>Patagioenas picazuro</i>	4
T16	<i>Nectandra lanceolata</i>	13	B16	<i>Turdus amaurochalinus</i>	4
T17	<i>Ocotea puberula</i>	13	B14	<i>Saltator similis</i>	3
T11	<i>Nectandra megapotamica</i>	11	B18	<i>Myiodynastes maculatus</i>	3
T24	<i>Banara parviflora</i>	6	B5	<i>Penelope obscura</i>	2
T7	<i>Pittosporum undulatum</i>	4	B7	<i>Procnias nudicollis</i>	2
T12	<i>Allophylus edulis</i>	3	B12	<i>Tyrannus melancholicus</i>	2
T21	<i>Annona rugulosa</i>	3	B21	<i>Chiroxiphia caudata</i>	2
T23	<i>Allophylus petiolulatus</i>	3	B2	<i>Cyanocorax chrysops</i>	1
T6	<i>Pimenta pseudocaryophyllus</i>	2	B15	<i>Tangara preciosa</i>	1
T8	<i>Psychotria vellosiana</i>	2	B17	<i>Colaptes melanochloros</i>	1
T18	<i>Myrcia splendens</i>	2	B19	<i>Thraupis bonariensis</i>	1
T20	<i>Hovenia dulcis</i>	2	B20	<i>Thlypopsis sordida</i>	1
T14	<i>Gymnanthes klotzschiana</i>	1			
T15	<i>Myrtacea sp</i>	1			
T19	<i>Celtis iguanaea</i>	1			
T25	<i>Styrax leprosus</i>	1			

The number of interactions represents the number of frugivory events sampled at forest patches, Curitiba, southern Brazil

presented a saturation trend (Supplementary material Appendix 1, Fig. A3). Interaction evenness was positively related to urban cover within a 500 m radius (Fig. 5, Table 1), which indicated that interaction patterns are more homogeneous in more urbanized landscapes. This model was five times more plausible than the second competing model (Table 1). In contrast, weighted nestedness increased with higher forest cover and decreased with lower number of patches. However, the no effect model was equally plausible and more parsimonious ($\Delta\text{AICc} < 2$), bringing considerable uncertainty to landscape effects on nestedness. Complementary specialization was not affected by landscape structure ($\Delta\text{AICc} > 2$ in comparison to the no effect model).

Discussion

We present the first study to investigate the combined effects of urban landscape structure and patch quality on the properties of urban plant-frugivore networks. We

observed that urban networks are small, nested and dominated by a core of generalist species that interact in similar frequencies. In addition to the prevalence of generalist species, total bird richness decreased and habitat specialist species were locally extinct in more urbanized landscapes. This led to a homogenization of urban bird communities and, as a consequence, of the whole networks. This loss specialized interactions may have cascading effects on the maintenance of some plant species, due to a decline in seed dispersal capability at the community level, and to the efficiency of ecosystems services.

As hypothesized, interaction evenness increased in forest patches with higher urban cover around them. This may be explained by the higher diet generalization of birds feeding on all resources available, coupled with the local extinction of rare and obligate frugivorous species that feed on more specific resources (Kaiser-Bunbury and Blüthgen 2015). Indeed, higher generalism was the driver of higher values of interaction evenness in plant-pollination networks

