



Housing or habitat: what drives patterns of avian species richness in urbanized landscapes?

Jacinta E. Humphrey · Angie Haslem ·
Andrew F. Bennett

Received: 7 December 2022 / Accepted: 12 April 2023 / Published online: 22 April 2023
© The Author(s) 2023

Abstract

Context Conservation of biodiversity in cities depends on ecologically sensitive urban planning, informed by an understanding of patterns of species distributions and richness. Because urbanized landscapes are heterogeneous mosaics, and many species move between different land-cover types, it is valuable to compare ‘whole landscapes’ (broad-scale spatially heterogeneous areas) that systematically differ in landscape structure.

Objectives We tested the relative influence of housing cover and canopy tree cover on avian species richness, to identify the components of landscape structure that most strongly influence landscape-scale

richness (i.e., the pooled richness of multiple sites within a whole landscape).

Methods We selected 30 residential landscapes (each 1 km²) in Melbourne, Australia, stratified to represent concurrent gradients of housing and canopy tree cover. Five point-count surveys were conducted at each of 10 sites per landscape (for a total of 50 surveys per landscape) and the data pooled to represent the whole landscape mosaic.

Results Up to 82% of variation in avian richness was explained by properties of the whole landscape. Housing cover was most dominant and a strong predictor for multiple response groups including native, terrestrial, forest, and aquatic birds. As housing cover increased, the richness of all groups decreased. Tree cover, primarily comprised of scattered trees in residential areas, had less influence on richness. Nonetheless, for forest birds, the extent of native vegetation surrounding a landscape had an important positive influence, indicating the value of potential source habitat for urban bird populations.

Conclusions Cities can be home to a diverse avifauna. The strong influence of landscape structure on species richness indicates a scope to plan and manage urbanized areas to support a diversity of birds that require natural habitat elements. We conclude that urbanizing environments can best be designed to benefit native birds by protecting patches of native vegetation (particularly large source areas) combined with localized higher housing cover, rather than uniform (lower) housing cover across the entire landscape.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10980-023-01666-2>.

J. E. Humphrey (✉) · A. Haslem · A. F. Bennett
Department of Environment and Genetics, La Trobe
University, Melbourne, Victoria 3086, Australia
e-mail: J.Humphrey@latrobe.edu.au

A. Haslem
e-mail: A.Haslem@latrobe.edu.au

A. F. Bennett
e-mail: A.Bennett@latrobe.edu.au

J. E. Humphrey · A. Haslem · A. F. Bennett
Research Centre for Future Landscapes, La Trobe
University, Melbourne, Victoria 3086, Australia
e-mail: A.Haslem@latrobe.edu.au · e-mail: A.Bennett@
latrobe.edu.au

Keywords Landscape-scale · Urban · Urbanization · Urban-rural gradient · Australia · Forest birds

Introduction

Landscape change through urbanization typically involves the systematic replacement of native vegetation or farmland with built infrastructure, impervious surfaces, and high human population densities (Hahs and McDonnell 2006; Banville et al. 2017). The resulting urban areas represent complex, heterogeneous mosaics of different land-uses, including industrial land, residential neighborhoods, private gardens, open green spaces, riparian corridors, and small patches of native vegetation (Breuste et al. 2008). Despite such changes, cities can form valuable habitats for a variety of fauna, including some threatened species (Ives et al. 2016; Soanes and Lentini 2019).

Birds are a particularly ubiquitous, abundant, and diverse taxonomic group in urban areas, and play a key role in connecting urban residents with nature (Cox and Gaston 2016). Strong positive associations have been demonstrated between avian species richness and human mental health (Cox et al. 2017; Methorst et al. 2021a), life satisfaction (Methorst, Rehdanz, Methorst et al. 2021a, b) and happiness (Cameron et al. 2020). Clearly, there are ecological and social benefits to maintaining avian diversity in cities. Successful conservation, however, will depend on ecologically sensitive urban planning informed by an understanding of what drives the distribution of bird species and patterns of avian richness. The challenge lies in ensuring that cities can accommodate both a growing human population and diverse bird communities.

Much research to date has compared the value of different types of urban land-cover for birds: for example, gardens (Daniels and Kirkpatrick 2006; van Heezik et al. 2013), urban green spaces (Sandström et al. 2006; Rega et al. 2015), wooded streetscapes (White et al. 2005; Ikin et al. 2013), riparian areas (Banville et al. 2017), and patches of native vegetation (Sewell and Catterall 1998). Attention has also been given to specific habitat features, such as the abundance of significant large trees (Barth et al. 2015; Threlfall et al. 2017), diversity of tree species (Ferenc et al. 2014), and the extent of understorey vegetation (Daniels and Kirkpatrick 2006; Threlfall

et al. 2017). Collectively, such work has enhanced understanding of how urbanization influences ecological patterns and processes (McDonnell and Hahs 2008; Alberti and Wang 2022), especially with regard to what makes urban habitats valuable for birds, and how habitat can be improved on a local scale.

These approaches to studying birds in urbanizing regions frequently share two characteristics. First, birds are surveyed along gradients of human influence, often an urban-rural gradient (McDonnell and Pickett 1990), which uses a space for time substitution to represent the process of urbanization (Pickett et al. 2011). Studies generally focus on a single broad measure of human influence, such as housing density (Pidgeon et al. 2014), human population density (Geschke et al. 2018), or distance from the city center (Connelly et al. 2020). However, the urban-rural gradient is complex (McDonnell and Pickett 1990), often inconsistently defined (Padilla and Sutherland 2019), and difficult to capture with a single measure (Padilla and Sutherland 2021). Recent studies (e.g., Padilla and Sutherland 2021; Alberti and Wang 2022) have demonstrated the benefits of considering multi-dimensional gradients of urbanization intensity.

Second, studies are typically site or patch-based, and data analysis and inference relate to the occurrence of bird species at the site or patch scale (e.g., White et al. 2005; Barth et al. 2015). Often such studies also include the influence of surrounding land-uses by establishing a buffer zone around individual sites, transects or patches (e.g., Mayorga et al. 2020; Malekian et al. 2021; Curzel et al. 2021). This approach, termed a ‘patch-landscape’ (McGarigal and Cushman 2002) approach, provides valuable evidence for the importance of landscape context in shaping avian communities. However, birds are mobile, and individuals often move between multiple sites or patches of the same, or different, habitat type within a broader heterogeneous landscape. Further, some land-uses may pose a barrier to movement within a landscape, or are of lower quality because they harbor predators, competitors, or human-induced disturbances (Shoffner et al. 2018).

Alternatively, in a ‘landscape’ approach (McGarigal and Cushman 2002; Bennett et al. 2006), a whole landscape is the unit of study (and of inference), with data pooled from multiple sites, transects or patches to represent the landscape. This approach recognises that landscape structure—the composition and configuration of different types of land-uses—has a profound

effect on the ecological processes that shape the occurrence, abundance and richness of species (Wu and Hobbs 2002; Fahrig 2005). Using a ‘whole of landscape’ approach to examine how landscape structure influences faunal assemblages has provided important insights on the distribution of birds in agricultural (e.g., Haslem and Bennett 2008; Zingg et al. 2018; Sirami et al. 2019) and forested (e.g., McGarigal and McComb 1995; Sitters et al. 2014) environments. A landscape approach has also proven valuable in urban areas because it captures the inherent heterogeneity of cities and has clear applications in urban design (e.g., Belaire et al. 2014; Geschke et al. 2018; Souza et al. 2019). Further, the landscape as a spatial unit of inference is likely to be more relevant for urban planners, policy makers and local government management authorities than individual gardens, parks or streets; and therefore, offers novel insights for conserving birds in cities.

In this study, we used a landscape approach, whereby bird data were pooled from multiple sites within 100 ha residential landscapes, to investigate the influence of urban development on avian species richness in Melbourne, Australia. By studying birds in spatially heterogeneous landscapes ($n=30$), explicitly stratified to sample concurrent gradients of housing cover and canopy tree cover, we aimed to: (i) investigate change in the biophysical properties of whole landscapes across an urbanization gradient; (ii) test the utility of a landscape approach with multiple gradients to study patterns of avian species richness in urbanized areas; (iii) determine the relative influence of housing cover, canopy tree cover, and other landscape properties on the richness of bird species; and (iv) compare the responses of different groups of birds to identify assemblages that are more (or less) vulnerable to urbanization. We predicted that: (i) the biophysical properties of landscapes would differ substantially across the urbanization gradient sampled; (ii) bird assemblages would respond strongly to the structure of ‘whole’ landscapes; (iii) avian species richness would decline with increasing housing cover and increase with canopy tree cover; and (iv) bird assemblages would respond to urbanization in different ways, with forest birds being most vulnerable due to their strong association with native vegetation.

Methods

Study area

The study area encompassed ~1300 km² in the northern and eastern suburbs of Greater Melbourne, a city of 4.92 million people in south-eastern Australia (Fig. 1). The selected area formerly supported native eucalypt forests and woodlands (Department of Environment Land Water and Planning 2021), but now comprises mostly residential land-use, interspersed with industry and commercial zones, urban parklands, riparian corridors, and intact patches of native vegetation. The climate is temperate: mean annual rainfall varies from 670 to 1260 mm across the region, with mean daily maximum temperatures of 13.4 °C in winter (July) and 26.7 °C in summer (January) (Bureau of Meteorology 2021).

