diversity

MDPI

Article

Bird Utilisation of Vertical Space in Urban Environments

Annalise J. Re [1], Andrew M. Rogers [1,2], Hugh P. Possingham [1] and Salit Kark [1,*]

[1] The Biodiversity Research Group, School of the Environment, Centre for Biodiversity and Conservation Science, The University of Queensland, Brisbane, QLD 4072, Australia; a.rogers@uq.edu.au (A.M.R.); h.possingham@uq.edu.au (H.P.P.)

[2] School of Agriculture, Food and Ecosystem Sciences, Faculty of Science, The University of Melbourne, Grattan Street, Parkville, VIC 3010, Australia

* Correspondence: s.kark@uq.edu.au

Abstract: In an increasingly urbanised world, it is important to understand how species interact with human-modified landscapes across all spatial dimensions. Urban areas, modified for higher density living, are characterised by buildings, airborne vehicles, and other uses of the airspace. These obstructions can alter the available vertical habitat space and hence impact species that rely on the vertical partitioning of resources. Nonetheless, studies in urban areas typically use 2D variables, which are unsuitable as proxies for 3D processes. To address this gap, bird surveys were conducted across three different types of urban environments that reflect a gradient of extensive to intensive within Brisbane, Australia. Bird activity was recorded across a range of heights. While exceptions occurred, we found that urban birds generally interacted with their environment at heights that reflected the taller structures along the urban gradient. Grouping species by urban tolerance (i.e., whether an urban avoider, adapter, or exploiter) and foraging level helped explain why some species could utilise certain height profiles across the urban structural gradient where others could not. A better understanding of how birds use urban vertical spaces can help identify habitat features that facilitate urban biodiversity and support conservation management in urban environments.

Keywords: birds; airspace; species; activity; urban planning; biodiversity; conservation

check for updates

Academic Editor: Michael Wink

Received: 27 September 2024
Revised: 19 December 2024
Accepted: 20 December 2024
Published: 27 December 2024

Citation: Re, A.J.; Rogers, A.M.; Possingham, H.P.; Kark, S. Bird Utilisation of Vertical Space in Urban Environments. *Diversity* **2025**, *17*, 16. https://doi.org/10.3390/d17010016

1. Introduction

With a majority of the world's population now living in urban areas, once-natural landscapes are progressively becoming more disturbed [1,2]. This shift is contributing to the global decline in biodiversity, with avian populations being no exception to the many species impacted by anthropogenic change [1,3]. Habitat loss, habitat fragmentation, and the alteration of local habitat, such as the disproportionate loss of key vegetation strata (i.e., understorey and canopy), are contributing forces to declining avian diversity in urban regions [4–6]. The structural heterogeneity of these altered environments, both natural and anthropogenic, has the potential to influence biodiversity and community composition, as well as behaviour and habitat preference in bird species [7,8]. If the focus of planners is to improve avian biodiversity across these diverse urban habitats, it is important to understand how birds are utilising the three-dimensional space available to them [9].

Urban environments may vary from highly dense city centres and sprawling suburbia to human-made parklands and other pockets of more natural habitat. This can present a host of challenges and opportunities for the species that occupy them. This matrix of different environments has the potential to host bird species with varying levels of habitat specialisation [9,10]. Urban parklands and other local habitat features, for example, have been proven to influence species distribution in highly urbanised areas [11]. Increased diversity due to the exploitation of new environments has also been described in the context of urban areas [12]. The added structural heterogeneity from anthropogenic features (e.g., buildings of varying heights) can create new resources and niches that some species may be able to exploit such as potential nesting and perching sites [12,13]. These structures may also influence species' behaviour such as how they forage, fly, and compete, and how they use the available airspace [14,15]. The value of these new vertical habitats to biodiversity (e.g., remnant verge-side vegetation, suburban yards/houses, and green infrastructure) is often overlooked [2,16,17]. Height variability in vegetation, buildings, and other anthropogenic structures can create novel habitats; however, little is known about whether birds are using this space [18–20].

Urban areas also present a host of new threats to bird species, which could influence how they are occupied. Increased human activity, urban noise, and artificial light all have influences on a species' ability to tolerate urban environments [6,21]. Similarly, tall buildings and other artificial structures are an obstruction to birds in flight, which may avoid these areas or risk fatal collisions [22,23]. Such structures can impact the ability of birds to disperse, source food, and reproduce amongst other activities [24,25]. Due to the potential disturbance that vertical anthropogenic structures may have on airborne species, the availability of vertical habitat and free airspace is an important consideration. Collision risk concerning buildings, wind farms, and other obstructions has also long been a challenge for birds navigating these urban spaces; however, research into bird flight activities on a local scale is still lacking [26,27]. Despite the contrasting threats and potential these urban habitats present, relatively little is known about whether birds are taking advantage of their novel structural variability [18–20].

Behavioural flexibility is one of the key factors driving a bird species' ability to exploit altered landscapes and it is inherently linked to the 3D space. A species' ability to perform key, life-sustaining behaviours at a range of strata allows them to fully utilise urban landscapes. This relationship is often studied in specific environments or for specific threats, or predictively in relation to habitat structure and functional traits [7,12,28,29]. Without knowing whether birds are interacting with novel vertical habitats and airspace in response to local threats in urban areas, insight cannot be gained into how to improve them for target bird species, e.g., designing green infrastructure that enhances biodiversity [29].

While little is currently known regarding how birds use their available vertical habitat in urban areas, birds have long been documented utilising the varying strata in natural areas for different behaviours and activities. In natural areas, resource partitioning of the available habitat space creates vertical niche differentiation for species occupying a similar area [30]. Foraging guilds, for example, are often categorised by the heights of the surrounding vegetation, highlighting the importance of 3D structuring to bird diversity and community composition [31,32]. Based on this idea, forests with a high open canopy, as well as a dense understory layer, should hold a high number of species due to having the most diversity in structure and habitat space, although not all studies have supported this finding [31,33]. Similarly, the loss of understorey species in urban areas supports the relevance of these vertical strata in novel environments [34,35]. Vegetation heterogeneity is one of the best predictors of bird species richness and composition across many natural environments [7,36–38], with vegetation height categories creating distinct structural niches [7,39]. This could be extrapolated to urban environments, where the added structural diversity of anthropogenic features is rarely studied, though it has been found to increase habitat heterogeneity and productivity [8,12,39]. While it is known that birds rely on vertical partitioning, the novel vertical airspace of urban areas is understudied.

Despite the prominence of urban bird studies, knowledge is still lacking on how 3D structures are influencing the suitability of urban habitats for bird species [39]. This study will hereby investigate the gaps in our understanding of the use of vertical space by birds in the context of urban areas to inform how birds respond to the anthropogenic risks associated with urban airspace [40]. Many airborne organisms occupy a range of elevations within their habitat, which begs the question of whether bird species are using the same range of elevations regardless of structural changes in their environment along the urbanisation gradient [24]. Similarly, we know that many studies have explored the importance of vertical niches to birds, at least within natural environments. Hence, we examined whether the heights that bird species are using vary across structurally diverse urban environments, by investigating if bird species (overall and individually) were observed at different heights depending on the urban environment type they are in (i.e., different vertical profiles). We then investigate what structural variables, such as building and vegetation heights, might explain variations in the observed heights both overall and for species groupings based on unifying traits. We predict that while some species' height profiles may remain consistent across the gradient, others would vary along with structural changes in each environment. Anthropogenic structures were of particular interest, with sites being selected to capture building variation. This information can help support urban planning decisions that aim to improve native, urban bird diversity and persistence.

2. Materials and Methods

We undertook bird activity surveys across the greater Brisbane area. Brisbane is the capital of Queensland, Australia, and has rapidly grown over the past two decades, with a current population of over 2.5 million people. We selected and classified our survey sites into three environment types, including (i) urban high (majority of buildings/structure > five stories, ~15 m), (ii) urban low (majority of buildings/structure below five stories), and (iii) urban parkland (little to no buildings or structures, mainly vegetation) (Figure 1). These categories were chosen to resemble a gradient of urban environments from a high to a low density of obstructive structures. Urban high environments were generally areas of more high-density living in urban hubs and the city centre, while urban low sites were mostly residential suburban sites with buildings of very similar heights and densities. For each category, we identified nine sites. The nine sites were surveyed seven times, each for 30 min at a time, leaving each environment type with 63 surveys (189 surveys total). Only one survey was conducted for each set of sites per day to reduce the impacts of weather variation. The total minimum amount of surveying per environment type was 1890 min. These surveys were conducted between 5.30 a.m. and 10 a.m., and we rotated the order in which sites were surveyed in the morning between days to reduce bias. A nested design was employed for selecting the locations of sites along an urban gradient (Figure A1). This helped reduce daily bias in sampling and ensure that species variation along the urban gradient was captured.

The sampling site area was a 400 $\times$ 400 m quadrat, where the observer traversed up to 1.5 km along a wandering transect. This was to ensure maximum visibility of birds between differing environments. The approach taken for the survey was similar to other studies, where the use of wandering transects is justified for spatially diverse species in different habitats with varying visibility [41,42]. Once a bird was sighted, their activity was monitored for 30 s, or until they left the line of sight, and its behaviour was classified into one of seven categories: flying over, flying through, foraging, perching, nesting, walking, or other (Table A1). Then, the height/elevation range (max and min) was recorded.

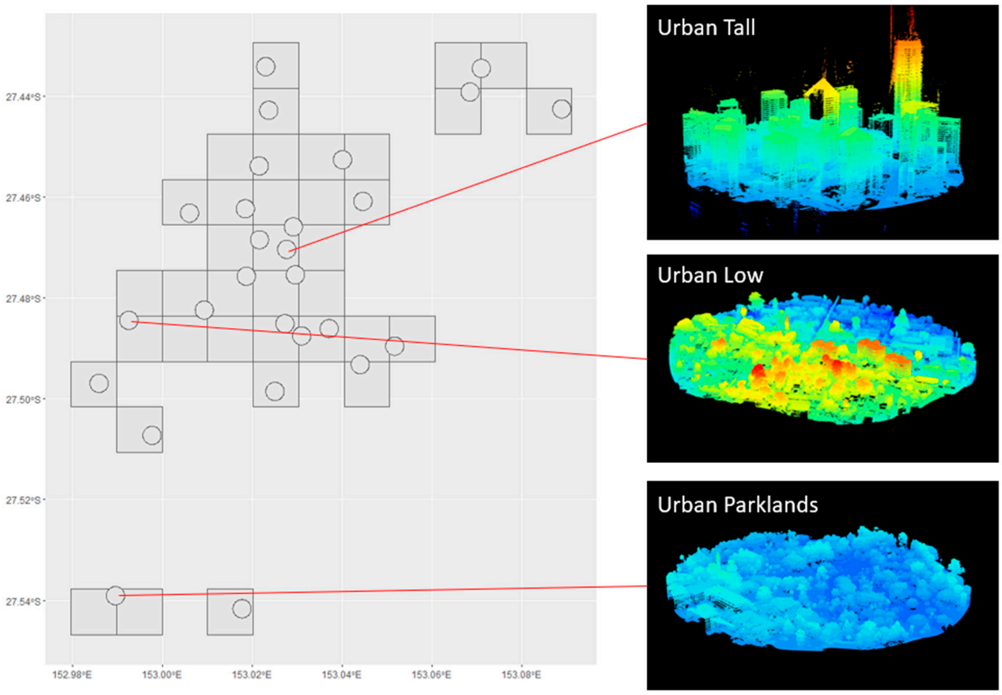


Figure 1. Visualisation of environment type differences using 3D LiDAR waveform data 2019, sourced from the QLD Department of Resources, for the definition of environment groupings: urban high (**left**), urban low (suburbia-centre), and urban parklands (**right**). The circles represent sites at their coordinates. The colours reflect heights within that study site (not comparable across sites).