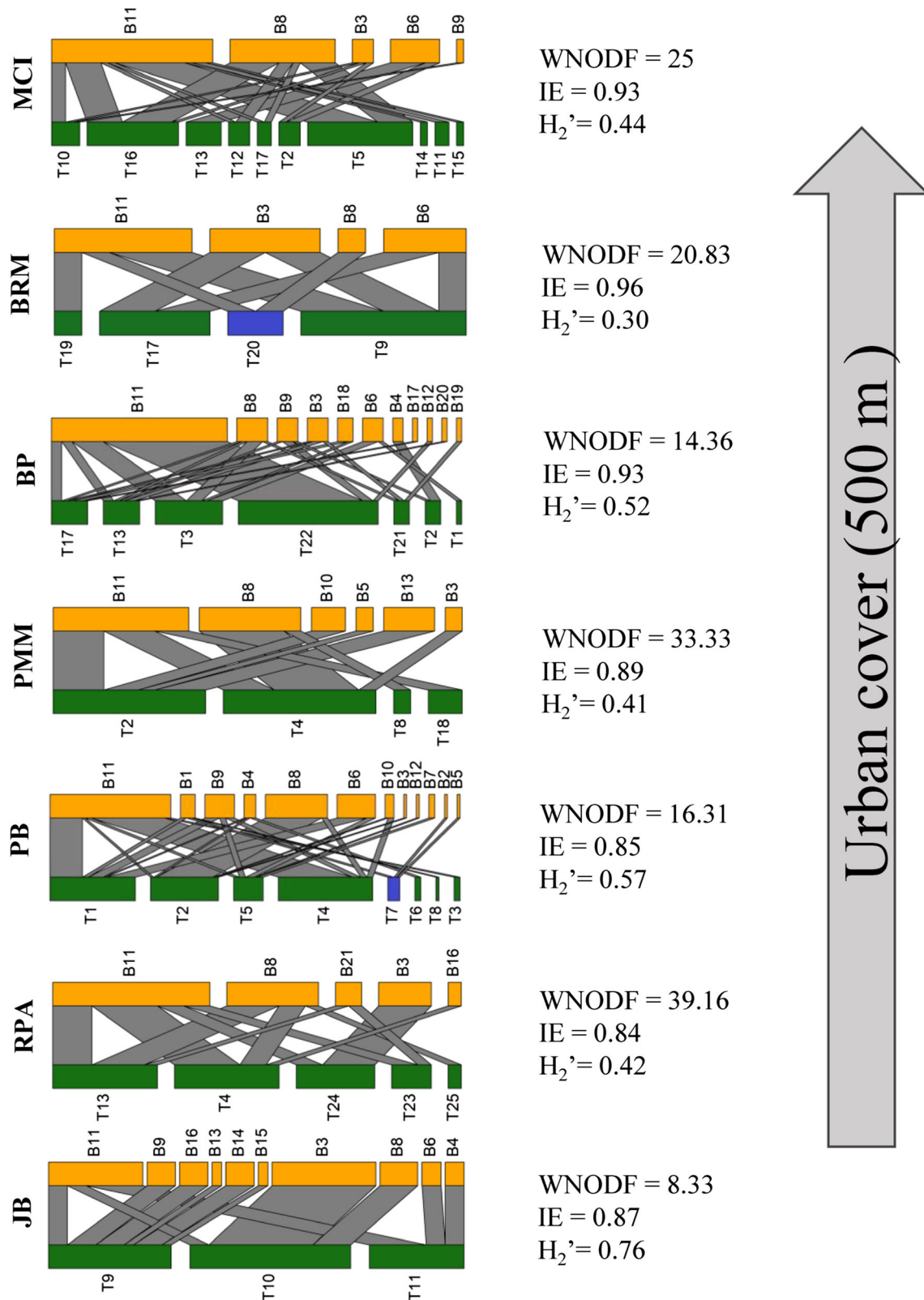
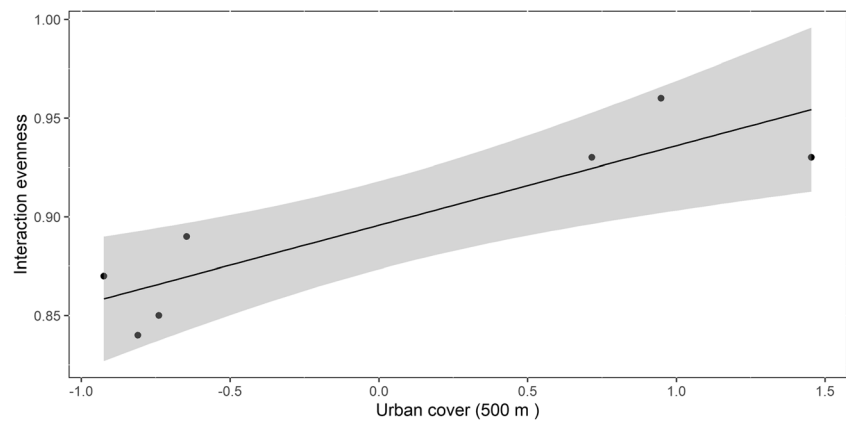


Fig. 4 Quantitative plant-frugivore networks sampled at forest patches, Curitiba, southern Brazil. Plant species and bird species are indicated by green and orange boxes, respectively. The arrow indicates the gradient of urban cover (500 m) in which the networks are inserted. Blue boxes

represent two exotic species of plant (*Pittosporum undullatus*, *Hovenia dulcis*). For abbreviate names of networks and code of plant and bird see Table 2

Fig. 5 Effect of urban cover on interaction evenness in frugivory networks from forest patches, Curitiba, southern Brazil. The values of urban cover are standardized



along a gradient of urbanization (Geslin et al. 2013). The increase in interaction evenness may be due to the attraction of tree fruit production in forest patches. Previous studies showed that the peak of fruit production is related to increasing bird richness (Wolfe et al. 2014) and network complexity (Ramos-Robles et al. 2016) due to the fruit abundance. It is possible that fruiting trees in forest patches in urbanized landscapes are more attractive and more easily accessible than other resources (e.g. invertebrates), thus concentrating the interactions.

The predominance of generalist species in urban networks is consistent with previous studies that investigated the role of urbanization on bird richness (Beissinger and Osborne 1982; Garaffa et al. 2009; Concepción et al. 2015). In more urbanized patches, the networks consisted of birds well adapted to urban landscapes (i.e. broad environmental tolerance and low dietary specificity) (Supplementary material Appendix 1 Table A3), which can move easily across the landscape exploring a wide range of resources (Marzluff et al. 2001). The lack of specialist species in urban landscapes is related to the lack of variety in resources and the low permeability that urban matrices represent to bird movement (Canedoli et al. 2018). Due to the prevalence of generalist species with redundant interactions in urban networks, nestedness, and network specialization were not affected by landscape structures.