Study design

We surveyed birds in 30 circular landscapes, each 1 km² in size (100 ha; 564 m radius), a landscape size widely used for studying birds (e.g., Zingg et al. 2018; Sambell et al. 2019; Sirami et al. 2019). Landscapes were selected to target heterogeneous residential areas (including small open green spaces, native vegetation patches and riparian areas), and avoided major roads, industrial zones, shopping centers, golf courses and public transport hubs. The 30 study landscapes each exhibited fine-scale variation, or heterogeneity, in land-cover types and biophysical properties (see Table 1 for examples). They were positioned ≥ 1 km apart and stratified to represent two main gradients of urbanization: housing cover and canopy tree cover.

For the housing cover gradient, we selected landscapes to represent three categories of housing density (see Theobald 2005): (i) Peri-urban (or Exurban, low density: 1–2 residential dwellings per ha (dph)); (ii) Suburban (medium density: 2–10 dph); and (iii) Urban (high density: >10 dph) (Appendix A). Our focus was on residential environments, so we did not sample inner City or outer Rural categories because they are more heavily dominated by commercial uses, or mixed lifestyle and agricultural land-uses, respectively. Sampling the full urbanization gradient (i.e., as depicted in Appendix A) may have reduced our capacity to detect trends across residential areas specifically, as subtle changes could have been diluted or masked by the significant differences regularly

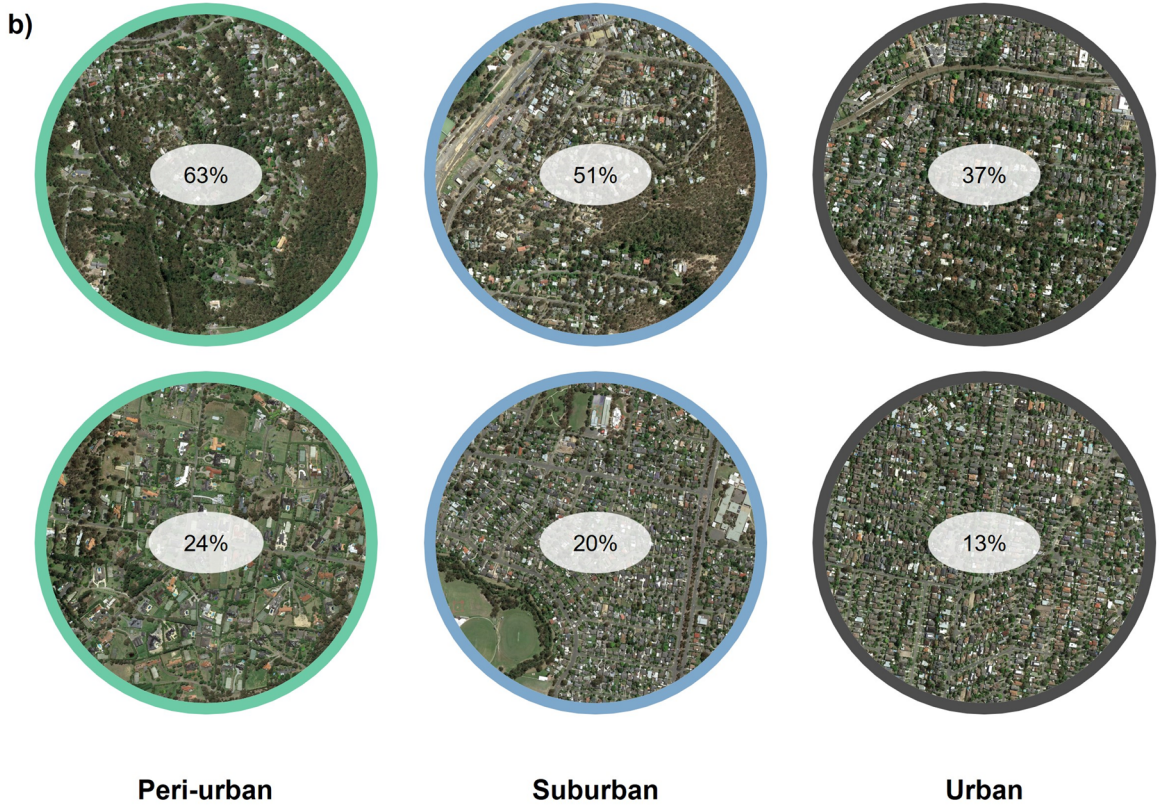
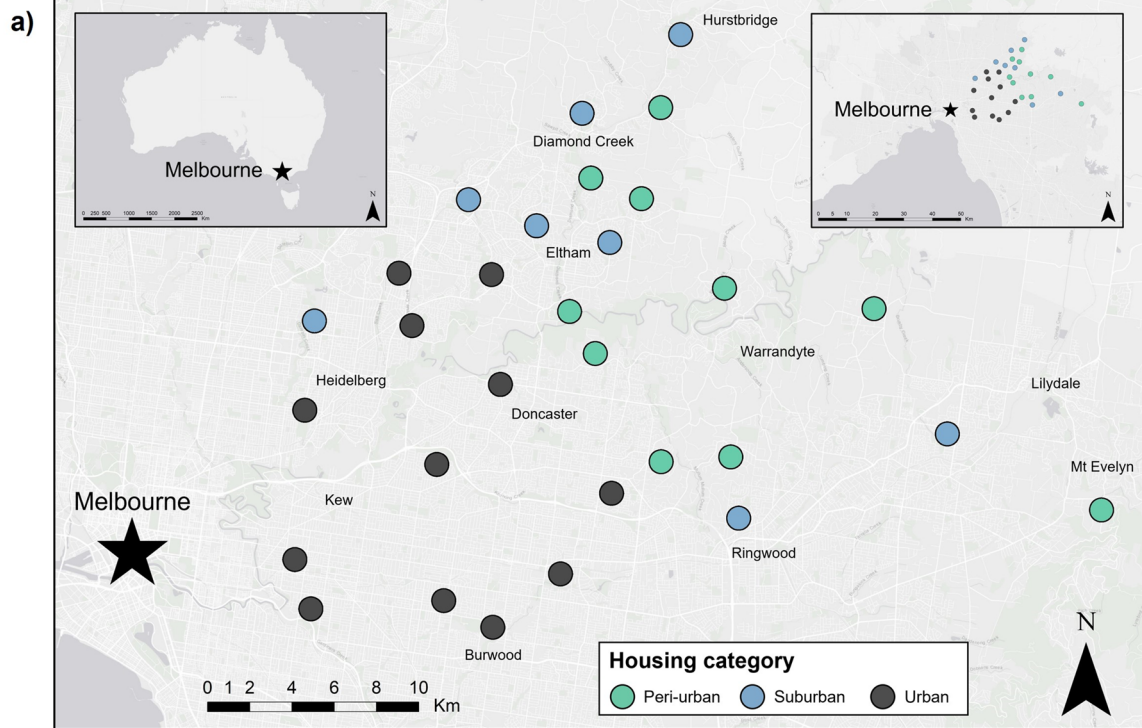


Fig. 1 **a** The study area in Melbourne, Australia, indicating the extent of land (light gray), water (dark gray), major roads (white lines), and the location of the 30 study landscapes (circles). **b** Aerial images of example landscapes from each housing category (Peri-urban in green, Suburban in blue, Urban in black) showing the upper (top row) and lower (bottom row) limits of canopy tree cover in each (indicated by the percentage value in the centre)

observed between the city center and undeveloped natural areas. For the canopy tree cover gradient, we selected landscapes representing a continuous gradient in the cover of canopy trees, spanning the maximum range available within each housing category (Peri-urban: 24–63%; Suburban: 20–51%; Urban: 13–37%). Tree cover was comprised mostly of canopy trees among residential land and urban parks. The number of residential dwellings per landscape was derived from the Vicmap Address—Address Point spatial layer (Department of Environment Land Water and Planning 2018) in ArcMap 10.7.1 (ESRI 2016), and canopy tree cover was initially visually estimated by observing aerial imagery (captured in 2017; sourced from Google Earth Pro 7.3.3.7786).

We selected an equal number of Peri-urban, Suburban and Urban landscapes ($n = 10$ each), ensuring half in each housing category ($n = 5$) contained a waterway, such as a natural flowing creek or drainage line. Waterways in Urban landscapes tended to be more modified than those in Peri-urban. Four landscapes were later reassigned once housing and canopy tree cover were systematically quantified (Table 1 and below). The final set of landscapes included 10 Peri-urban, 8 Suburban and 12 Urban ($n = 30$), spanning a housing gradient of 1.03–11.78 dph, and an estimated tree cover gradient of 13–63% cover (Appendix B).

Ten survey sites for birds were positioned in each landscape, distributed across four quadrants (≥ 2 sites per quadrant). The 10 sites were allocated among four land-cover types: residential, open green space, native vegetation patches, and riparian areas (see Fig. 2). In landscapes with waterways, two sites were allocated to riparian vegetation: one at the widest point, the second at a point where riparian width was considered representative of the landscape. For all other land-cover types, sites were allocated in proportion to their cover in the landscape, with one site allocated per 10 ha (or $\sim 10\%$ cover). All sites were spaced > 200 m apart, and > 50 m from the landscape boundary.

Potential sites were marked on a map of each landscape, then checked in the field for suitability.

Bird surveys

Bird surveys, conducted by the same observer (JEH), consisted of a 10-min point count covering 0.5 ha (40 m radius) at each site. All birds seen or heard within the 40 m radius were considered to be ‘on-site’; birds recorded > 40 m from the observer but within the landscape area were considered ‘off-site’.

