

ARTICLE

Disentangling direct and indirect effects of landscape structure on urban bird richness and functional diversity

Andrés Felipe Suárez-Castro^{1,2}  | Martine Maron^{1,3}  | Matthew G. E. Mitchell⁴  | Jonathan R. Rhodes^{1,3} 

¹Centre for Biodiversity and Conservation Science, The University of Queensland, Brisbane, Australia

²Australian Rivers Institute, University of Griffith, Nathan, Australia

³School of Earth and Environmental Sciences, The University of Queensland, Brisbane, Australia

⁴Institute for Resources, Environment and Sustainability, University of British Columbia, Vancouver, British Columbia, Canada

Correspondence

Andrés Felipe Suárez-Castro
Email: a.suarezcastro@griffith.edu.au

Funding information

Australian Research Council, Grant/Award Numbers: DP130100218, FT200100096; Colciencias. Department of Science, Technology and Innovation, Colombia, Grant/Award Number: Doctoral Fellowship, 529

Handling Editor: Beth Gardner

Abstract

As fragmented landscapes become increasingly common around the world, managing the spatial arrangement of landscape elements (i.e., landscape configuration) may help to promote the conservation of biodiversity. However, the relative effects of landscape configuration on different dimensions of biodiversity across species assemblages are largely unknown. Thus, a key challenge consists in understanding when it is necessary to focus on landscape configuration, in addition to landscape composition, to achieve multifunctional landscapes. We tested the effects of landscape composition (the percentage of tree cover and built infrastructure) and landscape configuration (degree of fragmentation) on landscape-level species richness and different metrics of functional diversity of urban birds. We collected data on different bird guilds (nectarivores/frugivores, insectivores) from Brisbane, Australia. Using structural equation models, we found that landscape structure (landscape composition and configuration) affected functional diversity via two main pathways: (1) through effects of landscape composition, mediated by landscape configuration (indirect effects), and (2) through direct (“independent”) effects of landscape composition and configuration, filtering species with extreme trait values. Our results show that landscape-level species richness declined with the extent of built infrastructure, but patterns of trait diversity did not necessarily correlate with this variable. Landscape configuration had a stronger mediating effect on some metrics of the functional diversity of insectivores than on the functional diversity of frugivores/nectarivores. In addition, fragmentation increased the effects of built infrastructure for some traits (body size and dispersal capacity), but not for others (habitat plasticity and foraging behavior). These results suggest that differential approaches to managing landscape structure are needed depending on whether the focus is on protecting functional diversity or species richness and what the target guild is. Managing landscape fragmentation in areas with high levels of built infrastructure is important if the objective is to protect insectivore species with uncommon traits, even if it is not

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial](https://creativecommons.org/licenses/by-nc/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.

© 2022 The Authors. *Ecological Applications* published by Wiley Periodicals LLC on behalf of The Ecological Society of America.

possible to preserve high levels of species richness. However, if the target is to enhance both functional diversity and species richness of multiple guilds, the focus should be on improving composition through the reduction of negative effects of built infrastructure, rather than promoting specific landscape configurations in growing cities.

KEYWORDS

habitat fragmentation, habitat loss, landscape sharing, landscape sparing multifunctional landscapes, species traits, urbanization

INTRODUCTION

As human-dominated landscapes become more common globally, new insights around how landscapes can be managed to conserve multiple components of biological diversity are increasingly valuable. This involves understanding how landscape change affects not only the number of species but also the distribution of functional traits in a species assemblage (i.e., functional diversity) that influence the maintenance of ecosystem processes (Gross et al., 2017; Mayfield et al., 2010). Importantly, species richness and functional diversity can show different responses to changes in landscape structure (landscape composition and configuration; Table 1) (Flynn et al., 2009; Hatfield et al., 2018; Suárez-Castro et al., 2020). Thus, a key challenge is to identify when a focus on managing landscape configuration is important for maximizing species richness and functional diversity.

Disentangling the pathways through which landscape structure affects functional diversity is challenging. The effects of landscape configuration on biodiversity should increase as the amount of habitat declines because the spatial distribution of remaining habitat shapes species opportunities to reach and settle in areas with available resources (Rybicki et al., 2019). However, the effects of landscape configuration on functional diversity can be highly variable and depend on the species assemblage evaluated (Bregman et al., 2014; Rocha-Santos et al., 2020). This is because there is high variation in the distribution of trait values across assemblages, and this increases the diversity of species responses to the spatial distribution of remaining habitats (Mori et al., 2013; Suárez-Castro et al., 2020). In addition, the effects of landscape structure on functional diversity depend on whether the focus is on trait richness or metrics that evaluate the abundance of trait values in a species assemblage (Hatfield et al., 2018; Suárez-Castro et al., 2020). Spatially explicit analyses are thus needed to understand the conditions under which functional diversity is expected to change due to changes in landscape structure and how this compares to impacts on species richness.

The effects of landscape structure on biodiversity can be classified as direct and indirect effects (Didham et al., 2012). For example, the number of species that occur in a landscape may mostly depend directly on the amount of remaining available habitat (Rybicki & Hanski, 2013).

TABLE 1 Key definitions of concepts used in this study.

Term	Definition
Assemblage	A taxonomically related group of species populations that occur together in space (Fauth et al., 1996)
Functional diversity	The variation of functional traits in an assemblage (Laliberté & Legendre, 2010)
Functional richness	The amount of functional space occupied by the species in an assemblage
Functional divergence	Represents how far species abundances are from the center of the trait functional space
Functional evenness	Describes how regularly species abundances are distributed in functional space (Mouchet et al., 2010)
Guild	A group of species that exploit the same class of resources in a similar way. We assume that species that belong to the same guild are also “functionally similar” (Stroud et al., 2015)
Landscape structure	The arrangement of landscape components, such as habitat patches or anthropogenic land uses across a landscape. It includes landscape composition (e.g., how much of each land cover or land use that exists) and configuration (e.g., the no. fragments, their size distribution, their shape, and spatial arrangement) (Tscharntke et al., 2012)
Landscape configuration	The spatial arrangement of landscape elements within a landscape
Landscape composition	The no. patch, land-cover, and habitat types represented in a landscape and their relative abundance

In this case, the direct relationship between habitat amount and species richness may be determined by the species–area relationship. However, as the amount of habitat available becomes limited, landscapes tend to become more fragmented, and processes related to the spatial distribution of the remaining habitat mediate the effects of habitat amount on biodiversity (Püttker et al., 2020; Villard & Metzger, 2014). This mediation pathway is an indirect effect. In addition, landscape configuration can also act directly on functional diversity by filtering traits such as dispersal capacity that allow species to cope with reduced connectivity and patch isolation (Barbaro et al., 2014; Ding et al., 2013). Evaluating the prevalence of direct and indirect effects can provide insights on how much we should focus on devoting resources to managing landscape structure to protect biodiversity.

Understanding direct and indirect drivers through which landscape structure alters functional diversity and species richness is particularly important in urban environments. Cities constitute important locations of landscape transformation and are one of the fastest-growing land-use types globally (McDonald et al., 2020; Seto et al., 2012). Although there are negative effects of urbanization on biodiversity at local scales, these could be mitigated by managing the spatial pattern and the structural complexity of remaining habitats (Fischer et al., 2014; Oliveira Hagen et al., 2017). For example, it has been hypothesized that urban growth form where areas of high density of built infrastructure are mixed with areas with large patches of vegetation may reduce local extinctions (Sushinsky et al., 2013). On the other hand, sprawling growth of urban areas may promote declines in native species richness, but it may help to maintain a wide range of blue and green spaces that enhance connectivity and, potentially, ecological functions at larger scales (Fahrig, 2017; Soga et al., 2014). Although we have a relatively good understanding of the effects of landscape composition on species richness in cities (Batáry et al., 2017), we have only limited understanding of how landscape configuration mediates the effect of landscape composition on both species richness and functional diversity in urban areas.

Here we test how landscape composition (amount of tree cover, percentage of built infrastructure) and landscape configuration (using measures of fragmentation of tree cover) simultaneously influence landscape-level species richness and functional diversity of urban birds using data from Brisbane, Australia. We chose birds as a focal study group because they are a taxonomically and functionally diverse group, even within highly modified landscapes. We evaluate this for different bird guilds and identify how fragmentation mediates the impacts

of landscape composition on different functional diversity indices. We focus on two guilds, frugivores/nectarivores and insectivores, because they are associated with different suites of ecological functions, and there is evidence that they respond differently to changes in landscape structure (Mayorga et al., 2020; Shanahan et al., 2011). Based on these results, we discuss how urban landscapes could be managed to potentially maximize the conservation of both species richness and functional diversity.