Changes in species composition are one of the most important factors altering network structure (Tylianakis and Morris 2017) and are associated with landscape structure (Hagen et al. 2012). The negative effect of urbanization on total bird richness may be associated with the abiotic filtering that urban areas impose on sensitive species (Crocì et al. 2008; Meffert and Dziöck 2013). Several studies have reported a decrease in total bird richness with increasing urbanization (Batten 1972; Marzluff et al. 2001; Gagné and Fahrig 2011) that resulted in compositional similarity between areas (i.e. biotic homogenization) because many habitat specialist species are lost and replaced by a few abundant generalist species which have

strong effects on network properties. On the other hand, forest cover had a positive effect on total bird richness (Fig. 2). Actually, forest cover together with other characteristics of vegetation structure, such as the presence of herbs, shrubs, and trees, have been shown to increase bird richness in urban environments (Beninde et al. 2015). We also recorded two important habitat specialist species *P. nudicollis* and *Cyanocorax caeruleus* (Emer et al. 2018), which are vulnerable and of near-threatened status, respectively (IUCN 2018). They were recorded in areas with higher forest cover, suggesting the effect of forest cover on species composition. Landscapes with higher forest cover offer a greater availability of conditions and resources (Ferreira et al. 2015), which may result in a greater co-occurrence of species that are adapted and species that are more sensitive to urbanization.

Interestingly, one of the areas with the highest forest cover (i.e. Reserva Marco Mazarotto – PMM) (Fig. 2) presented a small network with few birds and few plants (Supplementary material Appendix 1, Table A2). Comparing land use from 1984 and 2016, Google Earth images indicated a great change in the landscape due to the creation of a water reservoir, with the distance of the margins varying from 100 m to 600 m (Supplementary material Appendix 1, Fig. A4). This distance may be sufficient to prevent several bird species that inhabit the left bank of the reservoir from crossing the margins. Large water bodies are known to act as barriers for certain species of birds, preventing movements constrained by body size and dispersal ability (Hayes and Sewlal 2004; Weir et al. 2015). There may thus be a historical effect of land use on the size of this interaction network.

Conclusion

Although our sampling limitations of forest patches in urban areas are inherent to the characteristics of cities (i.e. low forest patch cover), our study was able to demonstrate how the properties of plant-frugivore networks vary across a gradient of

landscape structure and patch quality. On the one hand, patch size and quality can influence the provision of resources, which in turn allows species to persist, resulting in an increase likelihood of colonization in an inhospitable matrix. On the other hand, patch size and quality depend on the spatial arrangement of forest patches and matrix type (Gonzalez et al. 2011). Our results show that urban networks are mainly composed of birds well adapted to urban areas. This has two implications; one is that birds depending on bigger and better patches in a permeable matrix are already locally extinct. The other implication is that for urban exploiters, which can move easily in urban landscapes, their persistence is mostly driven by landscape effects, with minor effects of patch size and quality, which they can easily reach. Therefore, the resulting interactions they establish are distributed over all the remaining patches in the landscape, generating interaction networks that are generalist, with low nestedness values, and were interaction evenness is high.

We have demonstrated that urbanization can act as an environmental filter on the presence of birds and their interaction with fruit plants because only a subset of bird species from the total bird richness is able to persist in more urbanized areas (i.e. less forest cover). Urban networks were therefore composed of birds with a broad environmental tolerance (Bonier et al. 2007; Fontana et al. 2011). Although habitat specialist species are lost in urban landscapes, most generalist species still play a central role in frugivory networks (Martín González et al. 2010; Palacio et al. 2016) and are important for ecological processes such as seed dispersal (Richmond et al. 2005; Mellado and Zamora 2014) and forest regeneration. Although urbanization is characterized by a high frequency of exotic plants, mainly in forest edges (Lapaix et al. 2012), we found only two exotic plants in two networks, which represent 2% of all interactions. However, the homogenization in urban bird communities and the lack of dietary specialization by urban birds can promote the spread of exotic seeds, increasing the chances of invasion by exotic plant species in the long term.

Designing and planning cities to maximize biodiversity levels is challenging, due to frequent and intense landscape changes created by urbanization (Beninde et al. 2015). Small forest patches, public squares, and street arborization can serve as stepping-stones and facilitate the movement of frugivorous generalists in the landscape. Improving patch quality by preserving large trees and ancient remnants and controlling invasive species, may also have a positive effect on ecological interactions.