We used a laser rangefinder and building height data to record bird height using the heights of the surrounding features at each survey site (i.e., urban trees and buildings). The heights recorded were purposefully grouped into ranges that related directly to shrub, upper/lower canopy, and building heights to reduce the error that may result from estimating exact heights (ranging [0], [1–3 m], [3–8 m], [8–15 m], [15–25 m], [25–50 m], [50–100+ m]). Birds that were seen and heard were recorded. Only calls that were close enough for the observer to estimate a height range were recorded. In the case that a group of individuals (flock) was sited at a study site (>5 individuals), then the activity being performed by the greatest proportion of birds in the flock was selected, and a single individual was monitored for 30 s. The number of birds in the flock and the maximum and minimum height of the flock were recorded. The sampling of sites has been standardised to ensure equal effort was used for each environment type. An effort was made to continuously monitor previously recorded birds to reduce the risk of double counting, and if there was uncertainty, no new record was created as a precaution. To further address the issue of potential double counting, more sites with fewer surveys per environment type were incorporated. To address walking bias and visual vertical detectability biases, the amount of time spent surveying birds at different height strata was standardised. The height at which birds were observed was capped as 100 m+, and a vantage point was included in each transect to allow for reduced visibility bias from obstructions across each environment type. With these alterations to the survey design, assumptions were made that detectability differences between study sites had been mitigated. We also assumed that independent samples of bird flight height/activity were being taken during each sampling occasion.

We collected this information to investigate how birds used urban vertical habitat and airspace, with flight activity/height often acting as an explanatory factor for how birds respond to risks in this space, e.g., variation in migratory flight and variation in flight around wind turbines [40,43]. The study controls for seasonal and daily variation in species presence and focuses on spatial, not temporal, variation. Hence, spring and summer seasons were selected for sampling, given that this is when most species are active and breeding [41,44]. Migrants were not isolated in this study.

Bird species that occurred across all three environment types (urban high, urban low, and urban parklands) were the focus of this study. Species with the largest amount of data that occurred across all three site categories were used to analyse across-site variations. We compared how individual species' activity at a height varies across the urbanisation gradient. Then, we investigated the extent to which a species' height can be explained by the structural differences between environment types, and whether this varied after grouping species by various traits. In the context of this study, vertical habitat use includes the height ranges that species are active in (minimum, mean, and maximum height). For the analysis, we used the Kruskal-Wallis test for non-parametric data to compare species activity heights across the three environment types, both overall and for species that occurred across all three environments with greater than five minimum observations per category. We categorised the environment types by building and vegetation heights and quantified these structural differences using LiDAR data (Figure 1). We then used cumulative link mixed models (for ordinal data) to determine what structural variables explain the heights that species are using. This model was selected to better account for the ordinal and categorical nature of the height data collected. The models were run with observed height as the dependent variable and the structural characteristics of the survey sites as the explanatory variables (e.g., building heights and vegetation heights) (Table A2). This was run for the various species groupings based on their traits.

Structural data (height variables) were extracted from the 2019 LiDAR waveform data from the Department of Resources, QLD. First, the LAS dataset was classified, and then the LidR package [45] was used to extract standard (grid) metrics for points independently classified as buildings and vegetation (Figure 1). These include height minimum, maximum, mean, median, range, and percentiles in metres, as well as the area these classified categories covered. Foliage Height Diversity (FHD) median, max canopy, and medium vegetation layers were also available from the Department of Environment and Science (2014 LiDAR dataset), which were also incorporated. Next, the sites were voxelised into 1×1 m voxels and standard metrics were extracted again. This process creates 1×1 m cubes from within the LiDAR point cloud data to cover the extent of the points (i.e., 'features') and calculate metrics from within these. The average heights by voxel of vegetation and buildings at a site and the area they covered at a site were then used in the cumulative link models (Table A2). These metrics were then compared in a correlation matrix and highly correlated variables were removed. Many height-related variables were highly correlated.

To test for co-linearity on the remaining variables, we then calculated the variance inflation factors. These were calculated for a regression of the remaining variables, where VIFs > 5 were removed. Next, a stepwise generalised linear model of the Gaussian family was run using the remaining variables, all of which showed a significant relationship with observation height. Variables were scaled appropriately. There was not a lot of variation in standard metrics between 2014 and 2019; however, 2019 building heights were considered more accurate. The dependent variable was observations of activity within a given height bin. In this instance, if a bird was recorded traversing across multiple height bins, this was still recorded as observed activity across both those height classes. This model also incorporated two interaction effects (i.e., average building/vegetation height interacting with area coverage of buildings) since building height and coverage are not truly independent factors. Finally, this model included sites as a random effect, as they were nested. A test on the standard deviation of outputs was run to ensure that the models were a good fit.

This cumulative link model was initially run on species overall, and then the species were categorised into data subsets. The traits that species were subset by were decided upon from a review of the available literature and sourced from the *Handbook of Australian, New Zealand and Antarctic Birds* (HANZAB) [46], collated partially by [47] and the Australian Bird Dataset. Any remaining gaps were filled in from the HANZAB guide. The species were categorised into urban avoiders, adapters, and exploiters based on the observation results and the grouping created by Sol et al. [48]. This category represents their degree of urban tolerance, derived in the paper from species traits and range shifts moving along an urban gradient. Secondly, species were categorised by their feeding level, due to their relevance to their vertical habitat requirements, which was extracted from data in the HANZAB encyclopaedia (Table A4). These feeding levels were grouped based on vertical distribution (i.e., high, medium, and low) to avoid complications with having too many variables being compared/explained in the models. Thus, 'aerial' feeders and 'arboreal high' (upper canopy) feeders were grouped, as well as 'all' and 'arboreal all' (feeding across all levels), and 'arboreal low' (lower vegetation) and 'ground' feeders. These groupings were made as it is reasonable to predict that species with different foraging levels and urban tolerance may use heights differently. Therefore, running a single model combining all species may not provide such detailed information on which covariates were impacting heights given that certain individual species on the extremes of the spectrum could be skewing the results.

3. Results

3.1. Site Definition

Structural variables were extracted for each site in order to define the environment types and to be used in the cumulative link models (Figure 1). There was a high correlation between the various height-related variables, with a high correlation between building maximum, minimum, range, and mean, as well as vegetation maximum, minimum, range, and mean. The urban high environment was characterised by taller buildings and variable yet relatively low vegetation cover. The urban low environment (suburbia) was characterised as having many buildings with 0–15 m of height and similar vegetation cover to parklands. Parklands were characterised as having the lowest density of buildings and the tallest vegetation (Figures 1 and 2, Table A3). The median vegetation heights were similar for the urban high and urban low sites. The maximum canopy height was greatest in the parklands and lowest in urban high sites. The FHD index was similar across the sites (Table A3).

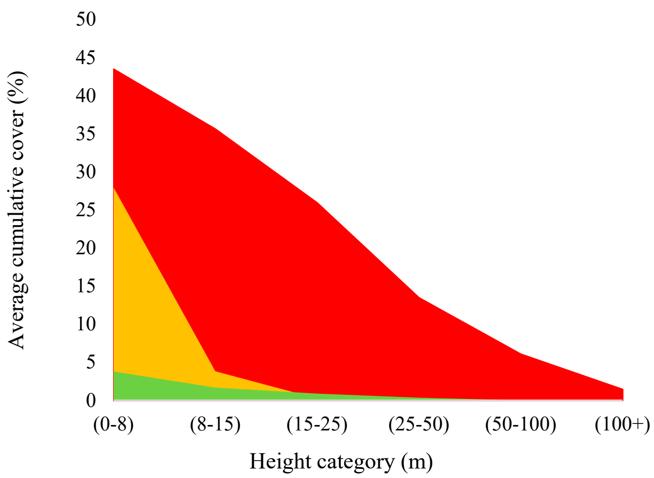


Figure 2. Cumulative percentage cover of buildings within distinct height categories across environment types (red = urban high, yellow = urban low, green = urban parklands).

3.2. Survey Results

During the 189 sampling occasions, a total of 10,858 individuals were observed. Overall sampling success (number of sampling occasions a species was observed) varied greatly across species. The greatest number of individual observations was in parklands (4911), with the second greatest in urban low (3791) and the lowest in urban high environments (2256) (Table 1). Species richness was the highest in parklands (90), followed by urban low (62), and lowest in urban high (36) environments. Only a subset of species occurred across all three environments, with certain groups seen in high numbers across all, while many others were only observed in parkland sites or occasionally straying into the urban low environments in small numbers (Table 1).

Table 1. Count of individuals seen for each species in each environment type. In brackets is the number of sampling occasions observed.

