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Urbanization homogenizes the interactions of plant-frugivore bird networks

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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

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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 Dziocck 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,

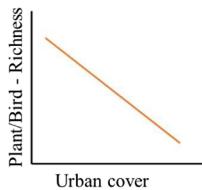
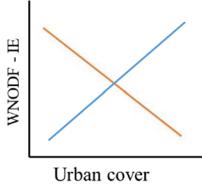
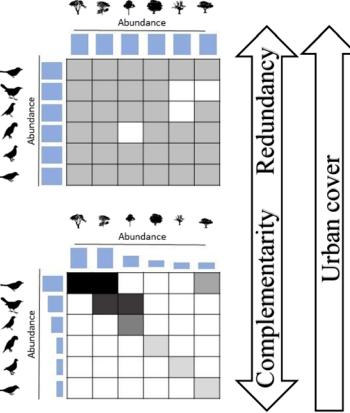
Hypothesis	Description	Expected Results
H1	Plant/Bird richness decrease within forest patches in landscapes with higher urban cover.	
H2	The lack of habitat/diet specialists in more urbanized area contributes to a decrease in nestedness ($WNODF$) – red line. Also, some species interact in higher frequencies than others, the dominance of generalist species in landscapes with higher urban cover leads to networks with high interaction evenness (IE) – 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.

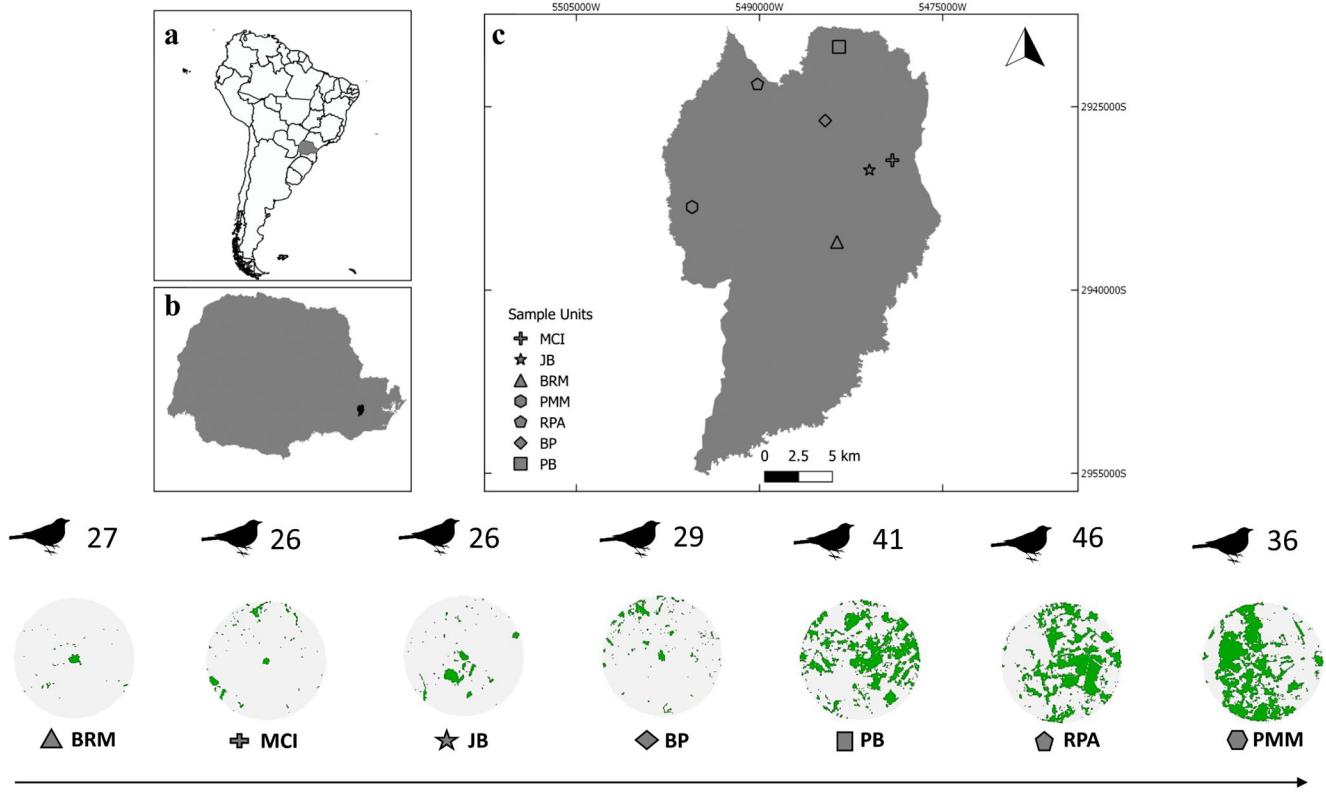


Fig. 2 Location of the sampled forest patches at Curitiba, southern Brazil (**a** to **c**). **a** represents South America. **b** Paraná state and Curitiba city (black area). **c** Sampled forest patches highlighted (symbols) within