Acknowledgments We thank Adalberto Penteado, Caio Graco Machado, Fernando Costa Straube, Gabriel De La Torre, James Joseph Roper, Leonardo Deconto, Lilian Manica, Marcel Lemos, Natalia Moretti Rongentta, Rafael Amorin, Tiago Machado de Souza and Vítor de Queiroz Piacentini for defining values of resistance to bird movement. We also thank Marcia Cristina Mendes Marques for critically reading a previous version of this manuscript.

Author contributions IS and IGV conceived the research; IS and CD collected the data; IS, DB, MD, BBN, VMS, CD, JWR, MCR, ACG, IGV analyzed the data; and IS, DB, MD, BBN, IGV wrote the paper.

Funding This study was funded by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES; scholarships to IS, VMS, BBN and CD), by Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq; grant no 445405/2014–7 and PQ scholarships no. 309453/2013–5 and no. 313801/2017–7 to IGV).

References

- Adriaenssens F, Chardon JP, De Blust G et al (2003) The application of 'least-cost' modelling as a functional landscape model. *Landsc Urban Plan* 64:233–247. [https://doi.org/10.1016/S0169-2046\(02\)00242-6](https://doi.org/10.1016/S0169-2046(02)00242-6)
- Alberti M (2008) Advances in urban ecology: integrating humans and ecological processes in urban ecosystems
- Almeida-Neto M, Ulrich W (2011) A straightforward computational approach for measuring nestedness using quantitative matrices. *Environ Model Softw* 26:173–178. <https://doi.org/10.1016/j.envsoft.2010.08.003>
- Bascompte J, Jordano P (2007) Plant-animal mutualistic networks: the architecture of biodiversity. *Annu Rev Ecol Evol Syst* 38:567–593. <https://doi.org/10.1146/annurev.ecolsys.38.091206.095818>
- Bastolla U, Fortuna MA, Pascual-García A et al (2009) The architecture of mutualistic networks minimizes competition and increases biodiversity. *Nature* 458:1018–1020. <https://doi.org/10.1038/nature07950>
- Batten LA (1972) Breeding bird species diversity in relation to increasing urbanisation. *Bird Study* 19:157–166. <https://doi.org/10.1080/00063657209476337>
- Beissinger SR, Osborne DR (1982) Effects of urbanization on avian community organization. *Condor* 84:75–83. <https://doi.org/10.2307/1367825>
- Beninde J, Veith M, Hochkirch A (2015) Biodiversity in cities needs space: a meta-analysis of factors determining intra-urban biodiversity variation. *Ecol Lett* 18:581–592. <https://doi.org/10.1111/ele.12427>
- Blüthgen N (2010) Why network analysis is often disconnected from community ecology: a critique and an ecologist's guide. *Basic Appl Ecol* 11:185–195. <https://doi.org/10.1016/j.baae.2010.01.001>
- Blüthgen N, Menzel F, Blüthgen N (2006) Measuring specialization in species interaction networks. *BMC Ecol* 6:1–12. <https://doi.org/10.1186/1472-6785-6-9>
- Bonier F, Martin PR, Wingfield JC (2007) Urban birds have broader environmental tolerance. *Biol Lett* 3:670–673. <https://doi.org/10.1098/rsbl.2007.0349>
- Boscolo D, Metzger JP (2009) Is bird incidence in Atlantic Forest fragments influenced by landscape patterns at multiple scales? *Landsc Ecol* 24:907–918. <https://doi.org/10.1007/s10980-009-9370-8>
- Boscolo D, Metzger JP (2011) Isolation determines patterns of species presence in highly fragmented landscapes. *Ecography* 34:1018–1029. <https://doi.org/10.1111/j.1600-0587.2011.06763.x>
- Bregman TP, Sekercioglu CH, Tobias JA (2014) Global patterns and predictors of bird species responses to forest fragmentation: implications for ecosystem function and conservation. *Biol Conserv* 169: 372–383. <https://doi.org/10.1016/j.biocon.2013.11.024>
- Burgos E, Ceva H, Perazzo RPJ et al (2007) Why nestedness in mutualistic networks? *J Theor Biol* 249:307–313. <https://doi.org/10.1016/j.jtbi.2007.07.030>
- Canedoli C, Manenti R, Padoa-Schioppa E (2018) Birds biodiversity in urban and periurban forests: environmental determinants at local and