Surveys were conducted in fair weather, avoiding high winds (≥ 20 km/hour), rain and high temperatures (> 30 °C). All surveys within a landscape for a single round were completed on the same day (except in unsuitable weather). Five rounds of bird surveys were undertaken (1500 surveys in total) from 2018 to 2019, including three rounds in the breeding season (September to December) and two in the non-breeding season (March to August). During each season, sites were surveyed at least once in the early morning (0–3 h after sunrise) and once in the late morning (3–6 h after sunrise). The order in which sites and landscapes were visited was randomized for each round.

Bird data were pooled from 50 surveys per landscape (including both on-site and off-site records) to calculate landscape-level species richness for five response groups: all native species, terrestrial species, forest species, aquatic species, and exotic bird species. Terrestrial and aquatic species were subsets of all native species. Aquatic species included taxa typically associated with streams, wetlands and lakes. Forest species, a subset of terrestrial species, included taxa that depend on native vegetation. Species were classified as forest species if included in $\geq 55\%$ of lists analysed by Fraser et al. (2015) and were also considered woodland, forest, or heathland-dependent by Radford and Bennett (2005). Taxonomy followed Menkhorst et al. (2017).

Measures of human disturbance

Prior studies have indicated that the number of human pedestrians, domestic dogs, and domestic cats in urban areas can have a negative impact on avian communities (Villegas and Garitano-Zavala 2010; MacGregor-Fors and Schondube 2011;

Table 1 A summary of variables used to describe the properties of each study landscape, including the mean, range of values, and a description

Landscape variable	Abbreviation	Mean	Range	Description
<i>Human infrastructure</i>				
Impervious cover (%)	Impervious	50.5	22.8–76.4	% Grid points intersecting impervious surfaces (buildings, roads, footpaths, carparks, rail corridors)
Housing cover (%)	Housing	24.2	9.2–38.7	% Grid points intersecting buildings (houses, shops, community centres, schools)
People (mean/round)	People	53.5	11.6–149.2	Average number of people observed per landscape
Dogs (mean/round)	Dogs	18.8	10.4–26.2	Average number of dogs observed per landscape
Cats (mean/round)	Cats	0.4	0.0–1.4	Average number of cats observed per landscape
<i>Tree cover</i>				
Canopy tree cover (%)	Tree Cover	33.6	13.3–63.1	% Grid points intersecting canopy trees
Exotic tree proportion	Tree Exotic	0.3	0.0–0.7	Proportion of canopy tree points intersecting non-native tree species
<i>Landscape composition</i>				
Open green space cover (%)	Open Green	8.6	0.0–31.0	% Grid points intersecting open green space (urban parks, sports fields, cleared paddocks)
Riparian cover (ha)	Riparian	3.2	0.0–17.6	Total area of the riparian zone (waterway, adjacent woody vegetation)
Compositional diversity (H)	Heterogeneity	1.0	0.7–1.4	Shannon-Wiener diversity index of five broad land-cover types: residential, gardens, open green space, native vegetation patches, and riparian areas
Maximum patch size (ha)	Max Patch	5.1	0.0–18.7	Maximum size of intact native vegetation patches per landscape
Mean patch size (ha)	Mean Patch	2.8	0.0–10.4	Average size of intact native vegetation patches per landscape
<i>Landscape context</i>				
Rainfall 2018/19 (mm/year) [^]	Rain 1819	787.9	696.2–1080.4	Mean annual rainfall (2018, 2019) derived from Bureau of Meteorology data
Rainfall long-term (mm/year) [^]	Rain Long	792.2	693.0–1265.5	Mean annual rainfall (1960–1990) derived from Bureau of Meteorology data
Vegetation within 1000 m (%)	Vege 1000	11.4	0.0–47.4	% Cover of native forest within 1000 m of landscape boundary
Vegetation within 1500 m (%)	Vege 1500	12.6	0.4–46.4	% Cover of native forest within 1500 m of landscape boundary
Vegetation within 2000 m (%)	Vege 2000	13.4	0.3–45.6	% Cover of native forest within 2000 m of landscape boundary

[^]Data sourced from the Bureau of Meteorology (2020)

Belaire et al. 2014). We incorporated these variables by counting the number of pedestrians, dogs and cats observed within a landscape during each visit. These direct counts were then averaged across the five rounds to give a mean value per landscape, per survey round.

Landscape properties

We collated variables to describe four broad properties of the study landscapes: human infrastructure, tree cover, landscape composition, and landscape context (Table 1).

Many of these variables were based on the extent of different land-cover types, which we quantified by using a grid of points overlaid onto an aerial image of each landscape (captured in December

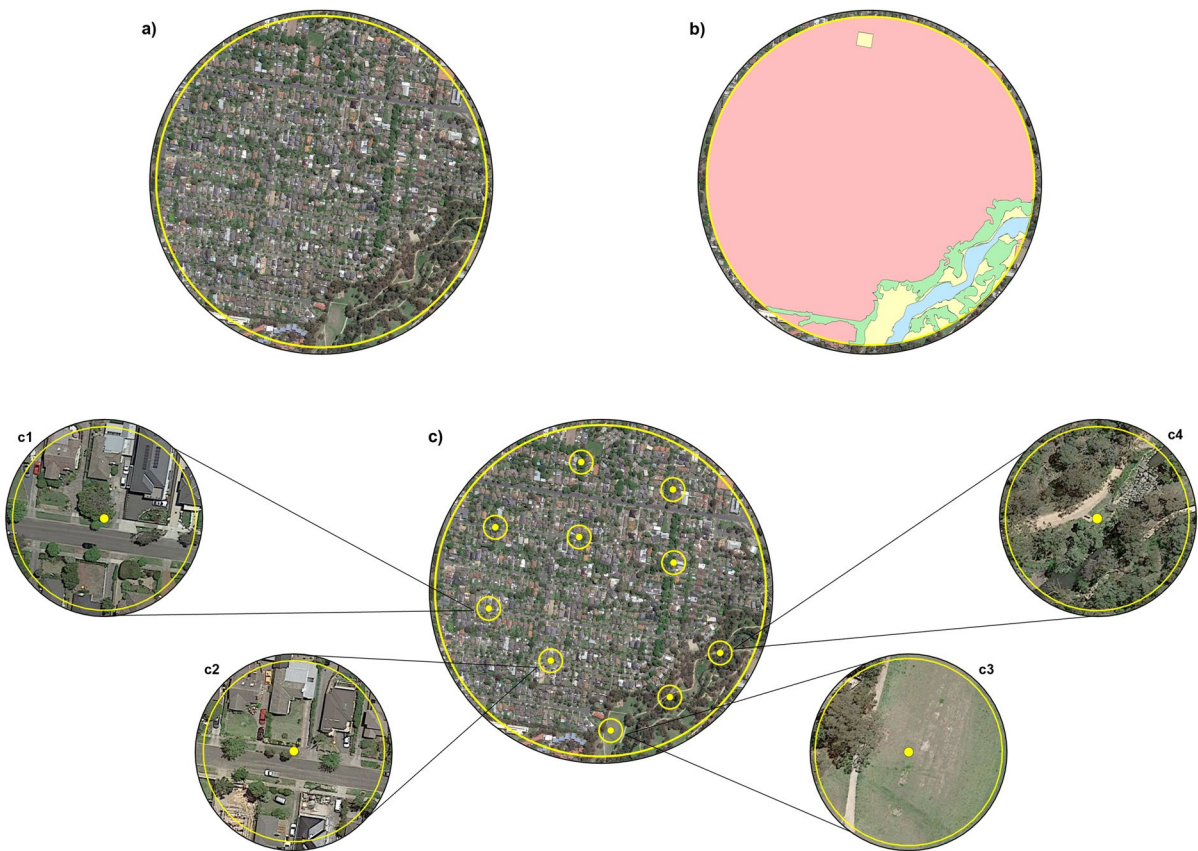


Fig. 2 An illustration of the site allocation process for an example Urban landscape. **a** An aerial image of the landscape showing the 100 ha circular boundary (solid yellow line). **b** The extent of each land-cover type was then visually estimated—here the land-cover types are digitised to show residential land (red), open green space (yellow), native vegetation (green), and riparian areas (blue). **c** Each site (yellow points)

covered an area of 0.5 ha (40 m radius; solid yellow lines). Aerial images are provided for some example sites: c1 and c2 depict residential sites where the observer stood on the foot-path; c3 shows an open green space site in a grassy area with a single eucalypt tree; c4 depicts a riparian site on the edge of a natural flowing creek

2018, coinciding with the first survey round). Points were spaced at 70 m intervals (mean=204; range=200–211 points per landscape) and systematically classified by land-cover type as residential (including all forms of human infrastructure), gardens (including road verges), open green space (urban parks, sports fields, cleared paddocks), native vegetation patches, or riparian (waterways and adjacent wooded vegetation) (Appendix C; see Fig. 3 for examples). Additional features were also recorded for each point, including whether it intersected buildings (houses, shops, community centres, schools), roads, footpaths, car parks, rail corridors, lawns, woody vegetation, or canopy trees (with multiple features possible for a single point) (Appendix C; Fig. 3). Where

multiple land-cover types were recorded for a single point (e.g., vegetation from a garden overhanging a road; a riparian area located within an open green space), the most dominant land-cover type was noted.