METHODS

Study area

Our study area was the Brisbane local government area (hereafter “Brisbane”), a city with a population of approximately 2.5 million located on the eastern coast of Queensland, Australia (27°28′ S, 153°07′ E; Figure 1). This region has a mean elevation of 540 m (range: 300–940 m), mean minimum and maximum temperatures of 16.3°C and 26.5°C, respectively, and a mean annual precipitation of 1006 mm. During summer (December–March) average temperatures range from 21°C to 29.8°C and the city has its highest average rainfall (426.6 mm). In winter (June–August), weather is generally dry and mild, with mean temperatures between 11°C and 21°C. Approximately half of the city (49%) has tree canopy coverage (Jacobs, 2014). In recent decades, the city has experienced extensive land clearing and fragmentation as a consequence of rapid urban growth, which in turn has led to declines in woodland birds (Catterall et al., 2010).

Survey design

We surveyed birds in 42 grids of 1 km². The grids were chosen to describe gradients of different amounts of tree cover and fragmentation. Although many bird species use areas larger than 1 km², most previous studies on the effects of landscape structure on urban bird diversity commonly showed that the scales at which predictor variables related most significantly to local bird assemblages were between 0.5 and 3 km² (Litteral & Shochat, 2017). In addition, 1 km² captures the size at which many local conservation planning actions, roughly the size of a neighborhood, are carried out within urban areas (Mitchell et al., 2016).

Grids were selected using stratified random sampling. First, we calculated the area of tree cover within each 1-km² grid using ArcGIS 10.2.1 (Environmental Systems Research Institute). Tree cover data were extracted from a high-resolution LiDAR layer of

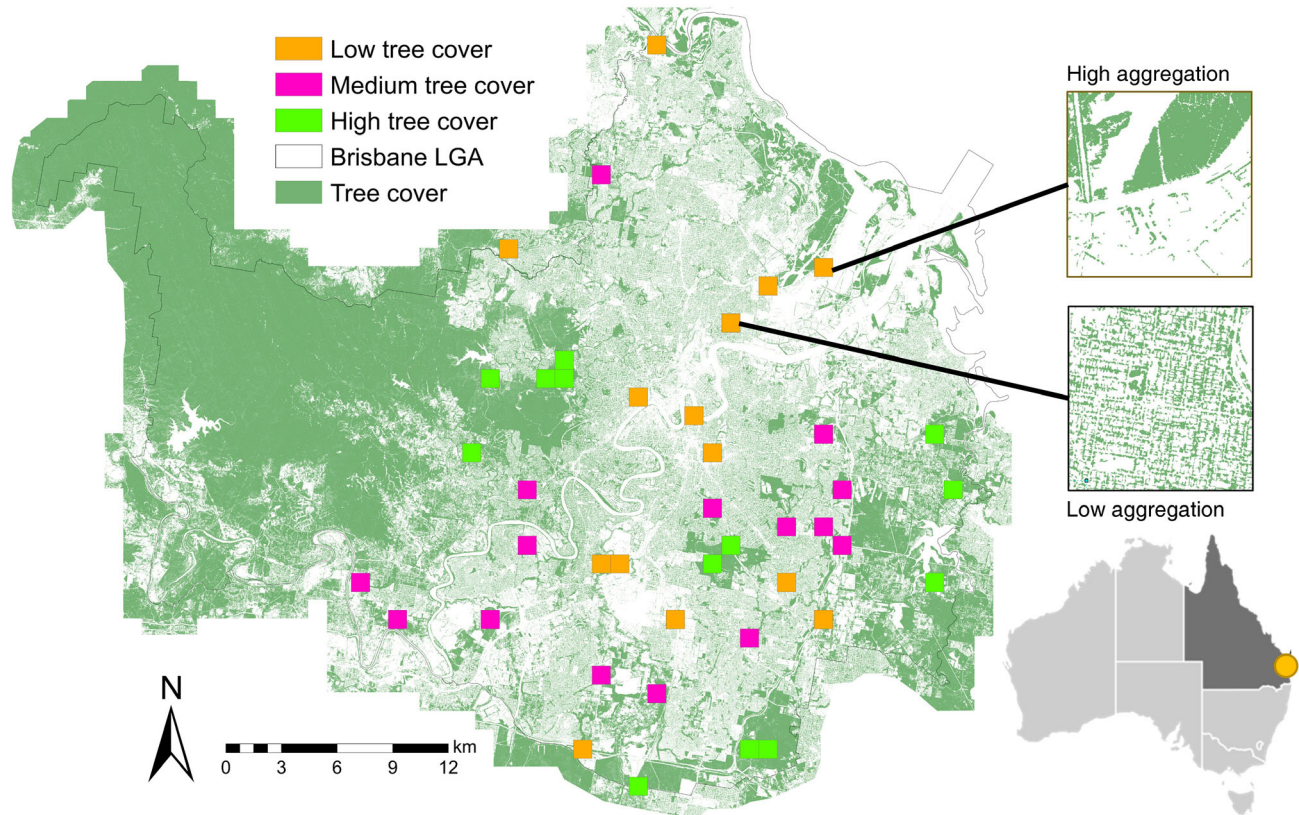


FIGURE 1 Brisbane local government area showing the landscape units used in this study. Landscape units were first selected based on tree cover (orange <35%, pink 35%–60%, bright green >60%). Each of these categories was stratified across different levels of fragmentation, ranging from low (clumpiness index > 0.8) to high (clumpiness index < 0.5) levels. Two units with similar levels of amount of tree cover and different levels of landscape fragmentation are shown in the right panel.

Brisbane for 2009 (see Mitchell et al. [2016] for details on how these data were processed). Each grid was then classified according to each of the following tree cover categories: low (10%–35%), medium (35%–60%), and high (>60%). For each category, we selected 14 landscape units stratified across different levels of fragmentation. We used the “clumpiness” metric, which measures spatial aggregation (McGarigal, 2002) but is relatively insensitive to variation in habitat extent, to measure fragmentation (Wang et al., 2014). This metric was calculated using a 5-m-resolution vegetation data layer within each grid and defining patches as four-neighbor contiguous cells using FRAGSTATS, version 4.2.598 (McGarigal, 2002). Within each vegetation cover category, fragmentation ranged from low (clumpiness index > 0.8) to high (clumpiness index < 0.5) (Figure 1). Within each 1-km² grid, we then selected three points to survey birds. To capture the heterogeneity within each landscape unit, we selected survey points in areas with different percentages of tree cover (<30%, 35%–60%, and >60%) when possible at the 1-ha scale. This process resulted in the selection of 126 survey points distributed across 42 landscape units.

For each selected 1-km² grid, we calculated the proportion of impervious surfaces and built infrastructure using the high-resolution LiDAR data. In addition, we calculated the average foliage height diversity (FHD), a relative density measure that describes how evenly vegetation is distributed across different vertical strata (Caynes et al., 2016; Mitchell et al., 2016). We included this variable because previous studies (e.g., Moudry et al., 2021) found that areas with high diversity in vertical vegetation structure promoted bird richness and the presence of rare species. Although vertical structure is usually measured as a local-scale variable, we were interested in evaluating whether this variable also had an influence at the landscape scale. More details on the calculation of the FHD index can be found in Caynes et al. (2016).

Bird surveys

We used 5-min point counts between dawn and 10:00 AM to estimate the density of all birds detected in each landscape unit. Point counts did not have a fixed radius,

and we recorded all the birds that were detected visually or aurally from that point. We used 5-min point counts because we were trying to increase the number of spatial replicates to collect information about relative abundances, rather than attempting to establish comprehensive data on site use. Each survey point was sampled twice in each of two seasons, summer (January–March 2016) and winter (mid-May–August 2016), for a total of four repeat surveys. Surveys in each point within each season were separated by at least 1 week. To avoid biases produced by local-scale habitat variables on wetland birds (e.g., the presence of lakes), we excluded those species. Although we recorded other guilds, such as strictly granivore species and raptors, they were not considered in the statistical analyses. We recorded distances of sightings using a rangefinder TruPulse 360B, and each bird was recorded if they were seen or heard. Birds recorded as flying over were omitted from the statistical analyses to avoid biases in recording species at a sampling point. Each bird detection was assigned to one of five distance classes from the sampling point (0–10, 10–20, 20–40, 40–50, and >50 m). Surveys were approved under Animal Ethics Number GPEM/047/15/ARC.