- landscape scales. *Urban Ecosyst* 21:779–793. <https://doi.org/10.1007/s11252-018-0757-7>
- Chacoff NP, Vázquez DP, Lomáscolo SB, Stevani EL, Dorado J, Padrón B (2012) Evaluating sampling completeness in a desert plant-pollinator network. *J Anim Ecol* 81:190–200. <https://doi.org/10.1111/j.1365-2656.2011.01883.x>
- Concepción ED, Moretti M, Altermatt F et al (2015) Impacts of urbanisation on biodiversity: the role of species mobility, degree of specialisation and spatial scale. *Oikos* 124:1571–1582. <https://doi.org/10.1111/oik.02166>
- Croci S, Butet A, Clergeau P (2008) Does urbanization filter birds on the basis of their biological traits? *Condor* 110:223–240. <https://doi.org/10.1525/cond.2008.8409>
- Crooks KR, Suarez AV, Bolger DT (2004) Avian assemblages along a gradient of urbanization in a highly fragmented landscape. *Biol Conserv* 115:451–462. [https://doi.org/10.1016/S0006-3207\(03\)00162-9](https://doi.org/10.1016/S0006-3207(03)00162-9)
- Cushman SA, McGarigal K (2004) Patterns in the species-environment relationship depend on both scale and choice of response variables. *Oikos* 105:117–124. <https://doi.org/10.1111/j.0030-1299.2004.12524.x>
- Devoto M, Bailey S, Craze P, Memmott J (2012) Understanding and planning ecological restoration of plant-pollinator networks. *Ecol Lett* 15:319–328. <https://doi.org/10.1111/j.1461-0248.2012.01740.x>
- Doherty TS, Driscoll DA (2018) Coupling movement and landscape ecology for animal conservation in production landscapes. *Proc R Soc B Biol Sci* 285:20172272. <https://doi.org/10.1098/rspb.2017.2272>
- Dormann CF, Fründ J, Bluthgen N, Gruber B (2009) Indices, graphs and null models: analysing bipartite ecological networks. *Open Ecol J* 2: 7–24. <https://doi.org/10.2174/1874213000902010007>
- Emer C, Galetti M, Pizo MA, Guimarães PR Jr, Moraes S, Piratelli A, Jordano P (2018) Seed-dispersal interactions in fragmented landscapes - a metanetwork approach. *Ecol Lett* 21:484–493. <https://doi.org/10.1111/ele.12909>
- Fahrig L (2003) Effects of habitat fragmentation on biodiversity. *Annu Rev Ecol Evol Syst* 34:487–515. <https://doi.org/10.1146/annurev.ecolsys.34.011802.132419>
- Ferraz G, Nichols JD, Hines JE et al (2007) A large-scale deforestation experiment: effects of patch area and isolation on Amazon birds. *Science* (80-) 315:238–241. <https://doi.org/10.1126/science.1133097>
- Ferreira PA, Boscolo D, Viana BF (2013) What do we know about the effects of landscape changes on plant–pollinator interaction networks? *Ecol Indic* 31:35–40. <https://doi.org/10.1016/j.ecolind.2012.07.025>
- Ferreira PA, Boscolo D, Carvalheiro LG, Biesmeijer JC, Rocha PLB, Viana BF (2015) Responses of bees to habitat loss in fragmented landscapes of Brazilian Atlantic rainforest. *Landsc Ecol* 30:2067–2078. <https://doi.org/10.1007/s10980-015-0231-3>
- Fletcher RJ, Reichert BE, Holmes K (2018) The negative effects of habitat fragmentation operate at the scale of dispersal. *Ecology* 99: 2176–2186. <https://doi.org/10.1002/ecy.2467>
- Fontana CS, Burger MI, Magnusson WE (2011) Bird diversity in a subtropical south-American city: effects of noise levels, arborisation and human population density. *Urban Ecosyst* 14:341–360. <https://doi.org/10.1007/s11252-011-0156-9>
- Fortuna MA, Bascompte J (2006) Habitat loss and the structure of plant-animal mutualistic networks. *Ecol Lett* 9:281–286. <https://doi.org/10.1111/j.1461-0248.2005.00868.x>
- Gagné SA, Fahrig L (2011) Do birds and beetles show similar responses to urbanization? *Ecol Appl* 21:2297–2312. <https://doi.org/10.1890/09-1905.1>
- Galetti M, Guevara R, Côrtes MC et al (2013) Functional extinction of birds drives rapid evolutionary changes in seed size. *Science* (80-) 340:1086–1091. <https://doi.org/10.1126/science.1233774>
- Garaffa PI, Filloy J, Bellocq MI (2009) Bird community responses along urban-rural gradients: does the size of the urbanized area matter? *Landsc Urban Plan* 90:33–41. <https://doi.org/10.1016/j.landurbplan.2008.10.004>
- Geslin B, Gauzens B, Thébault E, Dajoz I (2013) Plant pollinator networks along a gradient of urbanisation. *PLoS One* 8:e63421. <https://doi.org/10.1371/journal.pone.0063421>
- Gonzalez A, Rayfield B, Lindo Z (2011) The disentangled bank: how loss of habitat fragments and disassembles ecological networks. *Am J Bot* 98:503–516. <https://doi.org/10.732/ajb.1000424>
- Haddad NM, Brudvig LA, Clobert J, Davies KF, Gonzalez A, Holt RD, Lovejoy TE, Sexton JO, Austin MP, Collins CD, Cook WM, Damschen EI, Ewers RM, Foster BL, Jenkins CN, King AJ, Laurance WF, Levey DJ, Margules CR, Melbourne BA, Nicholls AO, Orrock JL, Song DX, Townshend JR (2015) Habitat fragmentation and its lasting impact on Earth's ecosystems. *Sci Adv* 1: e1500052–e1500052. <https://doi.org/10.1126/sciadv.1500052>
- Hagen M, Kissling WD, Rasmussen C, et al (2012) Biodiversity, species interactions and ecological networks in a fragmented world. In: *Advances in Ecological Research*. pp 89–210
- Hayes FE, Sewlal JN (2004) The Amazon River as a dispersal barrier to passerine birds: effects of river width, habitat and taxonomy. *J Biogeogr* 31:1809–1818. <https://doi.org/10.1111/j.1365-2699.2004.01139.x>
- Hodgson JA, Moilanen A, Wintle BA, Thomas CD (2011) Habitat area, quality and connectivity: striking the balance for efficient conservation. *J Appl Ecol* 48:148–152. <https://doi.org/10.1111/j.1365-2664.2010.01919.x>
- Hostetler M, Holling CS (2000) Detecting the scales at which birds respond to structure in urban landscapes. *Urban Ecosyst* 4:25–54. <https://doi.org/10.1023/A:1009587719462>
- IBGE Instituto Brasileiro de Geografia e Estatística (2018) Censo populacional. Accessed 02 Feb 2019
- IUCN International Union for Conservation of Nature (2018) IUCN red list of threatened species. Accessed 24 Oct 2018
- Jackson HB, Fahrig L (2015) Are ecologists conducting research at the optimal scale? *Glob Ecol Biogeogr* 24:52–63. <https://doi.org/10.1111/geb.12233>
- Kaiser-Bunbury CN, Blüthgen N (2015) Integrating network ecology with applied conservation: a synthesis and guide to implementation. *AoB Plants* 7:plv076. <https://doi.org/10.1093/aobpla/plv076>
- Lapaix R, Harper K, Freedman B (2012) Patterns of exotic plants in relation to anthropogenic edges within urban forest remnants. *Appl Veg Sci* 15:525–535. <https://doi.org/10.1111/j.1654-109X.2012.01195.x>
- Leblond M, Dussault C, Ouellet J-P (2013) Impacts of human disturbance on large prey species: do behavioral reactions translate to fitness consequences? *PLoS One* 8:e73695. <https://doi.org/10.1371/journal.pone.0073695>
- Liu Z, He C, Wu J (2016) The relationship between habitat loss and fragmentation during urbanization: an empirical evaluation from 16 world cities. *PLoS One* 11:e0154613. <https://doi.org/10.1371/journal.pone.0154613>
- Marques MCM, Roper JJ, Baggio Salvalaggio AP (2004) Phenological patterns among plant life-forms in a subtropical forest in southern Brazil. *Plant Ecol* (formerly Veg) 173:191–201. <https://doi.org/10.1023/B:VEGE.0000029325.85031.90>
- Martín González AM, Dalsgaard B, Olesen JM (2010) Centrality measures and the importance of generalist species in pollination networks. *Ecol Complex* 7:36–43. <https://doi.org/10.1016/j.ecocom.2009.03.008>