The origin of canopy trees may influence avian communities in urban areas, as native trees provide important feeding resources for many indigenous species (Young et al. 2007; Wood and Esaian 2020). For each point that fell on a canopy tree, we recorded whether it was native or exotic by comparing the colour of the foliage, the shape and density of the crown, and looking for evidence of leaf loss in autumn or winter. Most native canopy trees were Eucalypts which tend to have duller, grey-green foliage and more irregular and patchier crowns. The most




Land-cover type	Landscape features	Example points
1 Residential Including all built structures. May also include overhanging canopy trees.	Building Road / Footpath / Car park Rail corridor Canopy tree	
2 Gardens Including front and rear private gardens and road verges.	Lawn Woody vegetation Canopy tree	
3 Open green space Including urban parks, sports fields and cleared paddocks.	Lawn Woody vegetation Canopy tree	
4 Native vegetation Including patches of intact native vegetation not associated with waterways.	Woody vegetation Canopy tree	
5 Riparian areas Including waterways and adjacent woody vegetation.	Woody vegetation Canopy tree	

Fig. 3 A breakdown of the land-cover types and possible landscape features recorded using the grid point method, with example photos

common exotic canopy trees included pine (e.g., *Pinus radiata*), plane (*Platanus* spp.), and elm trees (*Ulmus* spp.) which have more vibrant, green foliage, denser crowns and were more likely to be deciduous. Where canopy trees could not be accurately assessed from aerial imagery alone, we used Google Street View or ground-truthing to identify trees to family level.

In addition, riparian zones in landscapes, and all patches of native vegetation within a landscape (> 1 ha) and within 2000 m of the landscape boundary (> 5 ha) were digitised and measured (Appendix C).

We represented human infrastructure at the landscape-scale by two spatially derived variables: total impervious cover (%) and housing cover (%)

(Table 1), both of which were highly correlated with the number of dwellings per landscape ($r=0.92$ and $r=0.91$, respectively). Tree cover was represented by two measures: total canopy tree cover (%) and the proportion of canopy tree cover comprised of exotic tree species (Table 1). Landscape composition was assessed by five metrics: open green space cover (%), riparian cover (ha), compositional diversity (heterogeneity; H), maximum patch size (native vegetation; ha), and mean patch size (native vegetation; ha) (Table 1). We assessed landscape compositional diversity by using the Shannon-Wiener diversity index, based on the relative proportion of dominant land-cover types in each 100 ha landscape (residential, gardens, open green space, native vegetation patches, and riparian areas; Table 1). Five variables relating to landscape

context were quantified: mean annual rainfall for the survey period (2018–2019) and over the long-term (1960–1990) (Bureau of Meteorology 2020); and the extent of native vegetation patches within a 1000 m, 1500 m, and 2000 m buffer of the landscape boundary (Table 1). We measured surrounding native vegetation because it may serve as a source area for forest bird species, the taxa of greatest conservation concern.

Data analysis

Assessment of survey effort

To assess bird survey effort, we generated a series of landscape-level species accumulation curves using the function ‘specaccum’ from the package ‘vegan’ (Oksanen et al. 2020). We used both the random permutation and collector methods to visualize the accumulation of species over 50 surveys per landscape. For many Suburban and Urban landscapes, species richness plateaued after 30 to 40 surveys; Peri-urban landscapes approached a plateau by 50 surveys (see Appendix D for example curves).

Landscape properties across an urbanization gradient

To examine variation in landscape properties across the gradient sampled, we carried out an ordination using non-metric multidimensional scaling (NMDS), based on a Bray-Curtis dissimilarity matrix of the landscape variables in Table 1. Landscape variables were fitted as environmental vectors using the function ‘envfit’ from the package ‘vegan’ (Oksanen et al. 2020). We also compared landscape properties between Peri-urban, Suburban and Urban landscapes using one-way ANOVAs and Tukey HSD post-hoc tests.

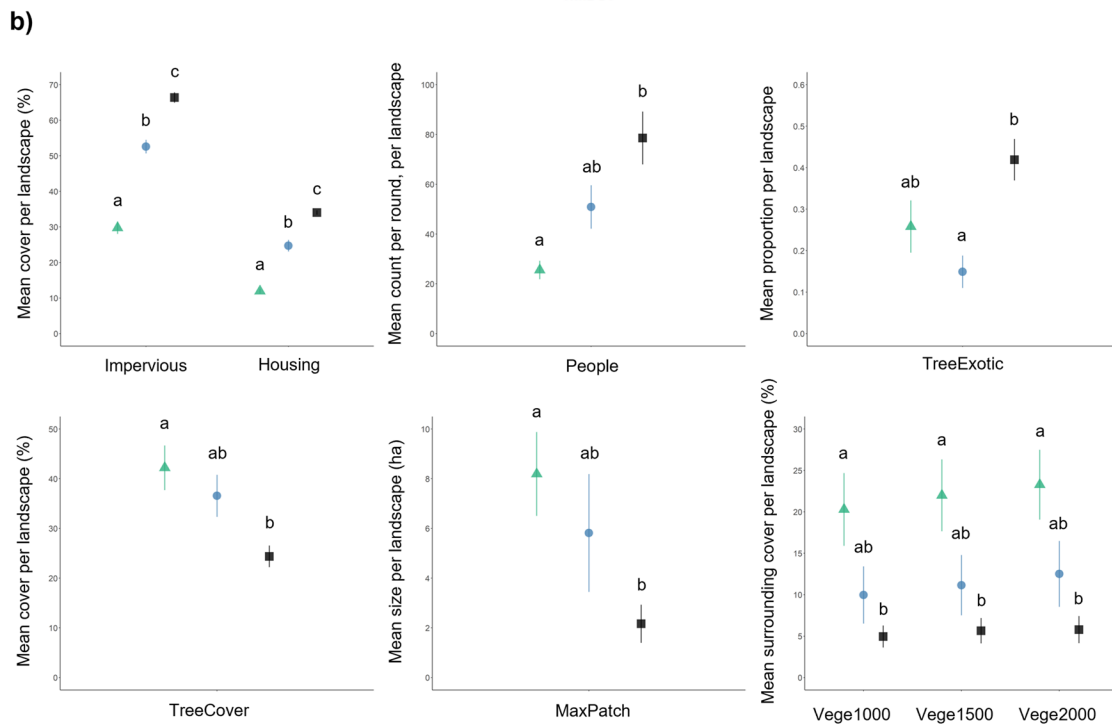
Predictors of avian species richness at the landscape-scale

We tested correlations between all pairs of landscape variables; where $r_s > 0.61$, one variable was excluded from subsequent analyses (Appendix E) (Dormann et al. 2013). Despite efforts to select landscapes along independent, concurrent gradients of housing cover and canopy tree cover, there was a moderate correlation between these variables ($r = -0.58$); however,

this was not considered strong enough to distort models (Dormann et al. 2013). Variables retained for modelling were those critical to the study design (i.e., housing cover, canopy tree cover) and those considered likely to have ecological influence (e.g., extent of surrounding native vegetation). The final set of variables included: housing cover, canopy tree cover, exotic tree proportion, open green space cover, riparian cover, rainfall long term, and surrounding native vegetation within 1000 m. All variables were standardised prior to further analysis.

Generalized linear models, assuming a Poisson distribution, were used to test hypotheses concerning the relative influence of landscape properties on avian species richness at the landscape-scale. We treated each of the four groups of variables as independent hypotheses which may explain variation in bird species richness: (i) Human infrastructure (Housing); (ii) Tree cover (Tree Cover + Tree Exotic); (iii) Landscape composition (Open Green + Riparian); and (iv) Landscape context (Rain Long + Vege 1000) (see Table 1) We predicted that avian species richness would be highest in landscapes with: (i) less housing cover; (ii) more canopy tree cover, but fewer exotic trees; (iii) more open green space and riparian areas; and (iv) higher annual rainfall and a greater extent of surrounding native vegetation.

We used a global model and the function ‘dredge’ from the package ‘MuMIn’ (Barton 2020), to compare all possible combinations of these hypotheses, for a total of 16 candidate models for each of the five bird response groups (native, terrestrial, forest, aquatic, exotic). The function ‘subset’ was used to ensure predictor variables representing the same hypothesis were included together (e.g., Tree Cover + Tree Exotic) (Barton 2020). We then ranked candidate models using Akaike’s information criterion corrected for small sample sizes (AIC_c), to identify the most parsimonious model for each bird group (Hurvich and Tsai 1989). Models were deemed similarly plausible when the difference between the AIC_c value (Δ_i) and the ‘best’ model (smallest AIC_c value) was less than two ($\Delta AIC_c < 2.0$) (Burnham and Anderson 2002). Where multiple models had $\Delta AIC_c < 2.0$, all associated variables were included in a single final model. For each final model, we plotted the residuals, calculated the dispersion ratio, and used Cook’s distance to check the leverage of individual observations (Cook and Weisberg 1984); there



◀Fig. 4 a A non-metric multidimensional scaling ordination of the 30 study landscapes based on the full complement of biophysical landscape properties, including measures of human infrastructure, tree cover, landscape composition, and landscape context. Environmental vectors are shown as grey lines. **b** Dot plots of the mean values for Peri-urban, Suburban and Urban landscapes for all variables where ANOVAs and Tukey HSD post-hoc tests showed moderate to strong evidence for a difference. The top row displays variables that increased across the housing cover gradient; the bottom row displays variables that decreased. The letter codes indicate differences between housing categories for which post-hoc tests showed moderate to strong evidence for a difference. See Table 1 for a description of variables and abbreviations of variable names

was no evidence of overdispersion and no landscapes with high leverage. For each bird response group, we plotted the modelled relationships (using ‘ggplot2’ (Wickham 2016)) for all variables with moderate to strong evidence for an effect on species richness (i.e., $P < 0.05$). All data analyses were carried out in R version 4.0.1 (R Core Team 2016) and R Studio version 1.1.419 (RStudio Team 2016). We interpret the analyses using the language of evidence, as described by Muff et al. (2022).