Data analysis

Abundance estimates

Multiple-covariate distance sampling (Thomas et al., 2010) was used to fit detection functions to the observed data separately for each species and to account for the effect of environmental factors for detection probability. We fitted two alternative models to the observed distribution of detections using half-normal or hazard key functions with season, detection type (i.e., if the bird was seen or heard only), and percentage of tree cover at the 1-ha resolution as potential covariates of detection probability of each species. For species recorded infrequently (<30 records), a common detection function was generated by grouping infrequently recorded species with more common species expected to have similar detectability (Allredge et al., 2007). These groupings were based on similarities in diet (i.e., frugivores, nectarivores, insectivores) and main foraging stratum (canopy, understory, ground). Within each group, we used species as a covariate to model the scale parameter. For each landscape, we then calculated density estimates and analytical 95% confidence intervals for each species using the model with the lowest Akaike information criteria (AIC). The density of each species at the 1-km scale was estimated as the average density across the three sites surveyed in each landscape unit.

Functional trait diversity indices and species richness calculation

To understand how landscape structure may affect functional diversity of bird guilds, we selected four traits: dispersal capacity, body size, habitat plasticity, and foraging behavior plasticity (hereafter foraging behavior). Body size can be linked to many ecosystem properties and may represent a universal trait to predict the effects of landscape structure on ecosystem functioning (Séguin et al., 2014). Dispersal capacity and foraging behavior help to infer species responses to changes in landscape structure and are important for pollination, seed dispersal, and pest control. Although habitat plasticity corresponds to an expression of multiple traits, including diet, morphology, and foraging strategies, we included this trait because it may reflect other aspects of the species life cycle (i.e., reproduction capacity) that are not reflected in the other traits we analyzed. Values of body size were sourced from Garnett et al. (2015). Fraser et al. (2017) provided values of dispersal capacity for each species using a model developed by Garrard et al. (2012). Their model predicts median dispersal distances based on wingspan and body mass collated from published studies worldwide and predicts that birds with a higher wingspan-to-mass ratio will have longer median dispersal distances. We used the values of foraging behavior and habitat plasticity provided by Luck et al. (2013). These authors derived these values based on the frequency with which a particular species was recorded using different foraging behaviors and habitats in different Australian regions.

We classified bird species into two different guilds based on diet: frugivores/nectarivores and insectivores, following Wilman et al. (2014). These authors translated descriptions of bird diets from multiple sources into standardized, semi-quantitative information about the relative importance of different food categories. We defined insectivores as those whose diet is more than 60% arthropods. Nectarivores and frugivores were those whose diet includes more than 60% fruits and nectar and most likely contribute to pollination and seed dispersal (see Suárez-Castro et al. [2022] for a complete list of species recorded in this study and their trait values). Frugivores and nectarivores were grouped into a single group since most species in Brisbane (e.g., rainbow lorikeet *Trichoglossus chlorolepidotus*, brown honeyeater *Lichmera indistincta*) that use plant resources include both nectar and fruits in their diet.

For each of these guilds we quantified species richness, functional richness (FRic), functional evenness (FEve), and functional divergence (FDiv) combining all traits based on the species density estimates at the 1-km² resolution. FRic corresponds to the range of trait values

in a given area and reflects how much functional space is occupied by a community. FEve quantifies how evenly the functional trait space is occupied by the community (Villéger et al., 2008). FEve values will be lowest when some parts of the functional space are empty whereas others are densely populated (Mouchet et al., 2010). FDiv measures the extent to which dominant species diverge in their trait values using trait dissimilarity weighted by species abundance (Villéger et al., 2008). All diversity calculations were performed with the dbFD function implemented in the FD package (Laliberté & Legendre, 2010) in R version 3.6.2 (R Development Core Team).

Statistical analysis

Structural equation modeling (SEM) (Grace, 2006) was used to examine the association between landscape structure and functional diversity and species richness metrics. In SEMs, variables are connected by paths that quantify the association between variables based on hypothesized causal relationships. For each functional metric (i.e., FEve, FDiv, and FRic), we constructed a causal model structure and direction of hypothesized relationships (Figure 2). Landscape composition variables (percentage of built infrastructure [impervious surface + buildings] and tree cover) and landscape configuration variables (clumpiness index) are reported at the 1-km² resolution. We also included a direct relationship between FHD and species richness and between FHD and functional diversity to represent how vegetation structure may affect the evaluated metrics. In the full model (Figure 2a), all the components of landscape structure directly affect patterns of species richness and functional diversity. In addition, fragmentation mediates the effects of tree cover and built infrastructure by assuming a causal relationship between these variables and fragmentation and the direct effect of fragmentation on species richness and functional diversity. Fragmentation is assumed to moderate the strength of the relationship between landscape composition and both species richness and functional diversity. We tested this model against a model that assumed moderation effects did not exist (Figure 2b) and a simple model where only direct effects were assumed (Figure 2c). To analyze the effects of landscape structure on individual traits, we used the same models using the community weighted mean (CWM) for each trait as the response variable. We calculated the CWM for each trait with the dbFD function implemented in the FD package (Laliberté & Legendre, 2010).

Following the recommendations by Weston and Gore (2006), we used multiple parsimony-based fit indices to determine which of the three models have the highest

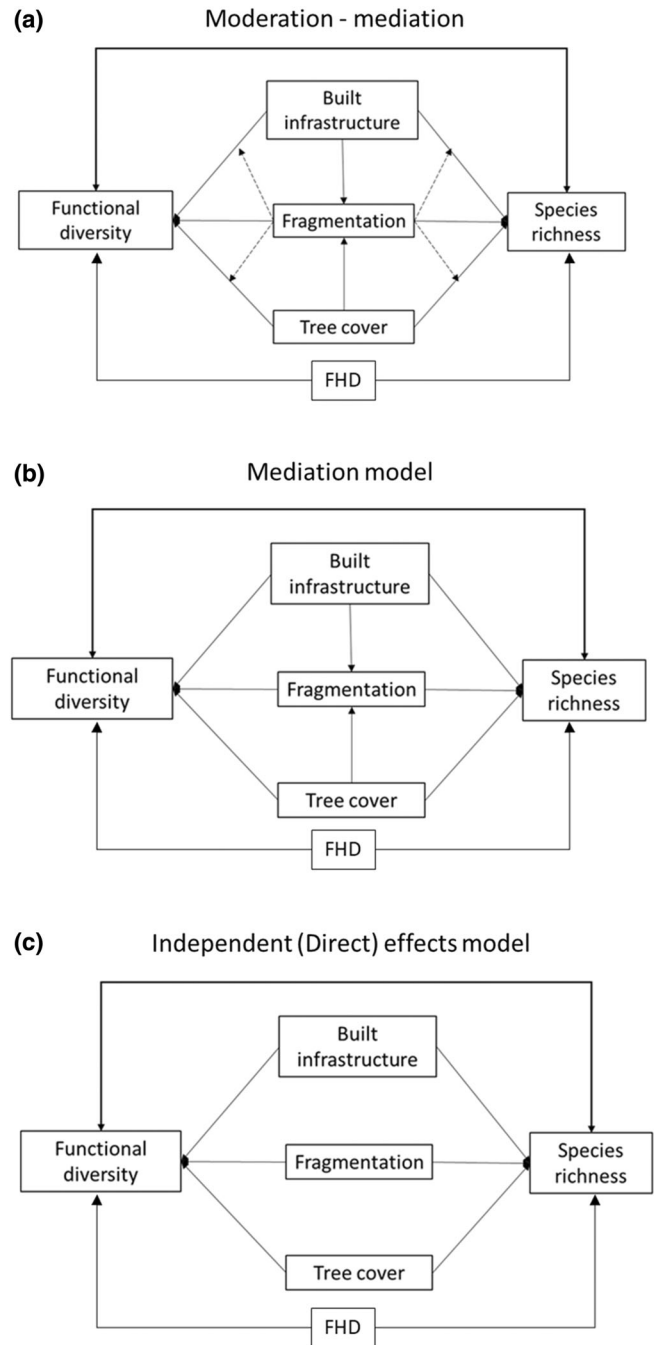


FIGURE 2 Conceptual model showing the main relationships between landscape structure and species richness and functional diversity. See explanation of pathways in the *Statistical analysis* section of the *Methods*. FHD, foliage height diversity.

parsimony. The three hypothetical models were compared using the Tucker–Lewis index (TLI) and the root mean square error of approximation (RMSEA). A TLI value of 0.95 or larger indicates good model fit, whereas RMSEA values <0.06 indicate good fit (Weston & Gore, 2006). The model with the lowest RMSEA and the highest TLI was considered the best. All response and explanatory variables were standardized (mean = 0, SD = 1) prior to

fitting the models. Analyses were performed using the lavaan package (Rosseel, 2012) in R version 3.6.2.