- Martin AE, Desrochers A, Fahrig L (2016) Homogenization of dispersal ability across bird species in response to landscape change. *Oikos*: 996–1003. <https://doi.org/10.1111/oik.03859>
- Marzluff JM, Ewing K (2001) Restoration of fragmented landscapes for the conservation of birds: a general framework and specific recommendations for urbanizing landscapes. *Restor Ecol* 9:280–292. <https://doi.org/10.1046/j.1526-100x.2001.009003280.x>
- Marzluff JM, Bowman R, Donnelly R (2001) Avian ecology and conservation in an urbanizing world. Springer US, Boston
- McConkey KR, Prasad S, Corlett RT et al (2012) Seed dispersal in changing landscapes. *Biol Conserv* 146:1–13. <https://doi.org/10.1016/j.biocon.2011.09.018>
- McKinney ML (2002) Urbanization, biodiversity, and conservation. *Bioscience* 52:883–890. [https://doi.org/10.1641/0006-3568\(2002\)052\[0883:UBAC\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2002)052[0883:UBAC]2.0.CO;2)
- McKinney ML (2006) Urbanization as a major cause of biotic homogenization. *Biol Conserv* 127:247–260. <https://doi.org/10.1016/j.biocon.2005.09.005>
- McPhearson T, Pickett STA, Grimm NB et al (2016) Advancing urban ecology toward a science of advancing urban ecology toward a science of cities. *Bioscience* 66:198–212. <https://doi.org/10.1093/biosci/biw002>
- Meffert PJ, Dziok F (2013) The influence of urbanisation on diversity and trait composition of birds. *Landsc Ecol* 28:943–957. <https://doi.org/10.1007/s10980-013-9867-z>
- Mellado A, Zamora R (2014) Generalist birds govern the seed dispersal of a parasitic plant with strong recruitment constraints. *Oecologia* 176:139–147. <https://doi.org/10.1007/s00442-014-3013-8>
- Mello MAR, Rodrigues FA, da CLF et al (2015) Keystone species in seed dispersal networks are mainly determined by dietary specialization. *Oikos* 124:1031–1039. <https://doi.org/10.1111/oik.01613>
- Miguet P, Jackson HB, Jackson ND et al (2016) What determines the spatial extent of landscape effects on species? *Landsc Ecol* 31:1177–1194. <https://doi.org/10.1007/s10980-015-0314-1>
- Morales JM, Moorcroft PR, Matthiopoulos J, Frair JL, Kie JG, Powell RA, Merrill EH, Haydon DT (2010) Building the bridge between animal movement and population dynamics. *Philos Trans R Soc London* 365:2289–2301. <https://doi.org/10.1098/rstb.2010.0082>
- Moreira EF, Boscolo D, Viana BF (2015) Spatial heterogeneity regulates plant-pollinator networks across multiple landscape scales. *PLoS One* 10:e0123628. <https://doi.org/10.1371/journal.pone.0123628>
- Newbold T, Hudson LN, Hill SLL et al (2015) Global effects of land use on local terrestrial biodiversity. *Nature* 520:45–50. <https://doi.org/10.1038/nature14324>
- Niebuhr BBS, Wosniack ME, Santos MC, Raposo EP, Viswanathan GM, da Luz MGE, Pie MR (2015) Survival in patchy landscapes: the interplay between dispersal, habitat loss and fragmentation. *Sci Rep* 5:1–10. <https://doi.org/10.1038/srep11898>
- Norris K (2012) Biodiversity in the context of ecosystem services: the applied need for systems approaches. *Philos Trans R Soc B Biol Sci* 367:191–199. <https://doi.org/10.1098/rstb.2011.0176>
- Palacio RD, Valderrama-Ardila C, Kattan GH (2016) Generalist species have a central role in a highly diverse plant-frugivore network. *Biotropica* 48:349–355. <https://doi.org/10.1111/btp.12290>
- Peel MC, Finlayson BL, McMahon TA (2007) Updated world map of the Köppen-Geiger climate classification. *Hydrol Earth Syst Sci* 11: 1633–1644. <https://doi.org/10.1127/0941-2948/2006/0130>
- Pena JCDC, Martello F, Ribeiro MC, Armitage RA, Young RJ, Rodrigues M (2017) Street trees reduce the negative effects of urbanization on birds. *PLoS One* 12:e0174484. <https://doi.org/10.1371/journal.pone.0174484>
- Perera AH, Drew CA, Johnson CJ (2012) Expert knowledge and its application in landscape ecology. Springer New York, New York