	Urban High	Urban Low	Urban Parkland	Total
Acanthizidae				
Acanthiza chrysorrhoa	-	-	3 (1)	3 (1)
Acanthiza nana	-	-	1 (1)	1 (1)
Acanthiza pusilla	-	-	4 (3)	4 (3)
Gerygone mouki	-	-	2 (2)	2 (2)
Sericornis magnirostra	-	-	1 (1)	1 (1)
Acrocephalidae				
Acrocephalus australis	-	1 (1)	5 (3)	6 (4)
Alcedinidae				
Dacelo novaeguineae	1 (1)	8 (7)	28 (17)	37 (25)
Todiramphus sanctus	-	1 (1)	1 (1)	2 (2)
Anatidae				
Aythya australis	-	-	5 (1)	5 (1)
Anas superciliosa	-	-	16 (10)	16 (10)
Chenonetta jubata	-	-	89 (11)	89 (11)
Anhingidae				
Anhinga novaehollandiae	2 (1)	1 (1)	1 (1)	4 (3)
Apodidae				
Apus pacificus	2 (2)	-	-	2 (2)
Hirundapus caudacutus	-	-	1 (1)	1 (1)
Ardeidae				
Ardea alba modesta	1 (1)	2 (2)	24 (7)	27 (10)
Bubulcus ibis	-	-	3 (2)	3 (2)
Egretta garzetta	-	1 (1)	2 (1)	3 (2)
Egretta novaehollandiae	-	-	1 (1)	1 (1)
Artamidae				
Artamus leucorynchus	4 (4)	12 (5)	9 (4)	25 (13)
Cracticus nigrogularis	51 (27)	89 (43)	137 (42)	277 (112)
Cracticus torquatus	18 (14)	159 (53)	97 (42)	274 (109)
Gymnorhina tibicen	64 (30)	159 (52)	146 (44)	369 (126)
Strepera graculina	113 (45)	67 (39)	90 (36)	270 (120)
Burhinidae				
Burhinus grallarius	-	-	44 (12)	44 (12)

Table 1. *Cont.*

	Urban High	Urban Low	Urban Parkland	Total
Cacatuidae				
Cacatua galerita	5 (3)	40 (6)	84 (20)	129 (29)
Cacatua sanguinea	6 (4)	52 (19)	29 (12)	87 (35)
Eolophus roseicapilla	2 (1)	51 (12)	19 (10)	72 (23)
Campephagidae				
Coracina novaehollandiae	2 (1)	23 (15)	26 (13)	51 (29)
Charadriidae				
Vanellus miles	14 (3)	21 (8)	177 (34)	212 (45)
Columbidae				
Columba leucomela	1 (1)	2 (2)	1 (1)	4 (4)
Columba livia domestica	261 (45)	214 (39)	15 (6)	490 (90)
Geopelia humeralis	-	-	1 (1)	1 (1)
Ocyphaps lophotes	3 (2)	106 (39)	20 (9)	129 (50)
Spilopelia chinensis	6 (4)	104 (46)	14 (10)	124 (60)
Corvidae				
Corvus orru	252 (53)	341 (58)	353 (54)	946 (165)
Cuculidae				
Cacomantis flabelliformis	-	11 (7)	10 (9)	21 (16)
Cacomantis pallidus	-	2 (2)	10 (6)	12 (8)
Cacomantis variolosus	1 (1)	8 (8)	19 (11)	28 (20)
Centropus phasianinus	-	1 (1)	2 (2)	3 (3)
Eudynamys orientalis	-	9 (6)	10 (9)	19 (15)
Scythrops novaehollandiae	-	1 (1)	3 (2)	4 (3)
Dicruridae				
Dicrurus bracteatus	-	-	4 (4)	4 (4)
Dicaeidae				
Dicaeum hirundinaceum	-	-	1 (1)	1 (1)
Estrildidae				
Neochmia temporalis	-	-	2 (2)	2 (2)
Taeniopygia bichenovii	-	1(1)	7 (2)	8 (3)
Hirundinidae				
Hirundo neoxena	544 (52)	140 (42)	370 (51)	1054 (145)
Petrochelidon ariel	60 (8)	3 (2)	45 (9)	108 (19)
Petrochelidon nigricans	1 (1)	5 (4)	10 (7)	16 (12)
Laridae				
Chroicocephalus novaehollandiae	1 (1)	-	4 (3)	5 (4)
Locustellidae				
Cincloramphus timoriensis	-	-	3 (1)	3 (1)
Maluridae				
Malurus cyaneus	1 (1)	21 (5)	110 (28)	132 (34)
Malurus melanocephalus	-	-	1 (1)	1 (1)
Megapodiidae				
Alectura lathami	-	7 (6)	15 (11)	22 (17)
Meliphagidae				
Entomyzon cyanotis	28 (16)	85 (30)	91 (30)	204 (76)
Lichmera indistincta	-	4 (3)	6 (5)	10 (8)
Lichenostomus leucotis	-	2 (1)	-	2 (1)
Manorina melanocephala	218 (44)	553 (62)	539 (54)	1310 (160)
Meliphaga lewinii	-	6 (1)	1 (1)	7 (2)
Melithreptus albogularis	-	10 (7)	7 (6)	17 (13)
Melithreptus lunatus	-	7 (4)	12 (9)	19 (13)
Myzomela sanguinolenta	-	-	1 (1)	1 (1)
Philemon citreogularis	-	8 (6)	49 (11)	57 (17)

Table 1. *Cont.*

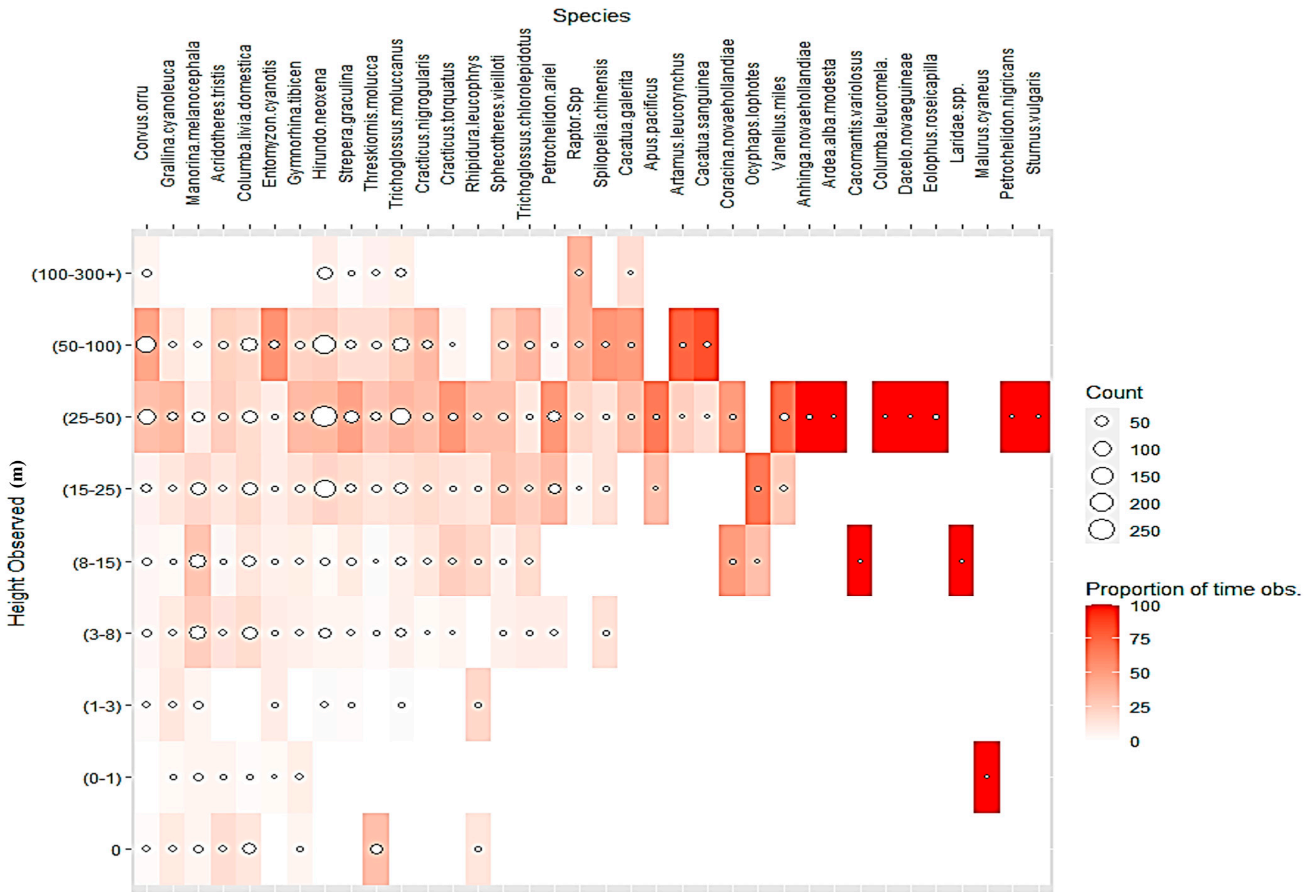
	Urban High	Urban Low	Urban Parkland	Total
Monarchidae				
Grallina cyanoleuca	58 (23)	67 (32)	120 (39)	245 (94)
Myiagra rubecula	-	-	5 (4)	5 (4)
Oriolidae				
Oriolus sagittatus	-	5 (5)	6 (5)	11 (10)
Sphecotheres vieilloti	38 (14)	200 (48)	180 (41)	418 (103)
Pachycephalidae				
Colluricincla harmonica	-	36 (14)	48 (15)	84 (29)
Colluricincla rufogaster	-	-	3 (3)	3 (3)
Pachycephala rufiventris	-	2 (1)	14 (12)	16 (13)
Pardalotidae				
Pardalotus punctatus	-	-	2 (2)	2 (2)
Pardalotus striatus	-	2 (2)	19 (11)	21 (13)
Phalacrocoracidae				
Microcarbo melanoleucos	-	-	13 (1)	13 (1)
Phalacrocorax sulcirostris	-	10 (8)	14 (10)	24 (18)
Phalacrocorax varius	-	6 (3)	20 (10)	26 (13)
Podargidae				
Podargus strigoides	-	-	6 (6)	6 (6)
Psittaculidae				
Alisterus scapularis	-	3 (3)	1 (1)	4 (4)
Platycercus adscitus	-	7 (1)	1 (1)	8 (2)
Trichoglossus chlorolepidotus	26 (8)	51 (19)	111 (24)	188 (51)
Trichoglossus moluccanus	300 (41)	801 (61)	608 (53)	1709 (155)
Psophodidae				
Psophodes olivaceus	-	1 (1)	2 (2)	3 (3)
Rallidae				
Gallinula tenebrosa	-	-	34 (17)	34 (17)
Porphyrio melanotus	-	-	6 (5)	6 (5)
Raptors				
Raptor spp.	20 (14)	15 (11)	12 (10)	47 (35)
Rhipiduridae				
Rhipidura albiscapa	-	1 (1)	6 (4)	7 (5)
Rhipidura leucophrys	12 (10)	8 (6)	66 (37)	86 (53)
Rhipidura rufifrons	-	2 (2)	6 (5)	8 (7)
Sturnidae				
Acridotheres tristis	50 (20)	120 (32)	23 (15)	193 (67)
Sturnus vulgaris	1 (1)	13 (11)	15 (11)	29 (23)
Threskiornithidae				
Threskiornis molucca	89 (34)	79 (33)	621 (51)	789 (118)
Threskiornis spinicollis	-	19 (5)	41 (16)	60 (19)
Unidentified				
Un. spp.	-	5 (3)	23 (9)	28 (12)
Zosteropidae				
Zosterops lateralis	-	-	4 (3)	4 (3)
Total	2256 (63)	3791 (63)	4811 (63)	10,858 (189)

Note: Raptors were generalised into the group *Raptor* spp. as they were a definite group of interest for urban high environments; however, they are harder to identify at greater heights, where they were mostly observed.