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

baring 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

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-

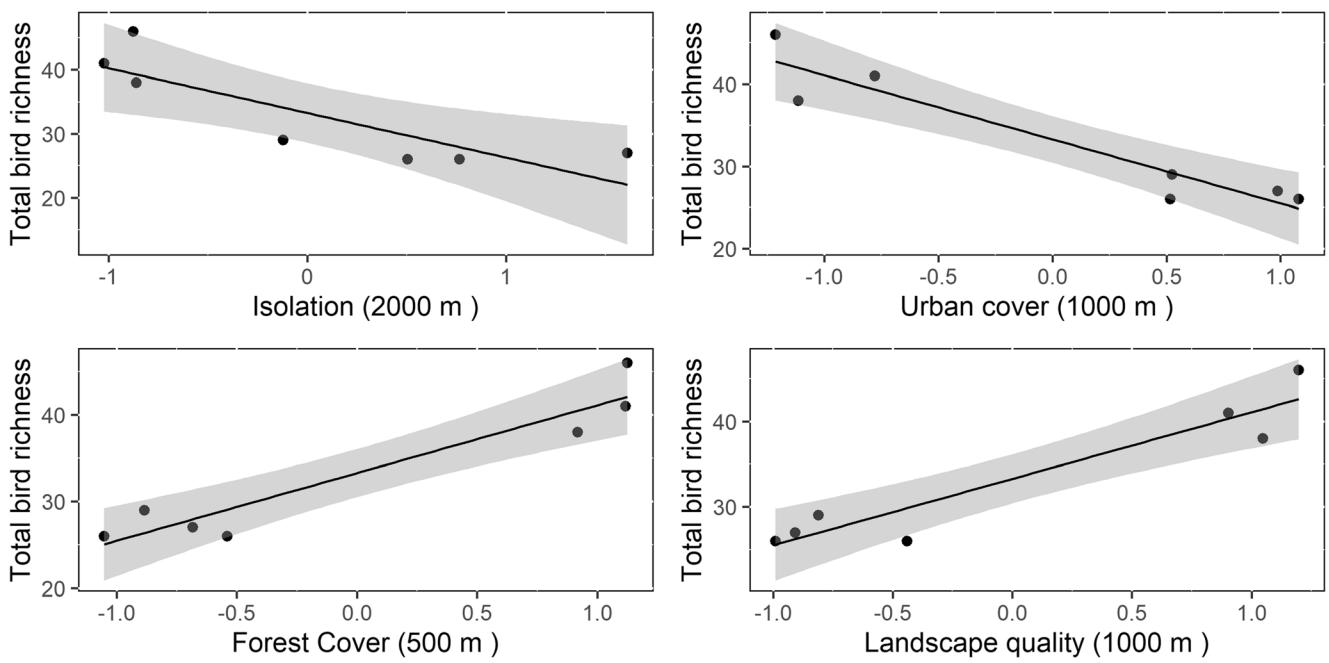


Fig. 3 Bird richness in urban landscapes at forest patches at Curitiba decreases with **a** the isolation between forest patches and **b** urban cover and increases with **c** forest cover and **d** landscape quality. The x-axis corresponds to the standardized values

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 (ΔAICc) 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	$\Delta AICc$	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 $\Delta AICc < 2$, 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 $\Delta AICc < 2$ were considered equally plausible. Model selection analyses were performed using the “AICmodavg” package in R 3.3.1.

All code and data are available in the GitHub repository: https://github.com/LEEClab/ms_Schneiberg_et al_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 ($\Delta AICc < 2$, $w_i = 0.24$) and landscape quality within 1000 m extent ($\Delta AICc < 2$, $w_i = 0.26$). Conversely, total bird richness decreased as the urban cover ($\Delta AICc < 2$, $w_i = 0.26$) and isolation increased ($\Delta AICc < 2$, $w_i = 0.11$), 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	Nº interactions	Code	Bird	Nº 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>Pachyramphus castaneus</i>	8
T13	<i>Eugenia uniflora</i>	20	B1	<i>Cacicus haemorrhouss</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>Myrtaceae 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 ($\Delta AIC_c < 2$), bringing considerable uncertainty to landscape effects on nestedness. Complementary specialization was not affected by landscape structure ($\Delta AIC_c > 2$ 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