Results

Landscape properties across an urbanization gradient

An NMDS ordination of the 30 landscapes (Fig. 4a) revealed that the main ordination axis (NMDS1) broadly represents a gradient in urban intensification. Low values of NMDS1 represent landscapes with greater cover of impervious surfaces and housing, a higher proportion of exotic tree cover, and more people observed per visit (Fig. 4a). In contrast, high values of NMDS1 represent landscapes with greater canopy tree cover, larger size (mean and maximum) of native vegetation patches, and a greater extent of native vegetation surrounding the landscape (Fig. 4a). All landscape variables, except the direct count of domestic dogs, explained a proportion of the variation observed among the 30 landscapes (Appendix F).

Most landscape variables showed clear differences across housing categories, with the strongest evidence for differences found between the low (Peri-urban) and high (Urban) ends of the gradient (Fig. 4b, Appendix G). Impervious surface cover, housing cover, people, and exotic tree proportion increased

across the housing cover gradient; canopy tree cover, maximum native patch size, and the extent of surrounding native vegetation (within 1000 m, 1500 m, and 2000 m) decreased (Fig. 4b; Appendix G).

The bird community

A total of 76 bird species was recorded, including 71 native and five exotic species (Appendix H). Ten native species were recorded in all 30 landscapes, including Australian magpie (*Gymnorhina tibicen*) and noisy miner (*Manorina melanocephala*). Two exotic species, common myna (*Acridotheres tristis*) and spotted dove (*Spilopelia chinensis*), also occurred in all landscapes. In contrast, 10 species were recorded in just one landscape: these included aquatic species such as Australasian darter (*Anhinga novae-hollandiae*) and forest birds such as scarlet robin (*Petroica boodang*).

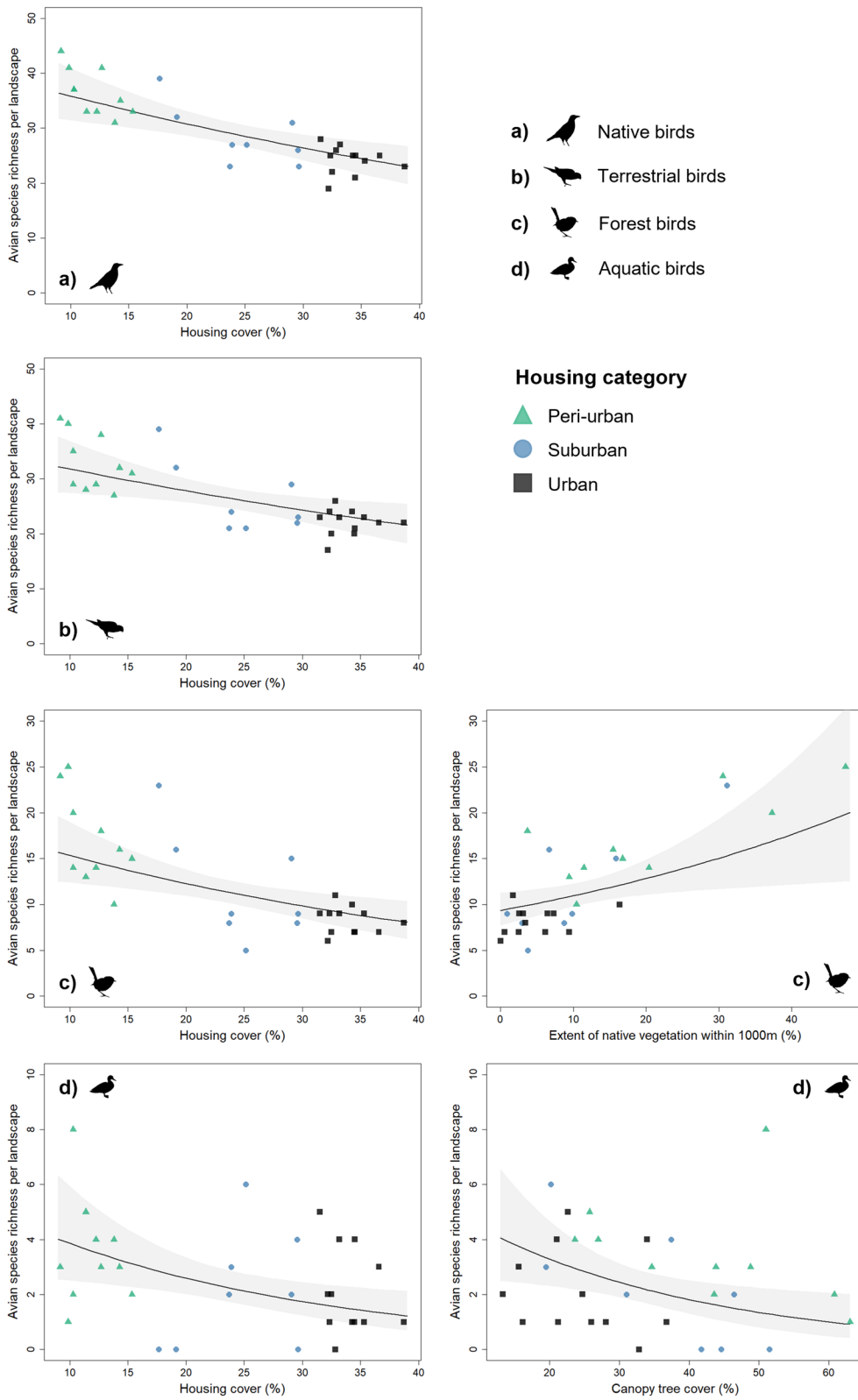
There was substantial variation between landscapes in the number of bird species recorded for each response group. The richness of native species ranged from 19 to 44 species per landscape (mean 29.4 species); 17–41 terrestrial species (mean 26.9); 5–25 forest species (mean 12.0); 0–8 aquatic species (mean 2.6); and 3–5 exotic species (mean 4.5).

Predictors of avian species richness at the landscape-scale

The best performing models for native species ($\Delta AICc < 2.0$) included measures of human infrastructure (Housing) and landscape context (Rain Long, Vege 1000) (Appendix I). The final model explained 82% of the variation in native species richness (Table 2). There was strong evidence ($P < 0.01$) for a negative effect of housing cover on native species richness at the landscape-scale (Fig. 5a).

For terrestrial species richness, all seven landscape properties were represented in the best performing models (Appendix I). The final (global) model explained 80% of the variation in terrestrial species richness (Table 2), with strong evidence ($P < 0.01$) that landscapes with greater housing cover have lower richness of terrestrial bird species (Fig. 5b).

The best performing models for forest species included measures of human infrastructure (Housing), landscape composition (Open Green, Riparian) and landscape context (Rain Long, Vege 1000)



◀**Fig. 5** Predicted relationships between the richness of bird response groups and landscape properties for which there was strong evidence: **a** native species, **b** terrestrial species, **c** forest species, and **d** aquatic species. For exotic birds, there was no evidence for a relationship between species richness and any of the landscape variables included in this study

(Appendix I). This combination of landscape properties explained 82% of the variation in forest bird richness (Table 2). There was strong evidence ($P < 0.01$) for a negative influence of housing cover on the richness of forest species in urbanizing landscapes, and moderate evidence ($P < 0.05$) for a positive relationship with the extent of surrounding native vegetation (Fig. 5c).

For aquatic species, the best performing models included measures of human infrastructure (Housing), tree cover (Tree Cover, Tree Exotic) and landscape composition (Open Green, Riparian) (Appendix I). The final model explained 63% of the variation (Table 2), with strong ($P < 0.01$) and moderate evidence ($P < 0.05$), respectively, that housing cover and canopy tree cover negatively affect the richness of aquatic birds in urbanized landscapes (Fig. 5d).

The best performing models for exotic species richness at the landscape scale included only human infrastructure (Housing) (Appendix I); however, the null model was equally parsimonious. There was little evidence for an effect of housing cover on the richness of exotic birds, and this model explained only 5% of the variation (Appendix I).

Discussion

This study investigated change in avian species richness along gradients of housing cover and canopy tree cover in a large, urbanized region. Importantly, we examined how the properties of ‘whole’ landscapes (1 km²) affect bird communities. There were marked differences in the spatial patterns of land cover between Peri-urban, Suburban and Urban landscapes. Species richness of several bird habitat groups also varied greatly between landscapes. Housing cover, the proportion of the residential landscape dominated by buildings, negatively influenced the richness of all bird groups, except for exotic species which were ubiquitous across the region. Forest species were also positively influenced by the extent of

native vegetation surrounding the landscape, suggesting that landscape context plays a key role for this assemblage. Landscape properties explained > 80% of the variation in richness for native, terrestrial and forest birds, demonstrating the value of a landscape approach for understanding patterns of avian species richness in urbanized areas. Our findings indicate there is scope to enhance habitat for avifauna in urban landscapes via improved management and planning.

Landscape change across an urbanization gradient

Landscapes sampled in this study showed complex patterns of variation in multiple landscape properties. The primary gradient contrasted landscapes with greater housing cover against those with more native vegetation cover. Landscapes with greater housing cover had greater impervious surface cover and more pedestrians observed during survey rounds. They also tended to have a greater proportion of exotic tree cover, reflecting the composition of residential gardens in older, more densely settled suburbs. Landscapes with greater canopy tree cover were characterised by larger patches of native vegetation, both within the landscape and at buffer distances of up to 2 km. This primary urbanization gradient aligns with trends observed in other regions, such as cities in North America (Melles et al. 2003; Padilla and Sutherland 2021), South America (Souza et al. 2019), and Europe (Suarez-Rubio and Krenn 2018). Housing cover values for Greater Melbourne (for 2018) were comparable to many cities in the conterminous United States in 2000 (Theobald 2005).