- Pinto SR, Melo F, Tabarelli M et al (2014) Governing and delivering a biome-wide restoration initiative: the case of Atlantic Forest restoration pact in Brazil. *Forests* 5:2212–2229. <https://doi.org/10.3390/f5092212>
- Ramos-Robles M, Andresen E, Díaz-Castelazo C (2016) Temporal changes in the structure of a plant-frugivore network are influenced by bird migration and fruit availability. *PeerJ* 4:e2048. <https://doi.org/10.7717/peerj.2048>
- Ribeiro da Silva F, Montoya D, Furtado R et al (2015) The restoration of tropical seed dispersal networks. *Restor Ecol* 23:852–860. <https://doi.org/10.1111/rec.12244>
- Ribeiro JW, dos Santos JS, Dodonov P et al (2017) Landscape corridors (LSCorridors): a new software package for modeling ecological corridors based on landscape patterns and species requirements. *Methods Ecol Evol* 38:42–49. <https://doi.org/10.1111/2041-210X.12750>
- Richmond CE, Breitung DL, Rose KA (2005) The role of environmental generalist species in ecosystem function. *Ecol Model* 188:279–295. <https://doi.org/10.1016/j.ecolmodel.2005.03.002>
- Rodewald AD, Rohr RP, Fortuna MA, Bascompte J (2014) Community-level demographic consequences of urbanization: an ecological network approach. *J Anim Ecol* 83:1409–1417. <https://doi.org/10.1111/1365-2656.12224>
- Sakai S, Metelmann S, Toquenaga Y, Telschow A (2016) Geographical variation in the heterogeneity of mutualistic networks. *R Soc Open Sci* 3:150630. <https://doi.org/10.1098/rsos.150630>
- Seto KC, Guneralp B, Hutyra LR (2012) Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. *Proc Natl Acad Sci* 109:16083–16088. <https://doi.org/10.1073/pnas.1211658109>
- Soares RGS, Ferreira PA, Lopes LE (2017) Can plant-pollinator network metrics indicate environmental quality? *Ecol Indic* 78:361–370. <https://doi.org/10.1016/j.ecolind.2017.03.037>
- Suarez-Rubio M, Wilson S, Leimgruber P, Lookingbill T (2013) Threshold responses of forest birds to landscape changes around exurban development. *PLoS One* 8:e67593. <https://doi.org/10.1371/journal.pone.0067593>
- Sutherland WJ, Newton I, Green R (2004) Bird ecology and conservation: a handbook of techniques. Oxford University Press, New York. <https://doi.org/10.1093/acprof:oso/9780198520863.001.0001>
- Tremblay MA, St. Clair CC (2011) Permeability of a heterogeneous urban landscape to the movements of forest songbirds. *J Appl Ecol* 48: 679–688. <https://doi.org/10.1111/j.1365-2664.2011.01978.x>
- Tschamtké T, Steffan-Dewenter I, Kruess A, Thies C (2002) Contribution of small habitat fragments to conservation of insect communities of grassland-cropland landscapes. *Ecol Appl* 12:354. <https://doi.org/10.2307/3060947>
- Tylianakis JM, Morris RJ (2017) Ecological networks across environmental gradients. *Annu Rev Ecol Evol Syst* 48. <https://doi.org/10.1146/annurev-ecolsys-110316-022821>
- Tylianakis JM, Tschamtké T, Lewis OT (2007) Habitat modification alters the structure of tropical host-parasitoid food webs. *Nature* 445: 202–205. <https://doi.org/10.1038/nature05429>
- Tylianakis JM, Laliberté E, Nielsen A, Bascompte J (2010) Conservation of species interaction networks. *Biol Conserv* 143:2270–2279. <https://doi.org/10.1016/j.biocon.2009.12.004>
- Valiente-Banuet A, Aizen MA, Alcántara JM et al (2014) Beyond species loss: the extinction of ecological interactions in a changing world. *Funct Ecol* 29:299–307. <https://doi.org/10.1111/1365-2435.12356>
- Vallejos MAV, Padial AA, Vitule JRS (2016) Human-induced landscape changes homogenize Atlantic forest bird assemblages through nested species loss. *PLoS One* 11:1–17. <https://doi.org/10.1371/journal.pone.0147058>
- Vitousek PM, Mooney HA, Lubchenco J, Melillo JM (1997) Human domination of Earth's ecosystems. *Science* (80-) 277:494–499. <https://doi.org/10.1126/science.277.5325.494>
- Weir JT, Faccio MS, Pulido-Santacruz P, Barrera-Guzmán AO, Aleixo A (2015) Hybridization in headwater regions, and the role of rivers as