RESULTS

A total of 84 terrestrial bird species were observed during the survey period (Suárez-Castro et al., 2022). Species richness for all the recorded birds in areas with a high percentage of built infrastructure (>70%) ranged from 13 to 24 species per 1-km² grid, whereas in areas with a low percentage of built infrastructure (<35%), species richness ranged from 22 to 41 species. The number of insectivore species recorded was higher (41) than the number of frugivores/nectarivores (25).

For all functional diversity metrics and the guilds evaluated, the structural equation models, including direct pathways for tree cover, percentage of built infrastructure, and fragmentation, as well as the mediating effects of fragmentation on landscape composition effects, had the best overall fit (TLI = 1, RMSEA = 0.048, df = 10). Including the direct causal pathway between FHD and either functional diversity or species richness did not improve overall model fit (TLI = 1, RMSEA = 0.435, df = 14). Therefore, because the vertical structure of the vegetation did not help to explain the effects of landscape structure on either species richness or functional diversity at the 1-km² resolution, we did not consider this variable in further analyses. The fit coefficients of the models considered for each guild are presented in Table 2.

The association between species richness and functional diversity depended on the metric analyzed (Figure 3; Appendix S1: Table S2). The correlation between FRic and species richness was highly positive for both guilds (Figure 3a,b). The correlation between species richness and FDiv was also positive and statistically significant ($p < 0.0001$), although it was higher for frugivores/nectarivores than for insectivores (Figure 3c,d). We did not find a correlation between FEve and species richness for the two guilds.

Direct effects of landscape composition on functional metrics and species richness differed between the two guilds (Figure 3; Appendix S1: Table S2). Built infrastructure had consistent negative effects on species richness for both guilds, but the effect on FRic (Figure 3a,b) and FDiv (Figure 3c,d) was higher for frugivores compared to insectivores. The effects of the proportion of tree cover on all the evaluated metrics and guilds were consistently lower than the effects of built infrastructure. The only exception was for FEve of insectivores, where an increase in the proportion of tree cover promoted lower levels of FEve (Figure 3f).

The direct and indirect effects of fragmentation on functional diversity metrics were highly variable and depended on the metric and the guild evaluated. Compared to the effects of landscape composition, the effects of fragmentation on FRic and species richness of frugivores/nectarivores were low (Figure 3b). In contrast, fragmentation had a strong negative effect on the FDiv of the insectivore guild (Figure 3c). Although the direct effects of fragmentation were always higher than indirect effects, we found evidence that fragmentation also mediated the negative effects of built infrastructure on FDiv and FRic of insectivores (Appendix S1: Table S2). No fragmentation effects were found on FEve for either guild (Figure 3e,f).

Landscape structure had various effects on the distribution of single traits. Built infrastructure promoted frugivore/nectarivore guilds with a higher proportion of species with high habitat plasticity, but that displayed a lower diversity of foraging behaviors (Figure 4). In addition, the effects of tree cover varied between guilds. We found a positive relationship between tree cover and dispersal for frugivores/nectarivores (Figure 4; Appendix S1: Table S3), but this variable did not affect the diversity of dispersal capacities of insectivores. On the other hand, tree cover had positive effects on frugivore/nectarivores with high habitat plasticity, whereas tree cover favored insectivores with low habitat plasticity (standardized coefficient = -0.41 , $p < 0.0001$). Fragmentation promoted species with large body size and high dispersal capacities for both guilds (Figure 4a,b). In addition, highly fragmented areas increased the proportion of insectivore species with high habitat plasticity and foraging behaviors (Figure 4; Appendix S1: Table S3).

DISCUSSION

Understanding the effects of landscape structure on different components of biodiversity and across multiple guilds is critical for managing multifunctional landscapes. Here we show that the effects of landscape structure on bird functional diversity and species richness are highly variable and depend on the metric and the guild evaluated. There is a clear negative effect of the extent of built infrastructure on species richness, but functional diversity showed a more complex relationship with landscape composition and landscape configuration. For example, we found that fragmentation increased the negative effects of built infrastructure on both the richness and the proportional abundance of insectivore traits. In contrast, functional diversity of frugivore/nectarivore species mainly depended on landscape composition rather than on fragmentation. Fragmentation also increased the effects of built infrastructure for some

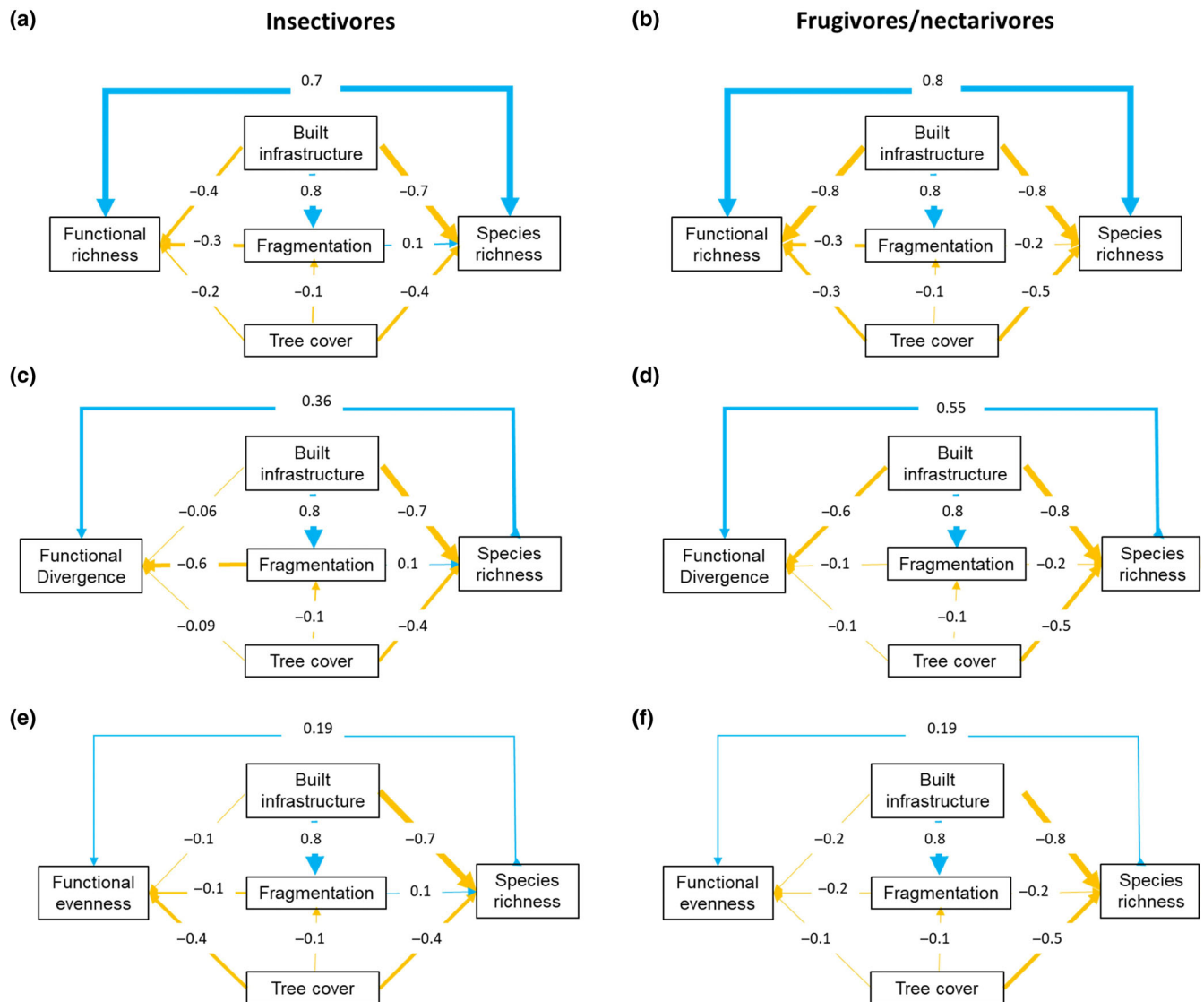


FIGURE 3 Structural equation models showing the direct effects of landscape structure on different functional components for the insectivore and the frugivore guilds. Numbers between arrows indicate standardized path coefficients, which allow for comparing relationship strengths within a model: (a, b) functional richness; (c, d) functional divergence; and (e, f) functional evenness. The line thickness represents the strength of the relationship. Blue: positive effect, orange: negative effect.

traits (body size and dispersal capacity), but not for others (habitat plasticity and foraging behavior). These results suggest that managing landscape configuration alone may not maximize functional diversity and species richness simultaneously for all guilds. Differential approaches to managing landscape structure are thus needed depending on whether the focus is on protecting functional diversity or species richness and what the target guild is (Figure 5).