3.3. Comparisons Across Urban Environment Types

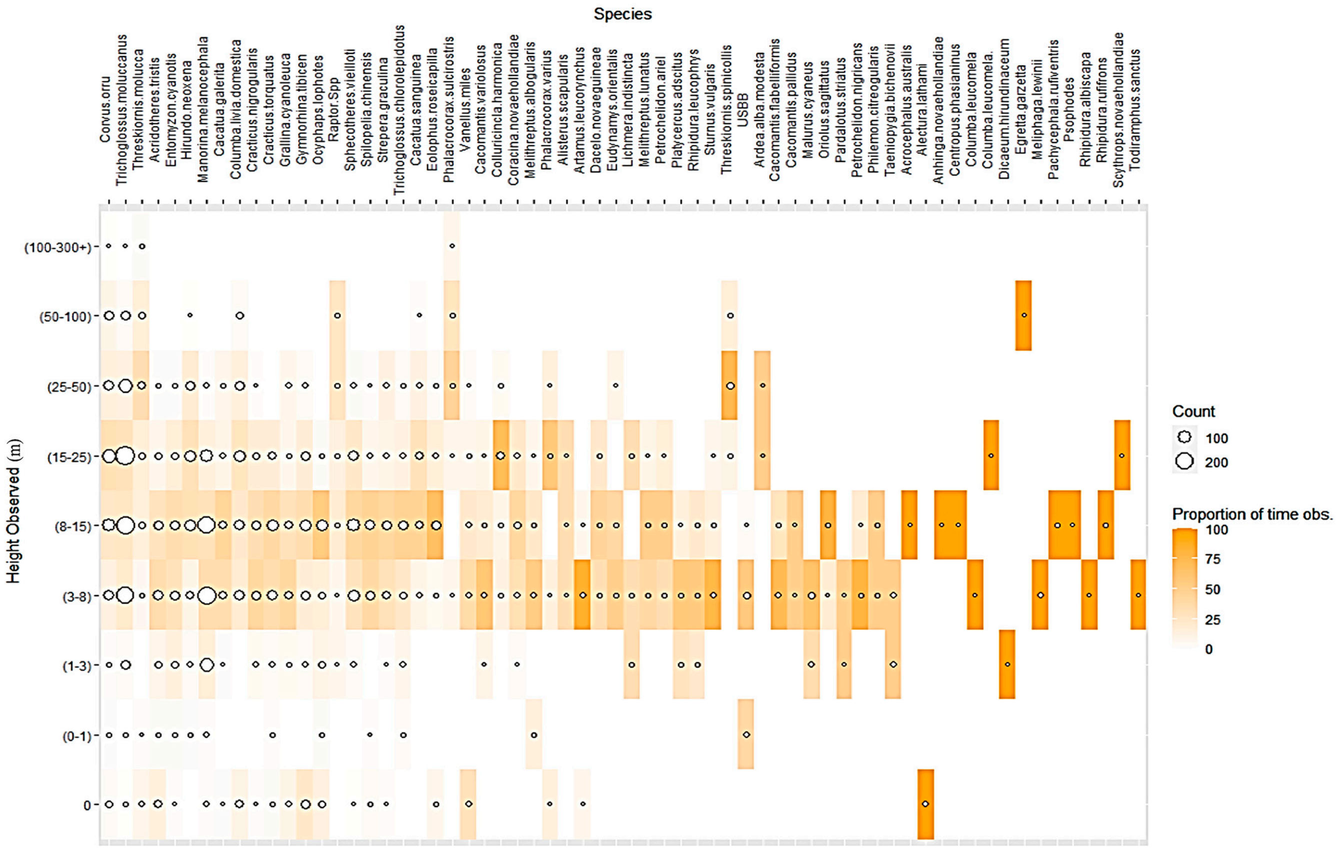
Overall, the height profiles used by the urban birds varied across the three types of environments along the urbanisation gradient. Species observed in urban high environments were flying at greater heights, with the greatest density of observations around the 25–50 m category both for individual species and across all species, with 50–100 m and 15–25 m being the next most used, respectively. The range of heights in which species activity was recorded was reduced overall for all species within the urban high environments. This trend was observed across species observed in this environment type, as well as within the height profiles of individual species. Species that appeared to be generalists (across all three environment types) such as *Corvus orru* (Torresian crow) and *Strepera graculina* (pied currawong) were often observed at the height of the tallest structures available in an environment (Figure 3). Even species that were only observed a handful of times in the urban high environments such as the *Dacelo novaeguineae* (laughing kookaburra), *Anhinga novaehollandiae* (Australasian darter), *Sturnus vulgaris* (common starling), *Coracina novaehollandiae* (black-faced cuckooshrike), and *Artamus leucorynchus* (white-breasted woodswallow) were observed occupying the upper height elevations (generally 25–50 + m).

Most of the observations in urban low environments fell into the 3–8 m and 8–15 m categories. Urban low environments still had a greater range of heights used both for individual species and across all species compared with urban high environments, with most species at some point observed in the 15–25 m category and often higher. These observed height profiles reflect the height of buildings within the environment type as identified in Figure 2.

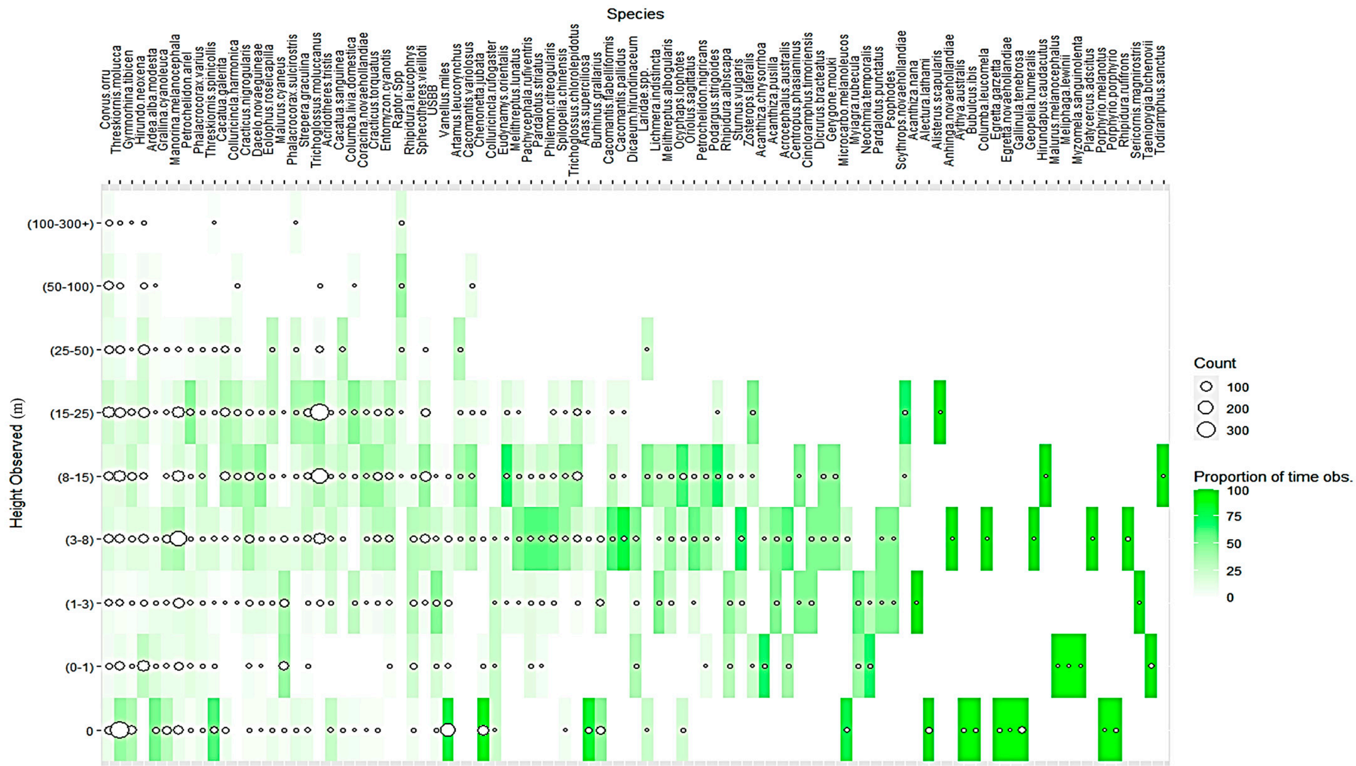


(**a**)

Figure 3. *Cont.*



(**b**)



(**c**)

Figure 3. Heatmaps representing the distribution of species across heights in (**a**) urban high sites, (**b**) urban low sites, and (**c**) urban parkland sites. Darker shades represent a higher proportion of observations in that height bin, for that species (vertical columns). The number of individuals observed is included as a point, with larger points representing larger counts.

Parklands had the greatest species richness and these species utilised the most diverse range of heights. More observations were made in the lower height categories and on the ground level within the urban parklands' environment type (Figure 3). Smaller honeyeaters and forest birds were more likely to be observed in parklands, compared to the more generalist species that could be observed across all three environments, and when they were observed outside of parklands, they were generally at lower height ranges (Table A3). Overall, certain height ranges were favoured across environments, and this was observed both among and within species.

Overall, there was a significant difference between the observed flight heights of birds across all three environment types (Kruskal–Wallis chi-squared = 1248.5, $p < 0.001$). Birds used a greater range of heights and, on average, flew approximately twice as high in urban high environments in comparison to urban low (Dunn's test Z score = 26.03, $p < 0.001$) and parkland sites (Dunn's test Z score = 35.09, $p < 0.001$). Flight heights in urban low environments were still significantly higher than in parkland environments (Dunn's test Z score = 10.27, $p < 0.001$) (Figure 4).