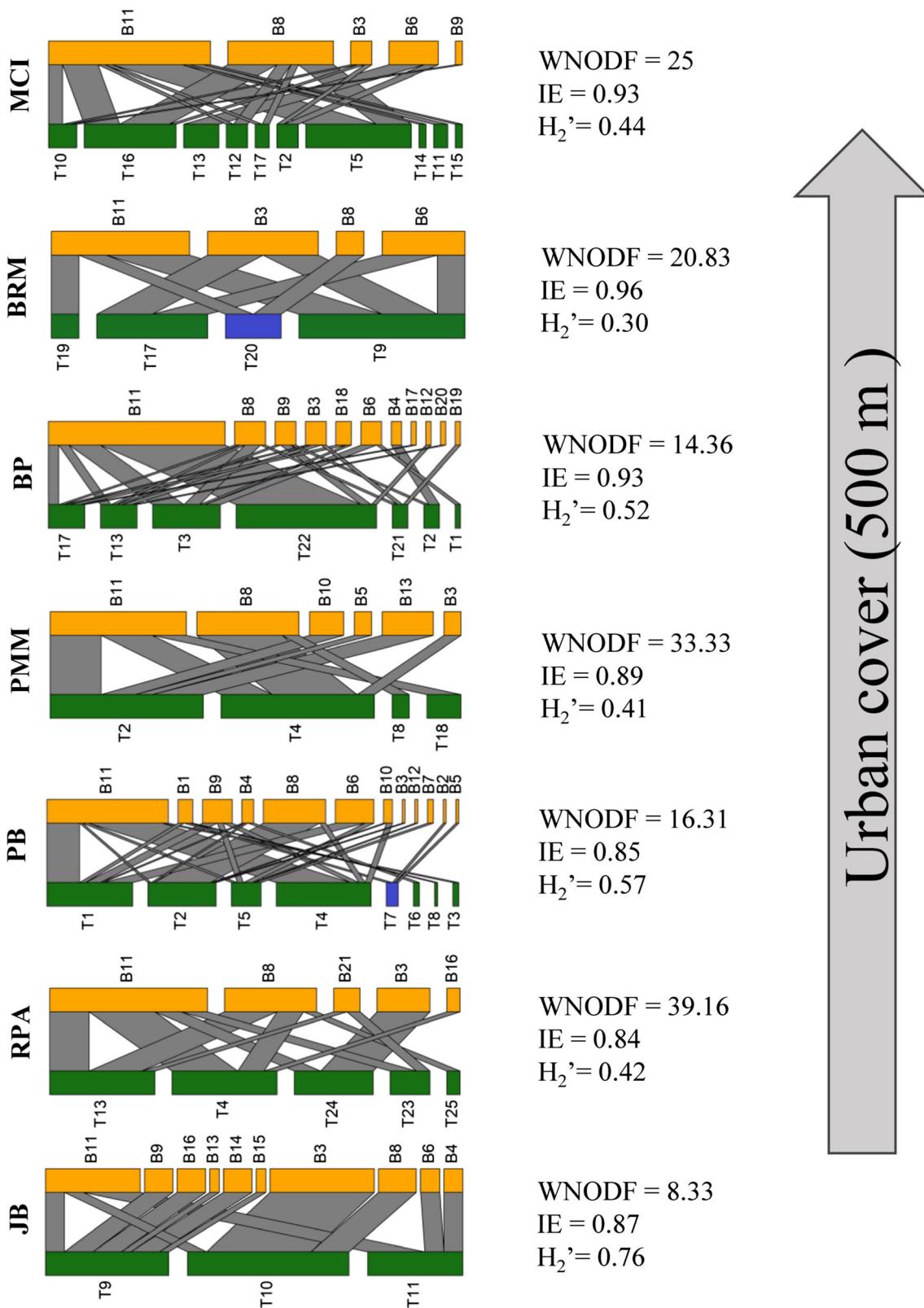
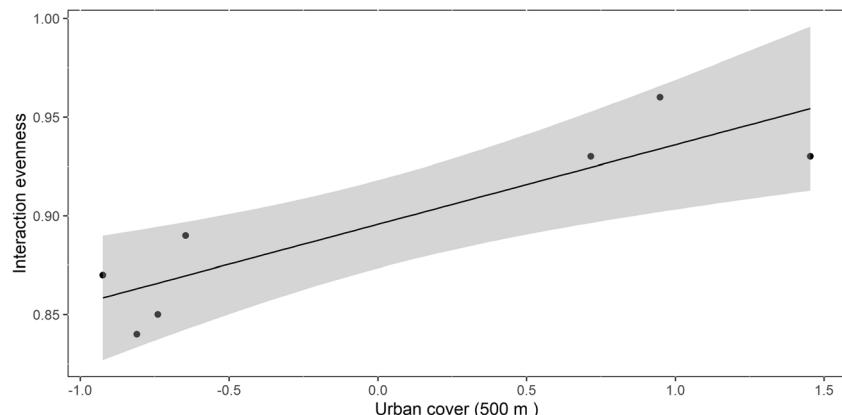


Fig. 4 Quantitative plant-frugivore networks sampled at forest patches, Curitiba, southern Brazil. Plant species and bird species are indicated by green and orange boxes, respectively. The arrow indicates the gradient of urban cover (500 m) in which the networks are inserted. Blue boxes

represent two exotic species of plant (*Pittosporum undulatus*, *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 (Croci et al. 2008; Meffert and Dziack 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.

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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.

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