Landscape structure also affected patterns of trait abundance independently of FRic for each guild. The relationship between FDiv and landscape structure shows that built infrastructure (for frugivores/nectarivores) and fragmentation (for insectivores) increased the similarity

in the trait values of the dominant species. We found that highly fragmented areas with low levels of tree cover had higher abundance of insectivores that had the following traits: large body size, high dispersal capacities, high habitat plasticity, and high diversity of foraging behaviors (Figure 4). Furthermore, tree cover was associated with insectivore species that had lower habitat plasticity, regardless of the level of fragmentation. Several studies reported a decline of species with high habitat plasticity and an increase of bird forest specialists associated with particular forest types, both in agricultural (Socolar & Wilcove, 2019) and urban areas (Liordos et al., 2021). This pattern can also be associated with an increase in the abundance and biomass of birds with high habitat plasticity in areas where the extent of

TABLE 2 Fit coefficients for all models considered in this study.

Functional diversity metric	Model	CFI	TLI	AIC	RMSEA	RMSEA CI lower	RMSEA CI upper
Insectivores							
FRic	Simple	1.00	1.00	449.87	0.00	0.00	0.00
	Mediation	1.00	1.00	307.73	0.00	0.00	0.00
	Moderation	0.32	−4.08	312.38	1.46	1.28	1.64
FEve	Simple	1.00	1.00	165.54	0.00	0.00	0.00
	Mediation	1.00	1.00	23.40	0.00	0.00	0.00
	Moderation	0.20	−5.03	27.80	1.46	1.28	1.64
FDiv	Simple	0.93	0.96	355.58	0.00	0.00	0.00
	Mediation	1.00	1.00	213.43	0.00	0.00	0.00
	Moderation	0.26	−4.53	213.14	1.46	1.28	1.64
Frugivores/nectarivores							
FRic	Simple	1.00	1.00	355.01	0.00	0.00	0.00
	Mediation	1.00	1.00	212.19	0.00	0.00	0.00
	Moderation	0.33	−4.03	214.93	1.46	1.28	1.64
FEve	Simple	1.00	1.00	159.54	0.00	0.00	0.00
	Mediation	1.00	1.00	17.20	0.00	0.00	0.00
	Moderation	0.18	−5.11	20.80	1.46	1.28	1.52
FDiv	Simple	1.00	1.00	556.58	0.00	0.00	0.00
	Mediation	1.00	1.00	440.43	0.00	0.00	0.00
	Moderation	0.30	−4.24	442.14	1.67	1.42	1.62

Abbreviations: AIC, Akaike information criterion; CI, confidence interval; CFI, comparative fit index; FRic, functional richness; FEve, functional evenness; FDiv, functional divergence; RMSEA, root mean square error of approximation; TLI, Tucker–Lewis index.

built infrastructure is high (Batáry et al., 2017; Brown & Graham, 2015; Coetzee & Chown, 2016; Evans et al., 2011).

We provide evidence that patterns of FEve and FDiv can vary for urban guilds with similar levels of species richness. One common pattern includes the coexistence of a few species with similar traits contributing most of the individuals (Batáry et al., 2017; Coetzee & Chown, 2016). In this case, high levels of FEve and low FDiv occur because the limited functional space will be filled by a small set of common species. On the other hand, the occurrence of less abundant, generalist species with uncommon traits can foster low levels of FEve and high divergence. In Brisbane, frugivore/nectarivore guilds tend to be dominated by large species in highly modified environments. However, some relatively small species with high habitat plasticity, such as the brown honeyeater (*L. indistincta*) and the mistletoebird (*Dicaeum hirundinaceum*), can still contribute to the diversity of each local guild. Contrasting responses of trait abundance to landscape change that are uncorrelated to species richness have been reported for both simulated communities (Mouchet et al., 2010; Suárez-Castro et al., 2020) and other avian assemblages (Ding et al., 2013; Ibarra & Martin, 2015).

Our results show the benefits of understanding when landscape structure promotes positive relationships between species richness and FRic. We show that landscape structure filters species less adapted to urban landscapes through the direct (“independent”) effects of landscape composition, particularly through the proportion of built infrastructure that has negative effects on FRic. Green area management policies that reduce the negative effects of impervious surfaces are thus key to protecting species richness and FRic simultaneously (Souza et al., 2019; Sultana et al., 2021). However, FRic can be enhanced in some cases even if it is not possible to maintain high levels of species richness. Built infrastructure affected species richness of insectivores more negatively than FRic. This suggests that for this guild, many species tend to share similar trait values, and the loss of some species does not necessarily translate to the loss of species traits. In this case, local-scale strategies focused on maintaining heterogeneous habitats with complex vegetation types within urban green spaces can be enough to protect FRic, even if the levels of built infrastructure are high (Callaghan et al., 2018; Mbiba et al., 2021; Oliveira Hagen et al., 2017).