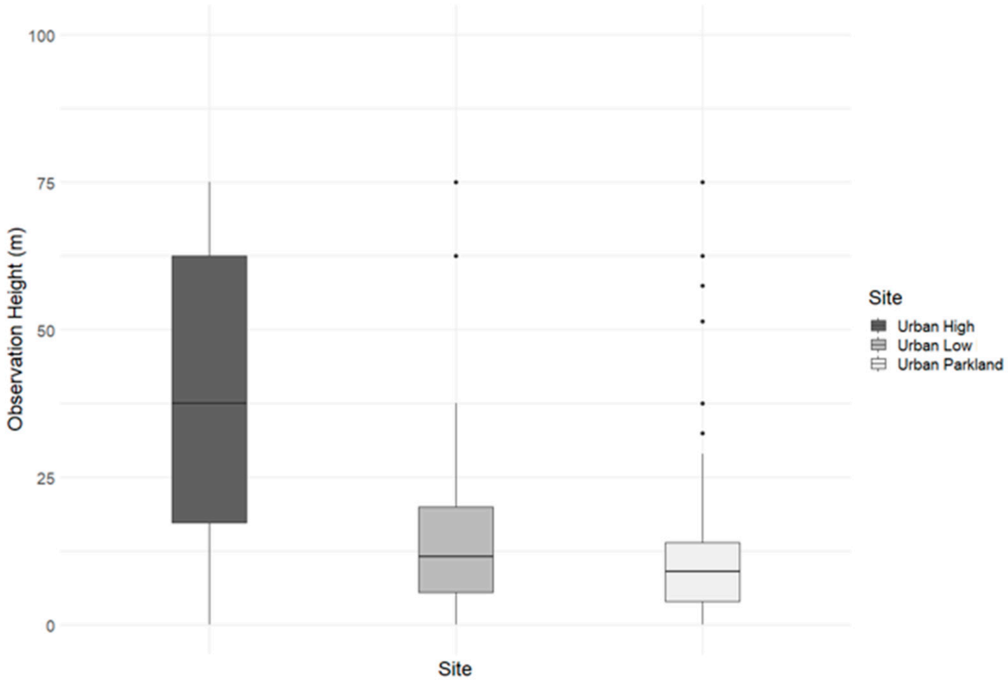


Figure 4. Summary boxplot depicting the range of heights for all species occurring across all three environment types.

Of the species observed, 10 out of 17 (59%) had a significantly higher height profile in urban high environments than parklands and suburbia, but the results displayed no significant difference between parklands and suburbia (Figure 5) (Australasian figbird: KW chi-sq = 26.26, $p < 0.001$, sample = 244; grey butcherbird: KW chi-sq = 26.96, $p < 0.001$, sample = 254; blue-faced honeyeater: KW chi-sq = 10.18, $p < 0.01$, sample = 134; noisy miner: KW chi-sq = 33.74, $p < 0.001$, sample = 714; rainbow lorikeet: KW chi-sq = 148.47, $p < 0.001$, sample = 680; Torresian crow: KW chi-sq = 171.43, $p < 0.001$, sample = 579; common myna: KW chi-sq = 19.84, $p < 0.001$, sample = 129; pied butcherbird: KW chi-sq = 91.19, $p < 0.001$, sample = 226; pied currawong: KW chi-sq = 102.24, $p < 0.001$, sample = 229; scaly-breasted lorikeet: KW chi-sq = 12.40, $p < 0.01$, sample = 78). Three species (18%), *Gymnorhina tibicen* (Australian magpies), *Grallina cyanoleuca* (magpie-larks), and *Hirundo neoxena* (welcome swallows), displayed significantly different height profiles across all three environment types (Australian magpie: KW chi-sq = 56.45, $p < 0.05$, sample = 265; magpie-lark: KW chi-sq = 39.66, $p < 0.05$, sample = 173; welcome swallow: KW chi-sq = 149.61, $p < 0.05$, sample = 383). The raptors observed flew higher in urban high environments compared to low (KW chi-sq = 6.70, $p < 0.05$, sample = 44), but otherwise showed no significant differences between environment types, as did the *Columba livia domestica* (domestic pigeon) (KW chi-sq = 15.78, $p < 0.001$, sample = 231). *Vanellus miles* (masked lapwings) flew significantly higher in urban high and urban low environments compared to parklands (KW chi-sq = 33.69, $p < 0.001$, sample = 73). The *Threskiornis moluccus* (Australian white ibis) was observed at significantly lower heights in parklands compared to urban high and urban low environments (KW chi-sq = 54.53, $p < 0.001$, sample = 321); however, it displayed no significant difference in their height uses between the urban low and high environments (Figure 5). Overall, there was a trend towards higher species activity being recorded in urban high environments, and around the same height for suburbia and parklands. Occasionally, when some species were seen showcasing greater activity at urban high sites (Figure 3), the range of heights they used was often reduced (Figures 4 and 5).

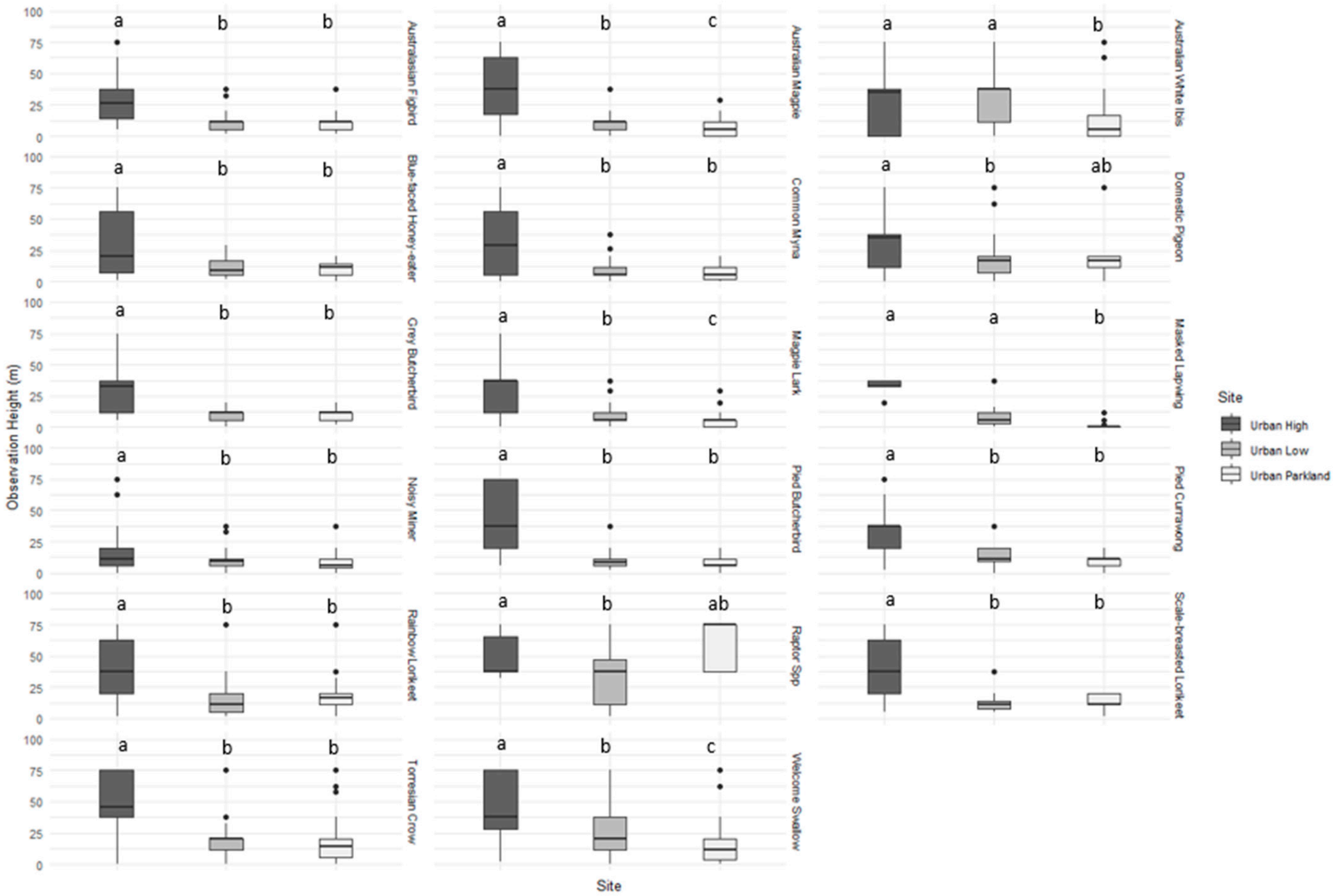


Figure 5. Boxplots depicting the range of heights for species occurring across all three environment types. Each boxplot represents a different species. In total, 17 species were selected, as they occurred across all the environments and had >5 counts at each. Kruskal–Wallis tests were run on each individual species to compare sites. The outcomes are represented by letters, where sites that have the same letter have no significant difference between flight heights at these sites.

The observational data note that, overall, species were observed more often interacting with the structures within their environment (either natural or anthropogenic) than not. This was observed in urban high, urban low, and urban parkland environment types. The average height at which species were not interacting with these structures was generally observed to be greater than when they were. The average heights at which species were interacting with their environment were reasonably similar between urban low environments and urban parklands; however, they appear to be much greater in urban high environments (Table 2). No statistics were analysed for observations of specific activities/behaviours and whether they were interacting with structures in their environment as sample sizes did not allow for sufficient power in the analysis.

Table 2. This table summarises general observation data, depicting whether species were seen interacting (shaded grey) or not interacting (white) with environmental structures, anthropogenic and natural, across the three environment types. The average height (m) is in the centre. Interacting can be defined as the foraging, perching, and nesting activities (as well as some in the other category, i.e., fighting) versus not interacting which is defined as the flying over and flying through activities. Species were included despite low numbers of records/observations.

Species	Urban High		Urban Low		Urban Parkland	
	Interacting	Not Interacting	Interacting	Not Interacting	Interacting	Not Interacting
Australasian Figbird	30.76	75.00	9.97	22.39	10.06	22.92
Australian Darter	37.50		11.50		5.50	
Australian Magpie	34.95	75.00	9.76	25.83	6.95	54.30
Australian White Ibis	28.79	92.50	11.24	48.00	7.08	38.98
Black-Faced Cuckoo	29.00		12.00	20.00	10.14	
Blue-Faced Honeyeater	31.36		9.45	17.10	10.28	20.00
Brush Cuckoo	11.50		7.19		14.07	
Common Myna	32.23	37.50	8.64	18.30	5.63	20.00
Common Starling	37.50		7.54		5.09	
Crested Pigeon	15.75		8.14		7.75	
Domestic Pigeon	30.54	64.29	12.24	29.18	12.50	38.33
Eastern Great Egret		37.50		28.75	10.65	
Fairy Martin	43.65		12.75		11.95	
Grey Butcherbird	29.59		10.51	8.50	10.57	
Laughing Kookaburra	37.50		12.71		10.39	
Little Corella	56.25	75.00	15.97	35.83	13.32	37.50
Magpie-Lark	29.83	75.00	8.31	37.50	5.73	20.00
Masked Lapwing	32.86		6.50	37.50	1.15	
Noisy Miner	14.83	20.00	8.40	21.23	8.18	23.10
Pied Butcherbird	43.49	75.00	8.73	22.80	8.08	20.00
Pied Currawong	39.96	45.83	12.00	30.94	9.73	15.75
Pink and Grey Galah	37.50		12.40	37.50	11.40	28.75
Rainbow Lorikeet	37.58	93.56	11.12	32.28	13.64	26.61
Raptor Spp	>100.00	>100.00	14.67	49.33	49.75	92.14
Scale-breasted Lorikeet	36.50	75.00	11.07	28.83	13.09	20.00
Spotted Turtle Dove	17.13	75.00	8.70	25.83	8.50	16.50
Sulphur-Crested Cockatoo	50.00	>100.00	8.79	25.83	14.10	20.00
Superb Fairy Wren	0.50		3.94		2.03	
Torresian Crow	52.80	76.74	13.06	39.84	12.63	42.03
Welcome Swallow	61.81	60.00	20.66	40.50	16.14	43.60
White-Breasted Woodswallow	65.63		6.70		14.38	20.00
Willy Wag Tail	22.36		5.71	11.50	3.57	