drivers of speciation in Amazonian birds. *Evolution* 69:1823–1834. <https://doi.org/10.1111/evo.12696>

Wilman H, Belmaker J, Simpson J et al (2014) EltonTraits 1.0: species-level foraging attributes of the world's birds and mammals. *Ecology* 95:2027–2027. <https://doi.org/10.1890/13-1917.1>

Wolfe JD, Johnson MD, Ralph CJ (2014) Do birds select habitat or food resources? Nearctic-neotropic migrants in northeastern Costa Rica. *PLoS One* 9:1–9. <https://doi.org/10.1371/journal.pone.0086221>

Zhao S, Liu S, Zhou D (2016) Prevalent vegetation growth enhancement in urban environment. *Proc Natl Acad Sci* 113:6313–6318. <https://doi.org/10.1073/pnas.1602312113>

Affiliations

Israel Schneiberg^{1,2}  • **Danilo Boscolo**³ • **Mariano Devoto**⁴ • **Vinicius Marcilio-Silva**^{1,5} • **Cilmar Antônio Dalmaso**⁶ • **John Wesley Ribeiro**⁷ • **Milton Cezar Ribeiro**⁷ • **André de Camargo Guaraldo**¹ • **Bernardo Brandão Niebuhr**⁷ • **Isabela Galarda Varassin**^{1,2}

¹ Programa de Pós-Graduação em Ecologia e Conservação, Universidade Federal do Paraná. Centro Politécnico, Jardim das Américas, Curitiba, PR 81531-990, Brazil

² Laboratório de Interações & Biologia Reprodutiva, Universidade Federal do Paraná. Centro Politécnico, Jardim das Américas, Curitiba, PR 81531-990, Brazil

³ Departamento de Biologia, Faculdade de filosofia, ciências e letras de Ribeirão Preto Universidade de São Paulo FFCLRP-USP Ribeirão Preto, São Paulo, Brazil

⁴ Universidad de Buenos Aires, Facultad de Agronomía, Cátedra de Botánica General, Argentina. Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Buenos Aires, Argentina

⁵ Laboratório de Ecologia Vegetal, Universidade Federal do Paraná. Centro Politécnico, Jardim das Américas, Curitiba, PR 81531-990, Brazil

⁶ Programa de Pós-Graduação em Ciências Florestais, Universidade Federal do Paraná. Jardim Botânico, Curitiba, PR 80210-170, Brazil

⁷ Laboratório de Ecologia Espacial e Conservação (LEEC), Departamento de Ecologia. Universidade Estadual Paulista, UNESP, Rio Claro, São Paulo, Brazil