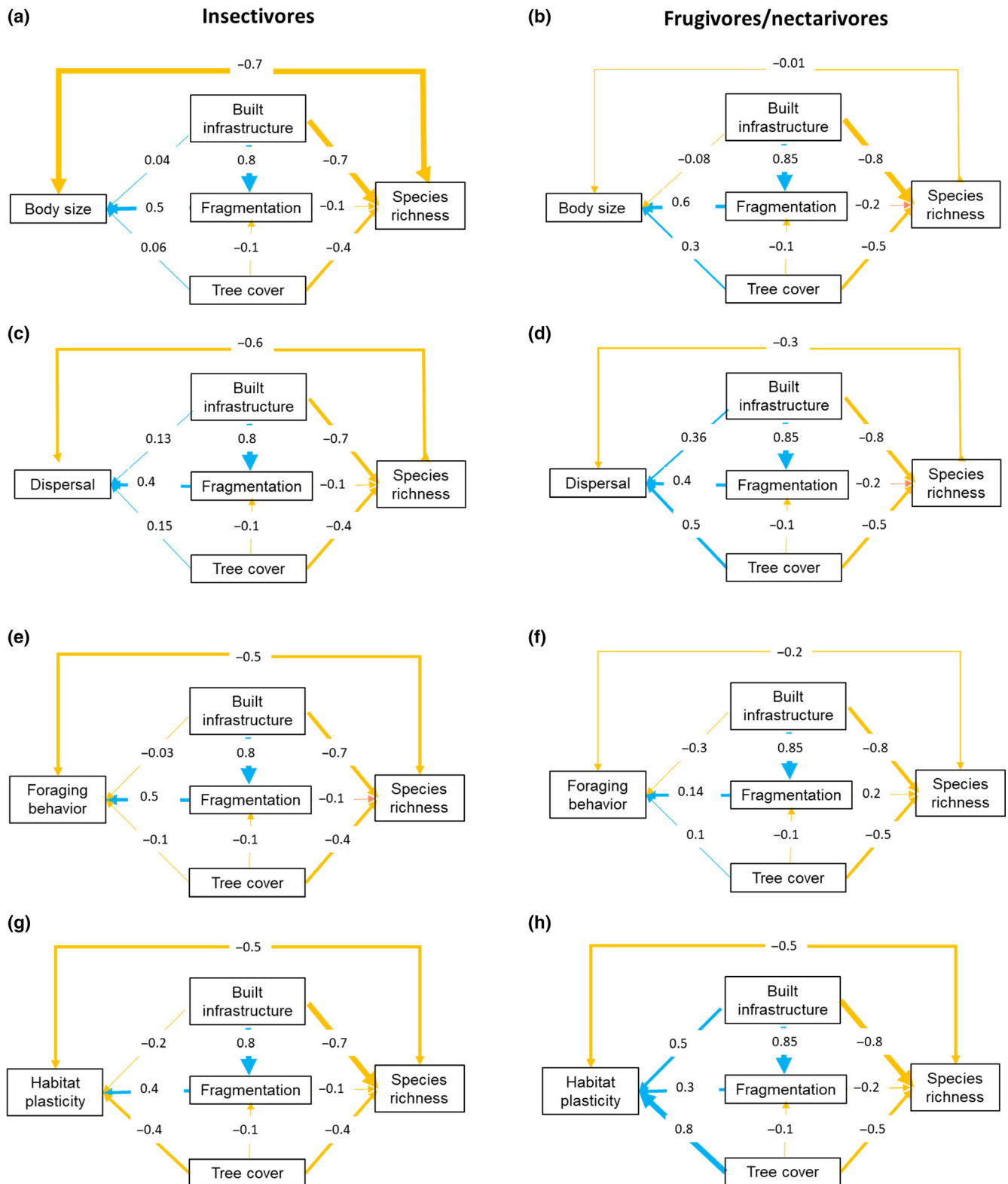


FIGURE 4 Structural equation models showing the direct effects of landscape structure on different species traits for the insectivore and the frugivore guilds. Numbers between arrows indicate standardized path coefficients, which allow for comparing relationship strengths within a model. The line thickness represents the strength of the relationship. Blue: positive effect, orange: negative effect.

The importance of focusing on managing landscape configuration in urban areas will depend on the management objective. We suggest that managing

landscape configuration is important if the objective is to enhance the abundance of less common traits of insectivore species. Previous work in Brisbane showed

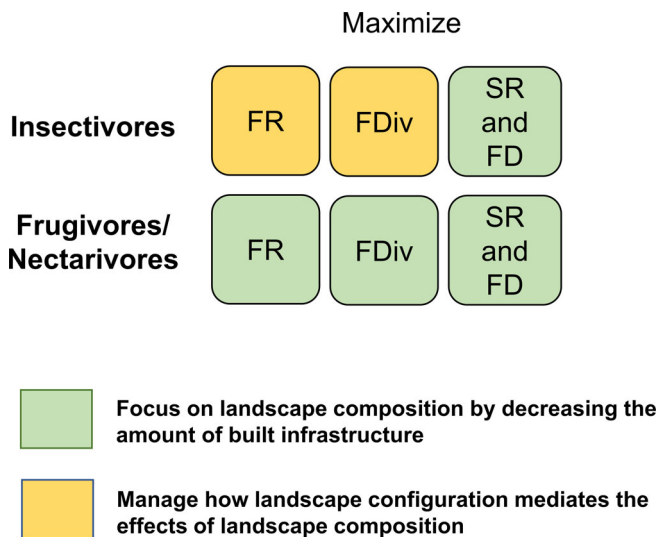


FIGURE 5 Landscape management approaches to maximizing the functional diversity (FD) of urban birds. If the objective is to enhance functional richness (FR), functional divergence (FDiv), and species richness (SR) simultaneously, the focus should be on improving landscape composition (e.g., setting aside urban reserves, improving habitat in remnant patches) rather than promoting specific landscape configurations in growing cities. Managing landscape configuration is important if the objective is to enhance the abundance of less common traits of insectivore species in our study landscapes. Minimizing fragmentation and enhancing the connectivity of remnant areas can increase FR and FDiv for insectivores, even if it is not possible to maintain high levels of species richness.

that maintaining landscape connectivity of medium-sized patches (>10 ha) can not only benefit bird species richness (Litteral & Shochat, 2017; Shanahan et al., 2011) but also reduce the dominance of large-bodied species (Catterall et al., 2010). The dominance of large-bodied species translates into low levels of FRic and FDiv, and so maintaining well-connected, medium-sized patches might be the best option when it comes to preserving species with extreme trait values (Catterall et al., 2010; Lim & Sodhi, 2004). On the other hand, if the aim is to enhance species richness at landscape scales while maintaining a high trait richness, the focus should be on reducing the negative effects of built infrastructure rather than on promoting certain habitat configurations. The negative effects of built infrastructure can be attenuated by promoting sensitive urban design practices (Garrard et al., 2018) that protect small patches (Wintle et al., 2019) and maintain native trees and shrub vegetation in gardens. Other management activities could include the management of riparian corridors using native plant species and increasing the complexity of the remaining vegetation (Ikin et al., 2014; Mayorga et al., 2020).

An enhancement to our study would be to conduct the analysis at multiple scales and while considering

the effects of species interactions. We conducted our analysis at a single scale, but future studies should take into consideration a multiscale approach. The effects of landscape structure are scale-dependent, and complex interactions operate simultaneously to shape species assemblages at patch and landscape extents. For example, previous work found that bird insectivory increases at edges and in small forest fragments (Barbaro et al., 2014; González-Gómez et al., 2006), and this increase may be explained by greater evenness in trait abundance distributions in edge than in interior bird assemblages (Barbaro et al., 2014). Testing this hypothesis requires evaluating edge effects that we did not include in our analyses. In addition, although we provide key insights about the effects of landscape structure on bird diversity, we did not consider how interactions between species may drive patterns of trait diversity (Rogers et al., 2020). An important area of research consists in analyzing how species network interactions reflect patterns of functional diversity in urban areas.

Our new insights could be integrated into an assessment of strategies to maximize bird functional diversity and species richness in urban environments roughly at the extent of a neighborhood. We show that landscape composition is the main driver of both species richness and FRic in urban environments. However, as the extent of built infrastructure increases and fragmented habitats become more common, accounting for landscape configuration can be important in promoting the abundance of species with less common traits. Our results suggest that approaches that aim to maintain small patches of vegetation distributed over large extents may help to maintain some species with unique traits (high FRic). However, we show that the overall trait distribution will be skewed toward common dominant traits for some guilds if the effects of fragmentation are ignored. Although local-scale management practices are always encouraged to protect urban biodiversity, these strategies may be ineffective if the effects of landscape structure are ignored.

AUTHOR CONTRIBUTIONS

All authors conceived the study. Andrés Felipe Suárez-Castro collected the data. Andrés Felipe Suárez-Castro and Jonathan R. Rhodes analyzed the data and wrote the paper with contributions from all authors. All authors contributed critically and gave final approval for publication.

ACKNOWLEDGMENTS

This work was supported by Australian Research Council Discovery Project DP130100218. Andrés Felipe Suárez-Castro was supported by a Colombian Ministry of Education (COLCIENCIAS 529) scholarship. Jonathan

R. Rhodes was supported by an ARC Future Fellowship (FT200100096). Constructive reviews from two anonymous reviewers substantially improved our manuscript. Open access publishing facilitated by Griffith University, as part of the Wiley - Griffith University agreement via the Council of Australian University Librarians.

CONFLICT OF INTEREST

The authors have declared no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Suárez-Castro et al., 2022) are available in Figshare at <https://doi.org/10.6084/m9.figshare.19501945.v2>.