3.4. Analyses of Flight Height as Explained by Site-Level Environment Variables

The results indicated a close relationship between the height of structures available in an urban environment, both building- and vegetation-based, and the observed species' flight heights (Figures 3–5, Table 3). Overall, building area (Est = 0.86, $p < 0.001$) and mean building (Est = 0.05, $p < 0.01$) and vegetation height (Est = 0.18, $p < 0.01$) had a strong positive and weak positive effect on all bird activity heights, respectively. Similarly, vegetation cover also showed a strong negative relationship with all bird activity heights (Est = −1.01, $p < 0.05$). It is interesting to note that Foliage Height Diversity (FHD) did not have a significant effect on the activity heights (Table 3). When grouping species by their feeding level, species that typically forage in the upper canopy and airspace showed significant relationships between flight heights and nearly all structural variables except FHD (Table 4; see Appendix A for further details). In comparison, only the more generalist foragers had their observed heights explained by the coverage of buildings (Est = 0.79, $p < 0.001$) and then also mean vegetation heights (Est = 0.28, $p < 0.001$), with both of these being positive relationships. Finally, low-level foragers showed significant relationships with building height (Est = 0.05, $p < 0.01$) and area (Est = 0.78, $p < 0.001$), although vegetation coverage was also important (Est = −1.02, $p < 0.05$) (Table 4). When species are grouped into urban tolerance categories of exploiters, adapters, and avoiders, we found that the observed height of urban adapters had weak/moderate relationships with vegetation (Est = 0.41, $p < 0.001$) and building heights (Est = 0.05, $p < 0.05$), as well as strong positive and negative relationships with building (Est = 1.29. $p < 0.001$) and vegetation (Est = −1.41, $p < 0.05$) cover, respectively (FHD excluded). Moreover, urban exploiter flight heights were only explained by building variables (height, Est = 0.04, $p < 0.01$; area, Est = 0.55, $p < 0.01$), including the interaction between height and area. Urban avoiders had a strong positive relationship with building area (Est = 1.21, $p < 0.001$) and vegetation area (Est = 2.00, $p < 0.05$) as well as an interaction effect (Table 5). Urban avoider flight heights did not significantly vary with building heights. An explanatory factor relating to buildings was always influencing species' flight heights across environments.

Table 3. Refined cumulative link mixed model with flexible variability between orders. The response variable is the observation heights of species activity, and this is explained by the environmental covariates below. Sub-sites are included as a random effect. Foliage Height Diversity (FHD) is incorporated as a defined metric. Levels of significance are displayed as an asterisk (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

Environmental Variables	Estimate	Std. Error	z Value	Pr (>∣z∣)
Mean building height (voxels)	0.05034	0.01612	3.123	0.00179 **
Building area	0.85996	0.19297	4.456	8.33×10^{-6} ***
FHD median	−1.19444	0.91900	−1.300	0.19370
Mean vegetation height (voxels)	0.17755	0.06881	2.580	0.00987 **
Vegetation area	−1.00911	0.50851	−1.984	0.04721 *
Interaction—mean building height: area	−0.02897	0.01112	−2.604	0.00922 **
Interaction—mean vegetation height: area	0.06746	0.05471	1.233	0.21758

Table 4. Significance output for cumulative link mixed model for species feeding level (vertical) subsets, with flexible variability between orders. The response variable is the observation heights of species activity, and this is explained by the environmental covariates below. Sub-sites are included as a random effect. Foliage Height Diversity (FHD) is incorporated as a defined metric. Levels of significance are displayed as an asterisk ('.' $p < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). See Appendix A for coefficient Tables A8–A13.

Environmental Variables	Pr (>∣z∣)		
	Aerial/Arboreal High	**All/Arboreal All**	**Ground/Arboreal Low**
Mean building height (voxels)	0.000174 ***	0.281	0.00816 **
Building area	3.70×10^{-9} ***	0.000645 ***	8.48×10^{-5} ***
FHD median	0.298	0.0519 .	0.498

Table 4. *Cont.*

Environmental Variables	Pr (>|z|)		
	Aerial/Arboreal High	All/Arboreal All	Ground/Arboreal Low
Mean vegetation height (voxels)	1.04×10^{-6} ***	0.000892 ***	0.706
Vegetation area	0.020050 *	0.553	0.0444 *
Interaction—mean building height: area	4.91×10^{-5} ***	0.120	0.0585 .
Interaction—mean vegetation height: area	0.187	0.995	0.153

Table 5. Significance output for cumulative link mixed model for species urban tolerance subsets, with flexible variability between orders. The response variable is the observation heights of species activity, and this is explained by the environmental covariates below. Sub-sites are included as a random effect. Foliage Height Diversity (FHD) is incorporated as a defined metric. Levels of significance are displayed as an asterisk ('.' $p < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). See Appendix A for coefficient Tables A8–A13.

Environmental Variables	Pr (>|z|)		
	Urban Avoiders	Urban Adapters	Urban Exploiters
Mean building height (voxels)	0.646	0.0443 *	0.00867 **
Building area	0.000211 ***	3.59×10^{-8} ***	0.00618 **
FHD median	0.106	0.271	0.420
Mean vegetation height (voxels)	0.113	7.51×10^{-6} ***	0.0635 .
Vegetation area	0.0190 *	0.0159 *	0.156
Interaction—mean building height: area	0.710	0.00664 **	0.0391 *
Interaction—mean vegetation height: area	0.0211 *	0.118	0.572

4. Discussion

The average height of both buildings and vegetation across the sites had a significant, positive effect overall on the observed bird heights. Overall, the observed flight heights also had a strong positive relationship with the building area and a strong negative relationship with the vegetation area. It could be inferred that, as predicted, some species' height profiles were varying along with structural changes in their environment. Bird species that were observed across all three environment types were flying higher at the urban high sites, which are characterised by tall anthropogenic structures (Figures 3–5) (Tables 4 and 5). They were also flying lower in areas with greater vegetation cover. Again, this could suggest that the height of urban structures is having an impact on birds in urban environments. Many species such as the Torresian crow and pied currawong, as well as some species less anticipated in intensive urban settings, were observed interacting with taller structures across the environments, including anthropogenic ones (Figure 3, Tables 2 and A3). Considering these interactions were characterised by activities such as perching, inter-perch flight, and foraging (Tables A6 and A7), it is possible that birds are using these structures to move through or survive within urban areas. However, sample sizes were small for observational data on specific activities, leading to a lack of statistical power and creating a significant gap for future research. Human-made urban features have, in some instances, been found to act as replacements for the vegetation layers normally occupied by some species [49], although it could be argued that this only holds true when species can use them for specific life-sustaining activities, i.e., nesting. It could also be the case that urban areas may simply favour species that thrive in naturally open environments (e.g., open forests) [9]. This study provides evidence to support the influence of a crowded urban airspace on bird flight heights, which has important implications for urban conservation.

A notable finding when investigating how individual species height profiles varied across the structurally diverse urban environments was that in urban high environments, species were observed predominantly in the greater height brackets (Figures 3a, 4 and 5). This sort of information could prove to be of importance when establishing urban greening principles. Some species were even observed there more often than they were in the urban low and parkland environments. *Raptor* species were a prime example of this. They spend a large proportion of their time soaring and even hunting in the upper airspace, which is reflected in their observed heights (Figure 5). This fits with what is known about these species. One study found that raptors have shown signs of improving their population numbers in urban areas, due to the tall perch and nesting points they provide as well as food subsidies. Raptors can exploit these resources with low competition, as well as at a lower energetic cost [22]. Similarly, species that are aerial feeders such as welcome swallows, or aerial migrants such as the Australian white ibis, may also more easily exploit the upper airspace in city environments to forage and travel, respectively (Table 5, Figure 5). Urban environments can provide opportunities to species in the form of improved perching locations where they can have an unobstructed, longer-distance view, as well as novel structures to nest on [50]. While it may be costly for certain species to cross roads frequently or fly up to the top of a tall building, for others, this might be a small expenditure for a greater food reward [51,52]. Although we observed birds interacting with structures at these greater elevations (Table 2), further research could focus on whether specific heights for urban greening are better at supporting life-sustaining behaviours. The potential for urban high areas to provide refuge for some species due to lower human disturbance, food, and perching locations could support the argument for implementing green roofs/structures in cities as a management tool for conservation planning. Other studies have found that green infrastructure can harbour species and support species movement, reflecting the ground level [53–55]. Studies on birds specifically have found them to be using green walls/roofs for key activities such as foraging, nesting, etc. [53]. This highlights the importance of incorporating 3D variables into urban planning, as it may unlock the potential for urban airspace and anthropogenic structures to support biodiversity.

The modelled relationships between the flight heights of specific species groupings (i.e., urban tolerance and feeding level) and the environmental covariates provide some explanation for why certain species height profiles remain consistent across structurally diverse urban environments while others vary. There was a significant positive relationship between adapter and exploiter species' flight heights and building heights, although it was weak. Both groupings also had moderate–strong relationships between their observed heights and building area/cover. Species in these groupings do seem to be varying their heights with buildings, perhaps indicating their ability to tolerate these environments. Many species that were classified as exploiters were the ones observed flying at greater heights in urban high environments and interacting with structures at these greater elevations which are likely to be tall buildings. Other studies support this finding, finding that urban exploiters used building structures (at least as perches) and the availability of greater heights regardless of vegetation. This likely contributed to their occupancy of all urban environment types along the gradient [10,51] (Tables A6 and A7). This relationship between height profiles across structurally diverse environments and urban tolerance has also been observed in another study for nesting heights at urban sites [51]. Further studies found that even in areas with lower suburban buildings, species were still altering their flight paths to adapt to the varied airflows and thermals created by the vertical obstructions [52,56]. This energy expenditure has implications for a species' ability to persist in and move through an environment. Hence, exploiter species' flight heights being influenced by building heights could be a product of their ability to maintain life-sustaining activities across structurally diverse environments. Further research on these species' groupings should consider three-dimensional (3D) space [52,56]. In the same fashion, urban adapter flight heights were influenced by all the environmental variables. There was a strong positive relationship between their observed heights and both building and vegetation heights (strong). The model also suggests they were flying lower as vegetation area increased and higher as cover decreased. This would explain their ability to adjust to the structural differences between environments (Table 4) [24]. Further research is required to explore factors that influence a bird's ability to exploit varying heights across diverse urban settings [56].