The second gradient identified by the ordination of landscape attributes, was represented by measures of landscape composition, notably the cover of open green space, cover of riparian vegetation and landscape heterogeneity. In residential environments, green spaces such as sports ovals, local parks and undeveloped cleared areas, along with retained streamside vegetation add visible heterogeneity to the landscape, a factor previously identified as an important feature of urban landscapes for birds (Souza et al. 2019). These findings, that urban landscapes encompass variation in multiple landscape properties, underscore the value of a landscape approach for understanding drivers of avian biodiversity.

Housing cover, as a key determinant of the structure and composition of urbanized landscapes,

Table 2 Generalized linear model outputs, assuming a Poisson distribution, for the final models relating the richness of each bird response group to properties of study landscapes

Bird group	Estimate	Std. error	z-value	P-value	R ² value
<i>Native species</i>					
Intercept	3.748	0.308	12.182	< 0.001	0.819
Housing	−0.406	0.116	−3.496	0.001	
Rain Long	−0.083	0.295	−0.281	0.779	
Vege 1000	0.094	0.063	1.485	0.138	
<i>Terrestrial species</i>					
Intercept	3.644	0.391	9.313	< 0.001	0.802
Housing	−0.355	0.131	−2.719	0.007	
Tree Cover	0.080	0.162	0.495	0.620	
Tree Exotic	−0.017	0.091	−0.182	0.856	
Open Green	−0.052	0.083	−0.632	0.527	
Riparian	−0.033	0.066	−0.501	0.616	
Rain Long	−0.116	0.337	−0.343	0.732	
Vege 1000	0.088	0.092	0.954	0.340	
<i>Forest species</i>					
Intercept	3.093	0.494	6.262	< 0.001	0.823
Housing	−0.589	0.194	−3.043	0.002	
Open Green	−0.097	0.123	−0.782	0.434	
Riparian	−0.043	0.097	−0.448	0.654	
Rain Long	−0.228	0.455	−0.503	0.615	
Vege 1000	0.261	0.106	2.451	0.014	
<i>Aquatic species</i>					
Intercept	2.278	0.687	3.315	< 0.001	0.625
Housing	−1.056	0.397	−2.658	0.008	
Tree Cover	−1.094	0.436	−2.508	0.012	
Tree Exotic	0.021	0.281	0.075	0.940	
Open Green	0.428	0.230	1.864	0.062	
Riparian	0.223	0.189	1.178	0.239	
<i>Exotic species</i>					
Intercept	1.434	0.231	6.196	< 0.001	0.048
Housing	0.077	0.233	0.329	0.742	

P-values in bold indicate variables with moderate to very strong evidence for a relationship

provides a useful measure for quantifying urban intensification (e.g., Pidgeon et al. 2014), as it is strongly correlated with several other landscape attributes (e.g., impervious surfaces, density of people), which have the potential to influence species richness at the landscape-scale. Despite deliberately designing our study to sample independent gradients of both housing cover and tree cover across urbanized landscapes, there was a moderate association between these variables ($r = -0.58$). This suggests it is difficult to maintain high levels of canopy tree cover (e.g., >40% landscape cover) in areas with greater housing cover. Conversely, at least in our study region, it was

rare that landscapes with low housing cover also had low canopy tree cover (<25%). This is likely because the study region was formerly covered by forest vegetation (Department of Environment Land Water and Planning 2021), and much land clearing has occurred due to urban expansion. This contrasts with other areas where urban development has expanded into cleared agricultural land, where prior tree cover is relatively low. Land-use history can have a strong influence on spatial patterns and conservation outcomes in urbanizing landscapes (Padilla and Sutherland 2021; Alberti and Wang 2022) and other environments (e.g., Lunt and Spooner 2005).

Relationships between avian species richness and landscape properties

Changes in the biophysical properties of landscapes influence the extent and quality of habitat available for species in urban areas (McKinney 2002). This occurs at multiple spatial scales: both local and landscape-scale habitat variables are influential (Melles et al. 2003; Mayorga et al. 2020; Curzel et al. 2021). Here, the extent of landscape-scale housing cover was a primary driver of the availability and suitability of habitat for native birds: as housing cover increased, fewer bird species were recorded in urbanized landscapes. These findings are consistent with other reports of a negative relationship between bird species richness and housing density (Pidgeon et al. 2014; Wood et al. 2015), or the extent of impervious surfaces (Chamberlain et al. 2019; Souza et al. 2019; Lerman et al. 2021; Suárez-Castro et al. 2022). The response to housing cover is not necessarily a direct relationship; rather, that increasing housing cover serves as a proxy for a range of other processes. Built structures such as houses, shops, roads and carparks all displace natural habitat and reduce the land available for land-cover types such as gardens, parks and patches of native vegetation which collectively provide more suitable and diverse habitat for most birds in urban landscapes (Sewell and Catterall 1998; Daniels and Kirkpatrick 2006; Sandström et al. 2006). Greater housing cover is also associated with increases in other human-induced disturbances, such as vehicle traffic and road strikes, domestic cats, air pollution, anthropogenic noise, and artificial light at night (Ciach and Fröhlich 2017; Shoffner et al. 2018).

Relative to housing cover, landscape-scale canopy tree cover did not have a strong influence on the richness of native, terrestrial or forest birds across the urbanization gradient sampled. This contrasts with other studies in urban environments which have reported a positive relationship between avian species richness and canopy tree cover, either for landscape units (Chamberlain et al. 2019; Callaghan et al. 2020) or sites with surrounding tree cover (Callaghan et al. 2018; Lerman et al. 2021). The lack of a relationship between landscape-scale tree cover and bird richness here may be due to several factors. First, it is likely that the form of tree cover in these predominantly residential landscapes affects the degree to which it influences bird species. Tree cover mostly

consisted of street trees and trees scattered among residential gardens and open parkland, rather than substantial intact patches of native vegetation. Whilst scattered trees undoubtedly provide habitat and feeding resources in urban areas (Wood and Esaian 2020), they are potentially of lesser value than intact patches of native forest (e.g., Haslem and Bennett 2008).

The origin of tree species in the urban environment is also important. In many landscapes, exotic trees contributed substantially to the overall tree cover. Whilst some bird species use resources provided by a combination of native and exotic plants (French et al. 2005; Daniels and Kirkpatrick 2006), a prevalence of introduced tree species reduces the amount of habitat for certain assemblages (Wood and Esaian 2020), such as insectivores and nectarivores that feed in eucalypt canopies (White et al. 2005; Young et al. 2007; Ikin et al. 2013). Third, this study sampled a gradient focussed primarily on residential landscapes, avoiding high-density inner city and near-natural landscapes at the urban fringe. It is likely that if a longer gradient was sampled, including the more extreme situations at either end, landscape-level tree cover would have had a greater influence on avian species richness. Finally, the positive influence of canopy tree cover may simply have been masked by the moderate negative correlation with housing cover.

Bird species that depend on natural habitats are considered ‘urban avoiders’ and are among the most sensitive to changes associated with urbanization (McKinney 2002; Conole and Kirkpatrick 2011; Ferenc et al. 2014; Shoffner et al. 2018). In southern Australia, woodland-dependent birds are a group of conservation concern due to the extensive loss and fragmentation of wooded habitats throughout their range (Radford et al. 2005; Ford 2011). Here, our results show that in addition to a negative response to increasing housing cover, forest-dependent birds were positively associated with surrounding tree cover (within 1000 m of the landscape boundary) comprising native vegetation in intact patches (≥ 5 ha). These results are consistent with the view that forest species are frequently lost from peri-urban suburbs and that forest remnants, either within or close to residential areas, are essential for the persistence of many species in this assemblage (Sewell and Catterall 1998; Palmer et al. 2008; Geschke et al. 2018; Shoffner et al. 2018). It is likely that intact forest areas adjacent to the study landscapes act as source populations for forest species

from which dispersal and spill over of individuals occurs into neighboring residential areas (see also van Heezik et al. 2010; van Heezik and Adams 2016).

The value of a landscape approach to understanding avian diversity in urban environments

We sampled birds at multiple sites and pooled the data to represent the richness of avifauna for ‘whole’ landscapes. There was much variation in richness between these residential landscapes (e.g., 5–25 species per landscape for forest birds); and importantly, such variation was strongly related to properties of the landscape, indicating that this is a valuable scale for seeking understanding. Between 80 and 82% of the variation in richness of all native species, terrestrial species, and forest species, respectively, was explained by landscape-scale properties. Less variation was explained for aquatic species (63%), which were not a primary focus, or for exotic species (5%) which were ubiquitous throughout the region.

There are multiple benefits of a landscape approach. First, it provides a means of measuring and understanding the consequences of the inherent heterogeneity of cities, which are complex mosaics of different land-uses (Breuste et al. 2008). Here, even primarily residential landscapes showed variation in multiple landscape properties (see also Padilla and Sutherland 2021), and our results provide an understanding of how bird groups respond to different aspects of habitat modification and urbanization. Second, a landscape approach explicitly recognises that bird species may move between different parts of the landscape and that ecological processes operate at spatial scales that incorporate multiple habitats or land-use types. For example, flowering of eucalypt trees in these landscapes provides a seasonal nectar source that some bird species exploit, and to do so they move between trees in residential gardens, along streets or in remnant patches of vegetation. Third, the findings from studies at this scale are highly relevant to urban planners, policy makers and local government management authorities, who must plan at broad scales rather than individual sites. Finally, the strong response of bird species to the overall properties of a landscape implies that individual actions—by local residents, community groups or government—matter, because they contribute to change in the wider landscape. For example, setting aside a local

area from housing to restore native bushland will alter the landscape structure, and influence the avifauna of the broader landscape.