ORCID

Andrés Felipe Suárez-Castro  <https://orcid.org/0000-0002-6621-3821>

Martine Maron  <https://orcid.org/0000-0002-5563-5789>

Matthew G. E. Mitchell  <https://orcid.org/0000-0002-3490-9314>

Jonathan R. Rhodes  <https://orcid.org/0000-0001-6746-7412>

REFERENCES

- Allredge, M. W., T. R. Simons, and K. H. Pollock. 2007. "A Field Evaluation of Distance Measurement Error in Auditory Avian Point Count Surveys." *The Journal of Wildlife Management* 71: 2759–66.
- Barbaro, L., B. Giffard, Y. Charbonnier, I. Van Halder, and E. G. Brockerhoff. 2014. "Bird Functional Diversity Enhances Insectivory at Forest Edges: A Transcontinental Experiment." *Diversity and Distributions* 20: 149–59.
- Batáry, P., K. Kurucz, M. Suarez-Rubio, and D. E. Chamberlain. 2017. "Non-linearities in Bird Responses across Urbanization Gradients: A Meta-Analysis." *Global Change Biology* 24: 1046–54.
- Bregman, T. P., C. H. Sekercioglu, and J. A. Tobias. 2014. "Global Patterns and Predictors of Bird Species Responses to Forest Fragmentation: Implications for Ecosystem Function and Conservation." *Biological Conservation* 169: 372–83.
- Brown, L. M., and C. H. Graham. 2015. "Demography, Traits and Vulnerability to Urbanization: Can we Make Generalizations?" *Journal of Applied Ecology* 52: 1455–64.
- Callaghan, C. T., R. E. Major, M. B. Lyons, J. M. Martin, and R. T. Kingsford. 2018. "The Effects of Local and Landscape Habitat Attributes on Bird Diversity in Urban Greenspaces." *Ecosphere* 9: e02347.
- Catterall, C. P., J. A. Cousin, S. Piper, and G. Johnson. 2010. "Long-Term Dynamics of Bird Diversity in Forest and Suburb: Decay, Turnover or Homogenization?" *Diversity and Distributions* 16: 559–70.
- Caynes, R. J. C., M. G. E. Mitchell, D. S. Wu, K. Johansen, and J. R. Rhodes. 2016. "Using High-Resolution LiDAR Data to Quantify the Three-Dimensional Structure of Vegetation in Urban Green Space." *Urban Ecosystem* 19: 1749–65.
- Coetzee, B. W. T., and S. L. Chown. 2016. "Land-Use Change Promotes Avian Diversity at the Expense of Species with Unique Traits." *Ecology and Evolution* 6: 7610–22.
- Didham, R. K., V. Kapos, and R. M. Ewers. 2012. "Rethinking the Conceptual Foundations of Habitat Fragmentation Research." *Oikos* 121: 161–70.
- Ding, Z., K. J. Feeley, Y. Wang, R. J. Pakeman, and P. Ding. 2013. "Patterns of Bird Functional Diversity on Land-Bridge Island Fragments." *Journal of Animal Ecology* 82: 781–90.
- Evans, K. L., D. E. Chamberlain, B. J. Hatchwell, R. D. Gregory, and K. J. Gaston. 2011. "What makes an urban bird?" *Global Change Biology* 17: 32–44.
- Fahrig, L. 2017. "Ecological Responses to Habitat Fragmentation per se." *Annual Review of Ecology, Evolution, and Systematics* 48: 1–23.
- Fauth, J. E., J. Bernardo, M. Camara, W. J. Resetarits, J. Van Buskirk, and S. A. Mccollum. 1996. "Simplifying the Jargon of Community Ecology: A Conceptual Approach." *The American Naturalist* 147: 282–6.
- Fischer, J., D. J. Abson, V. Butsic, M. J. Chappell, J. Ekroos, J. Hanspach, T. Kuemmerle, H. G. Smith, and H. Von Wehrden. 2014. "Land Sparing Versus Land Sharing: Moving Forward." *Conservation Letters* 7: 149–57.
- Flynn, D. F. B., M. Gogol-Prokurat, T. Nogeire, N. Molinari, B. T. Richers, B. B. Lin, N. Simpson, M. M. Mayfield, and F. Declerck. 2009. "Loss of Functional Diversity under Land Use Intensification across Multiple Taxa." *Ecology Letters* 12: 22–33.
- Fraser, H., C. E. Hauser, L. Rumpff, G. E. Garrard, and M. A. Mccarthy. 2017. "Classifying Animals into Ecologically Meaningful Groups: A Case Study on Woodland Birds." *Biological Conservation* 214: 184–94.
- Garnett, S. T., D. E. Duursma, G. Ehmke, P.-J. Guay, A. Stewart, J. K. Szabo, M. A. Weston, et al. 2015. "Biological, Ecological, Conservation and Legal Information for all Species and Subspecies of Australian Bird." *Scientific Data* 2: 150061.
- Garrard, G. E., M. A. Mccarthy, P. A. Vesk, J. Q. Radford, and A. F. Bennett. 2012. "A Predictive Model of Avian Natal Dispersal Distance Provides Prior Information for Investigating Response to Landscape Change." *Journal of Animal Ecology* 81: 14–23.
- Garrard, G. E., N. S. G. Williams, L. Mata, J. Thomas, and S. A. Bekessy. 2018. "Biodiversity Sensitive Urban Design." *Conservation Letters* 11: e12411.
- González-Gómez, P. L., C. F. Estades, and J. A. Simonetti. 2006. "Strengthened Insectivory in a Temperate Fragmented Forest." *Oecologia* 148: 137–43.
- Grace, J. B. 2006. *Structural Equation Modeling and Natural Systems*. Cambridge, UK; New York, NY: Cambridge University Press.
- Gross, N., Y. L. Bagousse-Pinguet, P. Liancourt, M. Berdugo, N. J. Gotelli, and F. T. Maestre. 2017. "Functional Trait Diversity Maximizes Ecosystem Multifunctionality." *Nature Ecology Evolution* 1: 132.
- Hatfield, J. H., M. L. K. Harrison, and C. Banks-Leite. 2018. "Functional Diversity Metrics: How they Are Affected by Landscape Change and how they Represent Ecosystem Functioning in the Tropics." *Current Landscape Ecology Reports* 3: 35–42.