Conversely, the activity heights of urban avoider species remained consistently low despite building heights increasing along the gradient (i.e., they were not significantly influenced by building height variation), although the model suggests they were flying higher as the coverage of buildings increased. This is likely due to these species occupying specific niches, i.e., low dense understorey vegetation, which provides protection against predators [6,7,57–59], and hence being unable to adapt to the availability of new structures [60] (Table 4). Many species were only observed in parklands, including small species such as thornbills, warblers, and gerygones. The great diversity of height profiles used in parklands is likely due to the presence of more vertically heterogeneous vegetation and native vegetation that can support forest specialists (Figure 3) [7]. As the cover of vegetation increased, so did these species' heights and vice versa (Table 4). In general, species with generalised niche requirements are active at heights aligning with novel/anthropogenic structures, while species with specialised niches avoid them [7,39,61] (Tables 4 and A4). Although smaller, specialist species often rely on low vegetation strata, the urban low and high environment sites had a lot of vegetation coverage, but not for those species (apart from the fairy wren) (Table A3). Therefore, although there is little evidence to suggest so in this study, it could be that anthropogenic disturbance is more influential in determining species composition. Disturbances such as noise pollution, lack of native habitat, roads, and human presence may drive birds to occupy higher spaces, which act as refuges, while emphasising why species reliant on low vegetation strata are more detrimentally impacted [6,50]. Other studies of bird species' response to disturbed land show a similar loss in species across the urban gradient, with low-structured vegetation as a significantly predictive factor [7,58]. Another key factor to consider is the presence of native versus non-native vegetation, which may also affect which species can persist in certain environments [7]. Targeting species of the lowest tolerance to urban areas and their vertical niche requirements could henceforth be a good conservation strategy to consider during urban development [7].

The flight heights of species grouped by their foraging level also varied with structural changes across the sites. This further highlights the potential significance of these structures to bird use of vertical space and consecutively urban conservation. For species foraging in lower feeding levels and on the ground, their observed heights had a strong positive relationship with building cover and a weak relationship with building height. This result is likely influenced by certain (common) ground-feeding birds exploiting urban food subsidies, e.g., domestic pigeons [14,62]. They have also been recorded perching at greater heights to avoid human disturbance. For species feeding at all levels, their flight heights remain consistent regardless of building height variation, suggesting that they could be unaffected by development and are simply exploiting the available vegetation, although they did tend to fly higher as urban cover increased, and at least somewhat interacted with these structures (Table 2). Finally, aerial/arboreal high forager heights were dependent on all variables, which suggests they could be utilising the greater availability of all structures, natural and anthropogenic alike (Table 5) [63]. This seems reasonable when considering that swallows would make up a large portion of this category. Opposite to what was anticipated, Foliage Height Diversity did not have any influence; this could be a result of the model's limitations, or it requires further investigation [19]. Different bird species will require different availabilities in heights and vegetation densities for feeding. Future research should look into the type of activity being performed at these heights in greater detail, e.g., how foraging height varies across inner-urban environments.

Overall, this study found substantial differences between how different groups of birds engage with and use the air and vertical spaces within a city. Notably, urban exploiters and adapters are unsurprisingly much more likely to be tolerant and adaptable to the built-up aspects of an urban environment. Urban avoiders are likely to be prone to disruption and displacement due to the anthropomorphic aspects of a city. This should be taken into account when designing and managing urban greenspaces for biodiversity, particularly in the context of green infrastructure, and how it can target the conservation of specific groups.

This investigation highlights the challenges that come with collecting data on species activity in three-dimensional space. Collecting height data introduces the additional issue of vertical detectability, which intersects with horizontal detectability issues across diverse study sites. Despite attempts to address this in the survey design, this could introduce bias to the study. Higher species counts in parklands and even urban low sites could be a result of reduced detectability (both vertical and horizontal) in the urban high sites. Similarly, despite standardising the time spent observing different strata, it is still possible that the surveyor was skewed to spending more time looking upwards at urban high sites, and hence, this could have biased the results to show more species being observed at greater heights. As it is, some behaviours are more conspicuous than others, as are certain species. This also varies across the urban environment in which the sampling occurs. Rather than aiming to record abundance and/or density measures, this study focused on creating an unbiased record of species activity within different flight height ranges. Future research should investigate how to address vertical detectability bias. The study focused on species occurring across all three environments as these were observed the most often. Despite this, data were still variable between sites for specific species which could have biased results from the Kruskal–Wallis tests. Small sample sizes for environments with a lower number of records could be providing an inaccurate measure of the true height species were using or could have given false positive/negative significance outputs. Comparisons between species, or that involve grouping species, could skew the data into over- or under-representing certain species groupings across height ranges and environments. This is because bird species occurring across all three environments, i.e., urban exploiters, are not easily defined nor are necessarily functionally similar. For this reason, bird species were assessed individually in the analysis approach and subset where possible. This is a fairly novel study in the field, with height data being collected across community assemblages and on a landscape scale [22,27,63].

Despite these limitations, this study demonstrates that we must continue to enhance our understanding of how bird species are adjusting to the novel vertical habitats created by urbanisation [3]. It is clear that species are active at, and have their flight heights influenced by, both the natural and anthropogenic structures in their environment alike. This knowledge has implications for how planners might tackle urban conservation and the potential that green infrastructure holds in this space. Future research needs to focus more specifically on individual species (or groups of interest, e.g., specific foraging guilds) and how their activities across vertical space are influenced by the structural diversity of urban environments. Similarly, a closer look at species dispersal, how they move through urban landscapes, and how they cross structures of varying heights would help reduce knowledge gaps on how species are using 3D space. This study also outlines the importance of developing more efficient ways to broadly collect these types of data and the difficulties associated with managing vertical detectability bias. Incorporating airspace data into future urban research and planning needs to be normalised. Future urban planning can benefit from focusing on the creation of 'green cities' through green infrastructure, targeted restoration plans, targeted artificial nesting sites, and so forth in urban landscapes [29,64].

Author Contributions: Conceptualisation, A.J.R., S.K. and A.M.R.; methodology, A.J.R., S.K. and A.M.R.; validation, A.M.R. and S.K.; formal analysis, A.J.R.; investigation, A.J.R.; software, A.J.R.; resources, S.K.; data curation, A.J.R. and S.K.; writing—original draft preparation, A.J.R.; writing—review and editing, A.J.R., S.K., A.M.R. and H.P.P.; visualisation, A.J.R.; supervision, S.K., A.M.R. and H.P.P.; project administration, S.K. and A.J.R.; funding acquisition, S.K. All authors have read and agreed to the published version of the manuscript.

Funding: This research was supported by an Australian Government Research Training Program (RTP) Scholarship 2021–2022. The purchasing of the 2019 LiDAR tiles was funded by The University of Queensland's School of Biological Sciences Grant awarded to Prof. Salit Kark and Prof. Noam Levin.

Institutional Review Board Statement: The animal study protocol was approved by the Institutional Review Board (or Ethics Committee) of The University of Queensland (ANRFA-2021/AE000985, 10/2021).

Data Availability Statement: The dataset is available upon request from the authors.

Conflicts of Interest: The authors declare no conflicts of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of the data; in the writing of the manuscript; or in the decision to publish the results.

Appendix A

Table A1. List of bird activities recorded in field surveys.

Activity	Symbol
Flying through	Ft
Flying over	Fo
Perching	P
Foraging	F
Nesting	N
Walking	W
Other	O

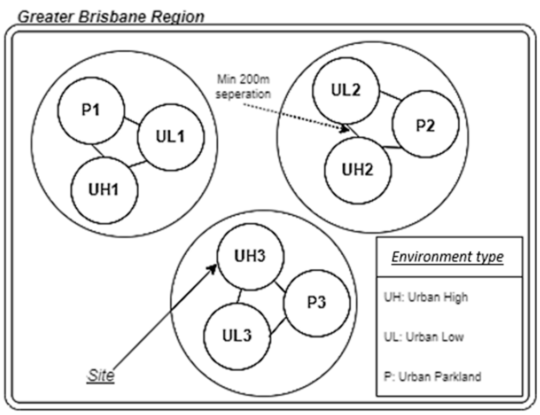


Figure A1. Schematic figure of nested sites (UH#, UL#, and P#). Sites were surveyed in sets of 3 (UH#, UL#, and P#) located within a wider locality in Brisbane. Sites are located a minimum distance of 200 m apart and make up a total quadrat area of 400 × 400 m, within which a wandering transect was up to a maximum length of 1.5 km per survey.

Table A2. Environmental variables for input into cumulative link models and their source.

Environmental Variable	Source
Mean building height (voxels)	Calculated from the 2019 LiDAR waveform data, Department of Resources, QLD
Building area	Calculated from the 2019 LiDAR waveform data, Department of Resources, QLD
FHD median	Calculated from Foliage Height Diversity, Brisbane 2014 data, Department of Environment and Science
Mean vegetation height (voxels)	Calculated from the 2019 LiDAR waveform data, Department of Resources, QLD
Vegetation area	Calculated from the 2019 LiDAR waveform data, Department of Resources, QLD
Interaction—mean building height: area	Calculated from the 2019 LiDAR waveform data, Department of Resources, QLD
Interaction—mean vegetation height: area	Calculated from the 2019 LiDAR waveform data, Department of Resources, QLD

Table A3. A summary of key vegetation structural variables across the three environment types. Variables were averaged from the sub-sites and were extracted from the 2019 LiDAR waveform data from the Department of Resources, QLD, using voxelisation (refer to Methods). The standard error is incorporated. Foliage Height Diversity (FHD) is incorporated as a defined metric for the structural variability of vegetation strata ranging from 0 to 1 (low to high).

Environment Type	Structural Variables			
	Vegetation Area (1 × 1 m Pixels)	Median Vegetation Height (m)	Median of Maximum Canopy Heights (m)	FHD Median
Urban High	39,599.67 ± 2500.78	5.07 ± 0.78	10.30 ± 0.69	0.72 ± 0.02
Urban Low	64,504.89 ± 2142.75	4.61 ± 0.26	8.14 ± 0.23	0.81 ± 0.03
Urban Parklands	70,601.78 ± 4675.00	10.02 ± 0.62	13.03 ± 0.88	0.82 ± 0.04

Table A4. Functional traits of species occurring across all three environment types.