Conclusion

Urbanizing landscapes in major cities are complex mosaics which have differing landscape properties, including varying extents of human infrastructure (e.g., housing cover) and tree cover (all tree cover, exotic trees). In residential landscapes across Melbourne, the extent of housing cover had the strongest influence on avian species richness at the landscape-scale. Residential housing offers little value as direct habitat for birds, and its presence restricts the amount of space available for other land-uses, such as gardens, parks or native vegetation, which offer more suitable habitat. Additionally, the limited canopy tree cover that remains in highly developed residential landscapes is often dominated by introduced tree species, which offer fewer resources for native avifauna. Heavily urbanized areas often lack nearby large patches of native vegetation which are essential for the persistence of forest birds.

Continued expansion of urbanized areas will come at a cost to biodiversity. The amount of land available is finite, and so there must be trade-offs between land allocated to housing and to other land-cover types such as native vegetation. Our findings suggest that benefits for native birds could best be achieved by protecting native vegetation, particularly source areas of intact habitat, and compensating with local areas of higher housing cover, rather than having uniform lower housing cover across the entire landscape.

Acknowledgements We acknowledge that this work took place on the lands of the Wurundjeri People of the Kulin Nations, and other lands where Traditional Owners are yet to be formally recognized. This study was funded by the Holsworth Wildlife Research Endowment and the Ecological Society of Australia, BirdLife Australia, the Australian Wildlife Society, and the Field Naturalists Club of Victoria. JEH was supported by an Australian Government Research Training Program (RTP) Stipend Scholarship. We thank the private landholders for providing access to property, and Jim Radford, Luke Collins, Matt White, and Rachel McIntosh for assistance with study design, remote sensing, and statistical analyses. We also thank three anonymous reviewers for their detailed

feedback which substantially improved this manuscript. The study was conducted with approval of the La Trobe University Animal Ethics Committee (Approval No. AEC18-11) and the Department of Environment, Land, Water and Planning (Permit No. 10008805).

Author contributions JEH: Conceptualization; Methodology; Funding acquisition; Project administration; Investigation; Formal analysis; Visualization; Writing—Original Draft; Writing—Review & Editing. AH: Conceptualization; Methodology; Formal analysis; Writing—Review & Editing; Supervision. AFB: Conceptualization; Methodology; Writing—Review & Editing; Supervision.

Funding Open Access funding enabled and organized by CAUL and its Member Institutions. This study was funded by the Holsworth Wildlife Research Endowment and the Ecological Society of Australia, BirdLife Australia, the Australian Wildlife Society, and the Field Naturalists Club of Victoria. JEH was supported by an Australian Government Research Training Program (RTP) Stipend Scholarship.

Data availability The datasets analysed in the present study are available from the corresponding author upon reasonable request.

Declarations

Competing interests Financial interests: The authors declare they have no known financial interests. Non-financial interests: Andrew F. Bennett is a current editor with the journal *Landsc Ecol*.

Ethical approval The study was conducted with approval of the La Trobe University Animal Ethics Committee (Approval No. AEC18-11) and the Department of Environment, Land, Water and Planning (Permit No. 10008805).

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

- Alberti M, Wang T (2022) Detecting patterns of vertebrate biodiversity across the multidimensional urban landscape. *Ecol Lett* 25:1027–1045
- Banville MJ, Bateman HL, Earl SR, Warren PS (2017) Decadal declines in bird abundance and diversity in urban riparian zones. *Landsc Urban Plan* 159:48–61
- Barth BJ, FitzGibbon SI, Wilson RS (2015) New urban developments that retain more remnant trees have greater bird diversity. *Landsc Urban Plan* 136:122–129
- Barton K (2020) MuMIn: Multi-model inference. R package version 1.43.17. <https://CRAN.R-project.org/package=MuMIn>
- Belaire JA, Whelan CJ, Minor ES (2014) Having our yards and sharing them too: the collective effects of yards on native bird species in an urban landscape. *Ecol Appl* 24:2132–2143
- Bennett AF, Radford JQ, Haslem A (2006) Properties of land mosaics: implications for nature conservation in agricultural environments. *Biol Conserv* 133:250–264
- Breuste J, Niemelä J, Snep RPH (2008) Applying landscape ecological principles in urban environments. *Landsc Ecol* 23:1139–1142
- Bureau of Meteorology (2020) Bureau of Meteorology. Australian Government. <http://www.bom.gov.au/>. Accessed 18 August 2020
- Bureau of Meteorology (2021) Bureau of Meteorology. Australian Government. <http://www.bom.gov.au/>. Accessed 30 August 2021
- Burnham K, Anderson D (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag
- Callaghan CT, Major RE, Lyons MB, Martin JM, Kingsford RT (2018) The effects of local and landscape habitat attributes on bird diversity in urban greenspaces. *Ecosphere* 9:e02347
- Callaghan CT, Poore AGB, Major RE, Cornwell WK, Wilshire JH, Lyons MB (2020) How to build a biodiverse city: environmental determinants of bird diversity within and among 1581 cities. *Biodivers Conserv* 30:217–234
- Cameron RWF, Brindley P, Mears M, McEwan K, Ferguson F, Sheffield D, Jorgensen A, Riley J, Goodrick J, Ballard L, Richardson M (2020) Where the wild things are! Do urban green spaces with greater avian biodiversity promote more positive emotions in humans? *Urban Ecosyst* 23:301–317
- Chamberlain DE, Henry DAW, Reynolds C, Caprio E, Amar A (2019) The relationship between wealth and biodiversity: a test of the luxury effect on bird species richness in the developing world. *Glob Chang Biol* 25:3045–3055
- Ciach M, Fröhlich A (2017) Habitat type, food resources, noise and light pollution explain the species composition, abundance and stability of a winter bird assemblage in an urban environment. *Urban Ecosyst* 20:547–559
- Connelly CA, Lennox E, Isaac B, Aulich V, Cooke R, Weston MA, White JG (2020) Tree cover is crucial but riparian areas provide a strategic focus for preserving an urban avooider in a fragmented urban ecosystem. *Emu* 120:304–312
- Conole LE, Kirkpatrick JB (2011) Functional and spatial differentiation of urban bird assemblages at the landscape scale. *Landsc Urban Plan* 100:11–23
- Cook R, Weisberg S (1984) Residuals and influence in regression. Wiley