- Ibarra, J. T., and K. Martin. 2015. "Biotic Homogenization: Loss of Avian Functional Richness and Habitat Specialists in Disturbed Andean Temperate Forests." *Biological Conservation* 192: 418–27.
- Ikin, K., P. S. Barton, I. A. Stirnemann, J. R. Stein, D. Michael, M. Crane, S. Okada, and D. B. Lindenmayer. 2014. "Multi-Scale Associations between Vegetation Cover and Woodland Bird Communities across a Large Agricultural Region." *PLoS Biology* 9: e97029.
- Jacobs, B. M., N. Mikhailovich, and C. Delaney. 2014. *Benchmarking Australia's Urban Tree Canopy: An I-Tree Assessment, Final Report*. Sydney, NSW: University of Technology Sydney.
- Laliberté, E., and P. Legendre. 2010. "A Distance-Based Framework for Measuring Functional Diversity from Multiple Traits." *Ecology* 91: 299–305.
- Lim, H. C., and N. S. Sodhi. 2004. "Responses of Avian Guilds to Urbanisation in a Tropical City." *Landscape and Urban Planning* 66: 199–215.
- Liordos, V., J. Jokimäki, M.-L. Kaisanlahti-Jokimäki, E. Valsamidis, and V. J. Kontsiotis. 2021. "Niche Analysis and Conservation of Bird Species Using Urban Core Areas." *Sustainability* 13: 6327.
- Litteral, J., and E. Shochat. 2017. "The Role of Landscape-Scale Factors in Shaping Urban Bird Communities." In *Ecology and Conservation of Birds in Urban Environments*, edited by E. Murgui and M. Hedblom. Cham: Springer International Publishing.
- Luck, G. W., A. Carter, and L. Smallbone. 2013. "Changes in Bird Functional Diversity across Multiple Land Uses: Interpretations of Functional Redundancy Depend on Functional Group Identity." *PLoS Biology* 8: e63671.
- Mayfield, M. M., S. P. Bonser, J. W. Morgan, I. Aubin, S. Mcnamara, and P. A. Vesik. 2010. "What Does Species Richness Tell us about Functional Trait Diversity? Predictions and Evidence for Responses of Species and Functional Trait Diversity to Land-Use Change." *Global Ecology and Biogeography* 19: 423–31.
- Mayorga, I., P. Bichier, and S. M. Philpott. 2020. "Local and Landscape Drivers of Bird Abundance, Species Richness, and Trait Composition in Urban Agroecosystems." *Urban Ecosystem* 23: 495–505.
- Mbiba, M., C. Mazhude, C. Fabricius, H. Fritz, and J. Muvengwi. 2021. "Bird Species Assemblages Differ, while Functional Richness Is Maintained across an Urban Landscape." *Landscape and Urban Planning* 212: 104094.
- McDonald, R. I., A. V. Mansur, F. Ascensão, M. L. Colbert, K. Crossman, T. Elmquist, A. Gonzalez, et al. 2020. "Research Gaps in Knowledge of the Impact of Urban Growth on Biodiversity." *Nature Sustainability* 3: 16–24.
- McGarigal, K., S. A. Cushman, M. C. Neel, and E. Ene. 2002. "FRAGSTATS: Spatial Pattern Analysis Program for Categorical Maps." Computer Software Program Produced by the Authors at the University of Massachusetts, Amherst. www.umass.edu/landeco/research/fragstats/fragstats.html.
- Mitchell, M. G. E., D. Wu, K. Johansen, M. Maron, C. Mcalpine, and J. R. Rhodes. 2016. "Landscape Structure Influences Urban Vegetation Vertical Structure." *Journal of Applied Ecology* 53: 1477–88.
- Mori, A. S., T. Furukawa, and T. Sasaki. 2013. "Response Diversity Determines the Resilience of Ecosystems to Environmental Change." *Biological Reviews of the Cambridge Philosophical Society* 88: 349–64.
- Mouchet, M. A., S. Villéger, N. W. H. Mason, and D. Moullot. 2010. "Functional Diversity Measures: An Overview of their Redundancy and their Ability to Discriminate Community Assembly Rules." *Functional Ecology* 24: 867–76.
- Moudrý, V., L. Moudrá, V. Barták, V. Bejček, K. Gdulová, M. Hendrychová, D. Moravec, et al. 2021. "The Role of the Vegetation Structure, Primary Productivity and Senescence Derived from Airborne LiDAR and Hyperspectral Data for Birds Diversity and Rarity on a Restored Site." *Landscape and Urban Planning* 210: 104064.
- Oliveira Hagen, E., O. Hagen, J. D. Ibáñez-Álamo, O. L. Petchey, and K. L. Evans. 2017. "Impacts of Urban Areas and Their Characteristics on Avian Functional Diversity." *Frontiers in Ecology and Evolution* 5: 84.
- Püttker, T., R. Crouzeilles, M. Almeida-Gomes, M. Schmoeller, D. Maurenza, H. Alves-Pinto, R. Pardini, et al. 2020. "Indirect Effects of Habitat Loss Via Habitat Fragmentation: A Cross-Taxa Analysis of Forest-Dependent Species." *Biological Conservation* 241: 108368.
- Rocha-Santos, L., M. M. Mayfield, A. V. Lopes, M. S. Pessoa, D. C. Talora, D. Faria, and E. Cazetta. 2020. "The Loss of Functional Diversity: A Detrimental Influence of Landscape-Scale Deforestation on Tree Reproductive Traits." *Journal of Ecology* 108: 212–23.
- Rogers, A. M., A. S. Griffin, B. J. Van Rensburg, and S. Kark. 2020. "Noisy Neighbours and Myna Problems: Interaction Webs and Aggression around Tree Hollows in Urban Habitats." *Journal of Applied Ecology* 57: 1891–901.
- Rosseel, Y. 2012. "lavaan: An R Package for Structural Equation Modeling." *Journal of Statistical Software* 1: 36.
- Rybicki, J., N. Abrego, and O. Ovaskainen. 2019. "Habitat Fragmentation and Species Diversity in Competitive Communities." *Ecology Letters* 23(3): 506–17.
- Rybicki, J., and I. Hanski. 2013. "Species–Area Relationships and Extinctions Caused by Habitat Loss and Fragmentation." *Ecology Letters* 16: 27–38.
- Séguin, A., É. Harvey, P. Archambault, C. Nozais, and D. Gravel. 2014. "Body Size as a Predictor of Species Loss Effect on Ecosystem Functioning." *Scientific Reports* 4: 4616. <https://doi.org/10.1038/srep04616>.
- Seto, K. C., B. Güneralp, and L. R. Hutyrá. 2012. "Global Forecasts of Urban Expansion to 2030 and Direct Impacts on Biodiversity and Carbon Pools." *Proceedings of the Royal Society of London, Series B: Biological Sciences* 109: 16083–8.
- Shanahan, D. F., C. Miller, H. P. Possingham, and R. A. Fuller. 2011. "The Influence of Patch Area and Connectivity on Avian Communities in Urban Revegetation." *Biological Conservation* 144: 722–9.
- Socolar, J. B., and D. S. Wilcove. 2019. "Forest-Type Specialization Strongly Predicts Avian Responses to Tropical Agriculture." *Proceedings of the Royal Society B: Biological Sciences* 286: 20191724.
- Soga, M., Y. Yamaura, S. Koike, and K. J. Gaston. 2014. "Land Sharing Vs. Land Sparing: Does the Compact City Reconcile

- Urban Development and Biodiversity Conservation?" *Journal of Applied Ecology* 51: 1378–86.
- Souza, F. L., F. Valente-Neto, F. Severo-Neto, B. Bueno, J. M. Ochoa-Quintero, R. R. Laps, F. Bolzan, and F. D. O. Roque. 2019. "Impervious Surface and Heterogeneity Are Opposite Drivers to Maintain Bird Richness in a Cerrado City." *Landscape and Urban Planning* 192: 103643.
- Stroud, J. T., M. R. Bush, M. C. Ladd, R. J. Nowicki, A. A. Shantz, and J. Sweatman. 2015. "Is a Community Still a Community? Reviewing Definitions of Key Terms in Community Ecology." *Ecology and Evolution* 5: 4757–65.
- Suárez-Castro, A. F., M. Maron, M. G. E. Mitchell, and J. R. Rhodes. 2022. "Suarez et al. Urban Birds Functional Diversity EAP21-0638." Figshare, Data Set. <https://doi.org/10.6084/m9.figshare.19501945.v2>.
- Suárez-Castro, A. F., M. M. Mayfield, M. G. E. Mitchell, L. Cattarino, M. Maron, and J. R. Rhodes. 2020. "Correlations and Variance among Species Traits Explain Contrasting Impacts of Fragmentation and Habitat Loss on Functional Diversity." *Landscape Ecology* 35: 2239–53.
- Sultana, M., L. Corlatti, and I. Storch. 2021. "The Interaction of Imperviousness and Habitat Heterogeneity Drives Bird Richness Patterns in South Asian Cities." *Urban Ecosystem* 24: 335–44.
- Sushinsky, J. R., J. R. Rhodes, H. P. Possingham, T. K. Gill, and R. A. Fuller. 2013. "How Should we Grow Cities to Minimize their Biodiversity Impacts?" *Global Change Biology* 19: 401–10.
- Thomas, L., S. T. Buckland, E. A. Rexstad, J. L. Laake, S. Strindberg, S. L. Hedley, J. R. B. Bishop, T. A. Marques, and K. P. Burnham. 2010. "Distance Software: Design and Analysis of Distance Sampling Surveys for Estimating Population Size." *The Journal of Applied Ecology* 47: 5–14.
- Tscharntke, T., J. M. Tylianakis, T. A. Rand, R. K. Didham, L. Fahrig, P. Batáry, J. Bengtsson, et al. 2012. "Landscape Moderation of Biodiversity Patterns and Processes - Eight Hypotheses." *Biological Reviews of the Cambridge Philosophical Society* 87: 661–85.
- Villard, M. A., and J. P. Metzger. 2014. "Beyond the Fragmentation Debate: A Conceptual Model to Predict when Habitat Configuration Really Matters." *Journal of Applied Ecology* 51: 309–18.
- Villéger, S., N. W. H. Mason, and D. Mouillot. 2008. "New Multidimensional Functional Diversity Indices for a Multifaceted Framework in Functional Ecology." *Ecology* 89: 2290–301.
- Wang, X., F. G. Blanchet, N. Koper, and A. Tatem. 2014. "Measuring Habitat Fragmentation: An Evaluation of Landscape Pattern Metrics." *Methods in Ecology and Evolution* 5: 634–46.
- Weston, R., and P. A. Gore. 2006. "A Brief Guide to Structural Equation Modeling." *The Counseling Psychologist* 34: 719–51.
- Wilman, H., J. Belmaker, J. Simpson, C. De La Rosa, M. M. Rivadeneira, and W. Jetz. 2014. "EltonTraits 1.0: Species-Level Foraging Attributes of the world's Birds and Mammals." *Ecology* 95: 2027.
- Wintle, B. A., H. Kujala, A. Whitehead, A. Cameron, S. Veloz, A. Kukkala, A. Moilanen, et al. 2019. "Global Synthesis of Conservation Studies Reveals the Importance of Small Habitat Patches for Biodiversity." *Proceedings of the National Academy of Sciences* 116: 909–14.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Suárez-Castro, Andrés Felipe, Martine Maron, Matthew G. E. Mitchell, and Jonathan R. Rhodes. 2022. "Disentangling Direct and Indirect Effects of Landscape Structure on Urban Bird Richness and Functional Diversity." *Ecological Applications* 32(8): e2713. <https://doi.org/10.1002/eap.2713>