- Cox DTC, Gaston KJ (2016) Urban bird feeding: connecting people with nature. *PLoS ONE* 11:e0158717
- Cox DTC, Shanahan DF, Hudson HL, Plummer KE, Siriwardena GM, Fuller RA, Anderson K, Hancock S, Gaston KJ (2017) Doses of neighborhood nature: the benefits for mental health of living with nature. *Bioscience* 67:147–155
- Curzel FE, Bellocq MI, Leveau LM (2021) Local and landscape features of wooded streets influenced bird taxonomic and functional diversity. *Urban For Urban Green* 66:127369
- Daniels GD, Kirkpatrick JB (2006) Does variation in garden characteristics influence the conservation of birds in suburbia? *Biol Conserv* 133:326–335
- Department of Environment, Land, Water and Planning (2018) Vicmap address—address point. Department of Environment, Land, Water and Planning, Victorian State Government
- Department of Environment, Land, Water and Planning (2021) Bioregions and EVC benchmarks. Department of Environment, Land, Water and Planning, Victorian State Government. <https://www.environment.vic.gov.au/biodiversity/bioregions-and-evc-benchmarks>. Accessed 14 December 2021
- Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carré G, Marquéz JRG, Gruber B, Lafourcade B, Leitão PJ, Münkemüller T, McClean C, Osborne PE, Reineking B, Schröder B, Skidmore AK, Zurell D, Lautenbach S (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36:27–46
- ESRI (2016) ArcGIS Desktop 10.7.1. ESRI Inc., Berkeley, California
- Fahrig L (2005) When is a landscape perspective important? In: Wiens JA, Moss MR (eds) *Issues and perspectives in landscape ecology*. Cambridge University Press, pp 3–10
- Ferenc M, Sedláček O, Fuchs R (2014) How to improve urban greenspace for woodland birds: site and local-scale determinants of bird species richness. *Urban Ecosyst* 17:625–640
- Ford HA (2011) The causes of decline of birds of eucalypt woodlands: advances in our knowledge over the last 10 years. *Emu* 111:1–9
- Fraser H, Garrard GE, Rumpff L, Hauser CE, McCarthy MA (2015) Consequences of inconsistently classifying woodland birds. *Front Ecol Evol* 3:83
- French K, Major R, Hely K (2005) Use of native and exotic garden plants by suburban nectarivorous birds. *Biol Conserv* 121:545–559
- Geschke A, James S, Bennett AF, Nimmo DG (2018) Compact cities or sprawling suburbs? Optimising the distribution of people in cities to maximise species diversity. *J Appl Ecol* 55:2320–2331
- Hahs AK, McDonnell MJ (2006) Selecting independent measures to quantify Melbourne's urban-rural gradient. *Landsc Urban Plan* 78:435–448
- Haslem A, Bennett AF (2008) Birds in agricultural mosaics: the influence of landscape pattern and countryside heterogeneity. *Ecol Appl* 18:185–196
- Hurvich C, Tsai CL (1989) Regression and time series model selection in small samples. *Biometrika* 76:297–307
- Ikin K, Knight E, Lindenmayer DB, Fischer J, Manning AD (2013) The influence of native versus exotic streetscape vegetation on the spatial distribution of birds in suburbs and reserves. *Divers Distrib* 19:294–306
- Ives CD, Lentini PE, Threlfall CG, Ikin K, Shanahan DF, Garrard GE, Bekessy SA, Fuller RA, Mumaw L, Rayner L, Rowe R, Valentine LE, Kendal D (2016) Cities are hotspots for threatened species. *Glob Ecol Biogeogr* 25:117–126
- Lerman SB, Narango DL, Avolio ML, Bratt AR, Engebretson JM, Groffman PM, Hall SJ, Heffernan JB, Hobbie SE, Larson KL, Locke DH, Neill C, Nelson KC, Padullés Cubino J, Trammell TLE (2021) Residential yard management and landscape cover affect urban bird community diversity across the continental USA. *Ecol Appl* 31:e02455
- Lunt ID, Spooner PG (2005) Using historical ecology to understand patterns of biodiversity in fragmented agricultural landscapes. *J Biogeogr* 32:1859–1873
- MacGregor-Fors I, Schondube JE (2011) Gray vs. green urbanization: relative importance of urban features for urban bird communities. *Basic Appl Ecol* 12:372–381
- Malekian M, Hadi M, Tarkesh M (2021) Landscape features affecting bird diversity and abundance at an urban landfill site: a case study in Central Iran. *Bird Study* 68:21–29
- Mayorga I, Bichier P, Philpott SM (2020) Local and landscape drivers of bird abundance, species richness, and trait composition in urban agroecosystems. *Urban Ecosyst* 23:495–505
- McDonnell MJ, Hahs AK (2008) The use of gradient analysis studies in advancing our understanding of the ecology of urbanizing landscapes: current status and future directions. *Landsc Ecol* 23:1143–1155
- McDonnell MJ, Pickett STA (1990) Ecosystem structure and function along urban-rural gradients: an unexploited opportunity for ecology. *Ecology* 71:1232–1237
- McGarigal K, Cushman SA (2002) Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. *Ecol Applic* 12:335–345
- McGarigal K, McComb WC (1995) Relationships between landscape structure and breeding birds in the Oregon Coast Range. *Ecol Monogr* 65:235–256
- McKinney ML (2002) Urbanization, biodiversity and conservation. *Bioscience* 52:883–890
- Melles S, Glenn S, Martin K (2003) Urban bird diversity and landscape complexity: species-environment associations along a multiscale habitat gradient. *Conserv Ecol* 7:1
- Menkhurst P, Rogers D, Clarke R, Davies J, Marsack P, Franklin K (2017) *The Australian bird guide*. CSIRO Publishing
- Methorst J, Bonn A, Marselle M, Böhning-Gaese K, Rehdanz K (2021) Species richness is positively related to mental health—a study for Germany. *Landsc Urban Plan* 211:104084
- Methorst J, Rehdanz K, Mueller T, Hansjürgens B, Bonn A, Böhning-Gaese K (2021) The importance of species diversity for human well-being in Europe. *Ecol Econ* 181:106917
- Muff S, Nilsen EB, O'Hara RB, Nater CR (2022) Rewriting results sections in the language of evidence. *Tree* 37:203–210

- Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGinn D, Minchin P, O'Hara RB, Simpson G, Solymos P, Stevens MHH, Szöcs E, Wagner H (2020) *vegan*: Community ecology package. R package version 2.5-7. <https://CRAN.R-project.org/package=vegan>
- Padilla BJ, Sutherland C (2019) A framework for transparent quantification of urban landscape gradients. *Landscape Ecol* 34:1219–1229
- Padilla BJ, Sutherland C (2021) Defining dual-axis landscape gradients of human influence for studying ecological processes. *PLoS ONE* 16:e0252364
- Palmer GC, Fitzsimons JA, Antos MJ, White JG (2008) Determinants of native avian richness in suburban remnant vegetation: implications for conservation planning. *Biol Conserv* 141:2329–2341
- Pickett STA, Cadenasso ML, Grove JM, Boone CG, Groffman PM, Irwin E, Kaushal SS, Marshall V, McGrath BP, Nilon CH, Pouyat Rv, Szlavecz K, Troy A, Warren P (2011) Urban ecological systems: scientific foundations and a decade of progress. *J Environ Manag* 92:331–362
- Pidgeon AM, Flather CH, Radeloff VC, Lepczyk CA, Keuler NS, Wood EM, Stewart SI, Hammer RB (2014) Systematic temporal patterns in the relationship between housing development and forest bird biodiversity. *Conserv Biol* 28:1291–1301
- R Core Team (2016) R: a language and environment for statistical computing (4.0.1). R Foundation for Statistical Computing, Vienna
- Radford JQ, Bennett AF (2005) Terrestrial avifauna of the Gippsland Plain and Strzelecki ranges, Victoria, Australia: insights from Atlas data. *Wildl Res* 32:531–555
- Radford JQ, Bennett AF, Cheers GJ (2005) Landscape-level thresholds of habitat cover for woodland-dependent birds. *Biol Conserv* 124:317–337
- Rega CC, Nilon CH, Warren PS (2015) Avian abundance patterns in relation to the distribution of small urban greenspaces. *J Urban Plan Dev* 141:A4015002
- RStudio Team (2016) RStudio: Integrated development for R (1.1.419). RStudio, Boston
- Sambell CE, Holland GJ, Haslem A, Bennett AF (2019) Diverse land-uses shape new bird communities in a changing rural region. *Biodivers Conserv* 28:3479–3496
- Sandström UG, Angelstam P, Mikusiński G (2006) Ecological diversity of birds in relation to the structure of urban green space. *Landscape Urban Plan* 77:39–53
- Sewell SR, Catterall CP (1998) Bushland modification and styles of urban development: their effects on birds in south-east Queensland. *Wildl Res* 25:41–63
- Shoffner A, Wilson AM, Tang W, Gagné SA (2018) The relative effects of forest amount, forest configuration, and urban matrix quality on forest breeding birds. *Sci Rep* 8:17140
- Sirami C, Gross N, Baillod AB, Bertrand C, Carrié R, Hass A et al (2019) Increasing crop heterogeneity enhances multitrophic diversity across agricultural regions. *Proc Natl Acad Sci USA* 116:16442–16447
- Sitters H, Christie FJ, di Stefano J, Swan M, Penman T, Collins PC, York A (2014) Avian responses to the diversity and configuration of fire age classes and vegetation types across a rainfall gradient. *For Ecol Manag* 318:13–20
- Soanes K, Lentini PE (2019) When cities are the last chance for saving species. *Front Ecol Evol* 17:225–231
- Souza FL, Valente-Neto F, Severo-Neto F, Bueno B, Ochoa-Quintero JM, Laps RR, Bolzan F, de Oliveira Roque F (2019) Impervious surface and heterogeneity are opposite drivers to maintain bird richness in a Cerrado city. *Landscape Urban Plan* 192:103643
- Suárez-Castro AF, Maron M, Mitchell MGE, Rhodes JR (2022) Disentangling direct and indirect effects of landscape structure on urban bird richness and functional diversity. *Ecol Appl*. <https://doi.org/10.1002/eap.2713>
- Suarez-Rubio M, Krenn R (2018) Quantitative analysis of urbanization gradients: a comparative case study of two European cities. *J Urban Ecol* 4:1–14
- Theobald DM (2005) Landscape patterns of exurban growth in the USA from 1980 to 2020. *Ecol Soc* 10:1
- Threlfall CG, Mata L, Mackie JA, Hahs AK, Stork NE, Williams NSG, Livesley SJ (2017) Increasing biodiversity in urban green spaces through simple vegetation interventions. *J Appl Ecol* 54:1874–1883
- van Heezik Y, Adams AL (2016) Vulnerability of native and exotic urban birds to housing densification and changing gardening and landscaping trends. *Urban Ecosyst* 19:1551–1563
- van Heezik Y, Smyth A, Adams A, Gordon J (2010) Do domestic cats impose an unsustainable harvest on urban bird populations? *Biol Conserv* 143:121–130
- van Heezik Y, Freeman C, Porter S, Dickinson KJM (2013) Garden size, householder knowledge, and socio-economic status influence plant and bird diversity at the scale of individual gardens. *Ecosyst* 16:1442–1454
- Villegas M, Garitano-Zavala Á (2010) Bird community responses to different urban conditions in La Paz, Bolivia. *Urban Ecosyst* 13:375–391
- White JG, Antos MJ, Fitzsimons JA, Palmer GC (2005) Non-uniform bird assemblages in urban environments: the influence of streetscape vegetation. *Landscape Urban Plan* 71:123–135
- Wickham H (2016) *ggplot2: elegant graphics for data analysis*. Springer-Verlag, New York
- Wood EM, Esaian S (2020) The importance of street trees to urban avifauna. *Ecol Appl* 30:e02149
- Wood EM, Pidgeon AM, Radeloff VC, Helters DP, Culbert PD, Keuler NS, Flather CH (2015) Long-term avian community response to housing development at the boundary of US protected areas: effect size increases with time. *J Appl Ecol* 52:1227–1236
- Wu J, Hobbs R (2002) Key issues and research priorities in landscape ecology: an idiosyncratic synthesis. *Landscape Ecol* 17:355–365
- Young KM, Daniels CB, Johnston G (2007) Species of street tree is important for southern hemisphere bird trophic guilds. *Austral Ecol* 32:541–550
- Zingg S, Grenz J, Humbert JY (2018) Landscape-scale effects of land use intensity on birds and butterflies. *Agric Ecosyst Environ* 267:119–128