Species	Urban Tolerance	Feeding Class	Feeding Level
Australasian Figbird	Urban Avoider/Suburban Adapter	Herbivorous	Arboreal High
Australian Darter	Urban Avoider	NA	NA
Australian Magpie	Urban Avoider/Suburban Adapter	Omnivorous	Ground
Australian White Ibis	Urban Adapter	Carnivorous	Ground
Black-Faced Cuckoo	Urban Avoider/Suburban Adapter	Insectivorous	Arboreal High
Blue-Faced Honeyeater	Urban Avoider/Suburban Adapter	Nectarivore/Frugivore	Arboreal All
Brush Cuckoo	Urban Avoider/Suburban Adapter	Insectivorous	Arboreal High
Common Myna	Urban Exploiter/Suburban Adapter	Omnivorous	All
Common Starling	Urban Avoider/Suburban Adapter	NA	NA
Crested Pigeon	Urban Avoider/Suburban Adapter	Granivorous	Ground
Domestic Pigeon	Urban Exploiter	Omnivorous	Ground
Eastern Great Egret	Urban Avoider	NA	NA
Fairy Martin	Urban Adapter	Insectivorous	Aerial
Grey Butcherbird	Urban Avoider/Suburban Adapter	Carnivorous	Arboreal All
Laughing Kookaburra	Urban Avoider/Suburban Adapter	Carnivorous	Arboreal All
Little Corella	Urban Avoider/Suburban Adapter	Omnivorous	Ground
Magpie-Lark	Urban Avoider/Suburban Adapter	Omnivorous	Ground
Masked Lapwing	Urban Avoider/Suburban Adapter	Insectivorous	Ground
Noisy Miner	Urban Exploiter	Omnivorous	All
Pied Butcherbird	Urban Avoider/Suburban Adapter	Omnivorous	All
Pied Currawong	Urban Exploiter	Omnivorous	All
Pink and Grey Galah	Urban Avoider/Suburban Adapter	Omnivorous	Ground
Rainbow Lorikeet	Urban Exploiter	Herbivorous	Arboreal High
Raptor Spp	Urban Exploiter	Carnivorous	Aerial
Scale-Breasted Lorikeet	Urban Avoider/Suburban Adapter	Herbivorous	Arboreal High
Spotted Turtle Dove	Urban Avoider/Suburban Adapter	Granivorous	Ground
Sulphur-Crested Cockatoo	Urban Avoider/Suburban Adapter	Granivorous	All
Superb Fairy Wren	Urban Avoider	Insectivorous	Arboreal Low

Table A4. *Cont.*

Species	Urban Tolerance	Feeding Class	Feeding Level
Torresian Crow	Urban Exploiter	Omnivorous	Ground
Welcome Swallow	Urban Exploiter	Insectivorous	Aerial
White-Breasted Woodswallow	Urban Avoider/Suburban Adapter	Insectivorous	Aerial
Willy Wag Tail	Urban Avoider/Suburban Adapter	Insectivorous	Ground

Table A5. Average heights from mid-point with standard deviation for all bird species, for each environment type. Species are ordered from top to bottom by how many environment types they occur across (i.e., species that occurred across all environments are at the top).

Species	Site		
	Urban High	Urban Low	Urban Parkland
Acridotheres tristis	32.4 ± 27.2	9.3 ± 6.5	6.5 ± 5.7
Anhinga novaehollandiae	37.5 ± 0	11.5 ± 0	5.5 ± 0
Ardea alba modesta	37.5 ± 0	28.8 ± 8.8	10.7 ± 16.3
Artamus leucorynchus	65.6 ± 16.2	6.7 ± 2.4	15.5 ± 8.3
Cacatua galerita	93.75 ± 62.8	14.5 ± 9.7	14.5 ± 6.6
Cacatua sanguinea	65.63 ± 16.2	22.7 ± 14.8	18.5 ± 11.3
Cacomantis variolosus	11.5 ± 0	7.2 ± 3.6	14.1 ± 17.4
Columba livia domestica	32.4 ± 24.9	18.7 ± 15.2	20.3 ± 19.2
Coracina novaehollandiae	29.0 ± 0	12.9 ± 4.5	10.8 ± 5.5
Corvus orru	57.3 ± 37.6	22.7 ± 19.3	20.8 ± 26.8
Cracticus nigrogularis	45.0 ± 24.2	9.6 ± 5.7	8.2 ± 5.0
Cracticus torquatus	29.6 ± 16.3	10.5 ± 5.3	10.6 ± 5.2
Dacelo novaeguineae	37.5 ± 0	12.7 ± 5.0	10.4 ± 5.5
Entomyzon cyanotis	31.4 ± 27.6	10.2 ± 6.7	10.9 ± 6.0
Eolophus roseicapilla	37.5 ± 0	14.0 ± 7.4	14.3 ± 11.4
Grallina cyanoleuca	31.0 ± 22.4	8.9 ± 7.9	5.9 ± 6.6
Gymnorhina tibicen	36.8 ± 25.2	10.6 ± 8.3	9.3 ± 20.3
Hirundo neoxena	61.8 ± 52.9	22.1 ± 12.7	17.2 ± 23.2
Malurus cyaneus	0.5 ± 0	3.9 ± 1.6	2.0 ± 2.5
Manorina melanocephala	14.9 ± 12.9	9.0 ± 5.8	8.7 ± 7.3
Ocyphaps lophotes	15.8 ± 4.3	8.1 ± 4.8	7.8 ± 4.5
Petrochelidon ariel	43.7 ± 21.8	12.8 ± 3.8	12.0 ± 10.1
Petrochelidon nigricans	37.5 ± 0	6.7 ± 2.4	7.1 ± 3.7
Raptor Spp	117.1 ± 70.4	35.5 ± 26.4	76.7 ± 62.2
Rhipidura leucophrys	22.4 ± 13.6	6.4 ± 3.1	3.6 ± 2.8
Sphecotheres vieilloti	32.8 ± 23.0	10.9 ± 5.5	10.8 ± 5.8
Spilopelia chinensis	28.7 ± 26.0	9.3 ± 5.2	9.2 ± 3.7
Strepera graculina	40.1 ± 30.5	14.5 ± 10.5	9.9 ± 6.2
Sturnus vulgaris	37.5 ± 0	7.5 ± 4.2	5.1 ± 2.5
Threskiornis molucca	37.1 ± 43.5	36.5 ± 37.4	11.9 ± 19.2
Trichoglossus chlorolepidotus	40.8 ± 23.8	13.2 ± 8.4	13.5 ± 5.5
Trichoglossus moluccanus	48.7 ± 41.6	17.0 ± 16.2	16.4 ± 9.9
Vanellus miles	32.9 ± 5.7	9.3 ± 10.3	1.2 ± 2.6
Columba leucomela	37.5 ± 0	20 ± 0	-
Apus pacificus	35 ± 2.5	-	5.5 ± 0
Gelochelidon nilotica	11.5 ± 0	-	16.3 ± 15.7
Acrocephalus australis		11.5 ± 0	2.2 ± 2.4
Alectura lathami		0 ± 0	0 ± 0
Cacomantis flabelliformis		7 ± 2.6	8.4 ± 4.8
Cacomantis pallidus		8.5 ± 3.0	8.4 ± 5.2
Centropus phasianinus		11.5 ± 0	2 ± 0
Colluricincla harmonica		16.7 ± 7.8	17.4 ± 14.6
Columba leucomela		5.5 ± 0	5.5 ± 0
Egretta garzetta		75 ± 0	0 ± 0
Eudynamys orientalis		12.2 ± 9.9	12.2 ± 4.0

Table A5. *Cont.*

Species	Site		
	Urban High	**Urban Low**	**Urban Parkland**
Lichmera indistincta		6. 0 ± 5.7	4.6 ± 3.7
Meliphaga lewinii		5.5 ± 0	0.5 ± 0
Melithreptus gularis		11.5 ± 0	8.3 ± 3.2
Melithreptus lunatus		8.1 ± 4.5	7.9 ± 3.8
Myiagra inquieta		2.0 ± 0	3.5 ± 2.1
Nesoptilotis leucotis		12.3 ± 3.1	12.3 ± 5.9
Oriolus sagittatus		10.3 ± 2.4	7.3 ± 3.0
Pachycephala rufiventris		11.5 ± 0	6.2 ± 2.7
Pardalotus striatus		3.8 ± 1.8	6.4 ± 3.3
Phalacrocorax sulcirostris		67.3 ± 55.4	35.5 ± 50.8
Phalacrocorax varius		20.6 ± 10.1	13.5 ± 10.9
Philemon citreogularis		8.5 ± 3.0	7.44 ± 4.8
Psophodes		11.5 ± 0	3.75 ± 1.75
Rhipidura albiscapa		5.5 ± 0	6.6 ± 4.9
Rhipidura rufifrons		11.5 ± 0	5.5 ± 0
Scythrops novaehollandiae		20.0 ± 0	17.2 ± 4.0
Taeniopygia bichenovii		4.5 ± 0	0.5 ± 0
Threskiornis spinicollis		56.5 ± 23.3	20.3 ± 44.5
Todiramphus sanctus		5.5 ± 0	11.5 ± 0
USBB		6.4 ± 2.6	3.5 ± 2.7
Alisterus scapularis		8.5 ± 3.0	-
Lichenostomus leucotis		5.5 ± 0	-
Platycercus adscitus		6 ± 3.1	-
Platycercus elegans		20 ± 0	-
Acanthiza chrysorrhoa			3.0 ± 2.5
Acanthiza nana			2.0 ± 0
Acanthiza pusilla			4.0 ± 1.5
Anas superciliosa			2.6 ± 6.0
Atrichornis clamosus			2.0 ± 0
Aythya australis			0 ± 0
Bubulcus ibis			0 ± 0
Burhinus grallarius			0.5 ± 1.2
Chenonetta jubata			1.2 ± 3.3
Cincloramphus timoriensis			4.5 ± 0
Colluricincla rufogaster			1.8 ± 1.9
Dicrurus bracteatus			8.5 ± 3.0
Egretta novaehollandiae			0 ± 0
Gallinula tenebrosa			0 ± 0
Geopelia humeralis			5.5 ± 0
Gerygone mouki			10.3 ± 1.3
Hirundapus caudacutus			11.5 ± 0
Malurus melanocephalus			0.5 ± 0
Microcarbo melanoleucos			2.8 ± 2.8
Myiagra rubecula			1.5 ± 0.6
Myzomela sanguinolenta			0.5 ± 0
Neochmia temporalis			1.0 ± 0.5
Pardalotus punctatus			3.75 ± 1.8
Platycercus eximius			12.8 ± 7.3
Podargus strigoides			11.9 ± 4.2
Porphyrio melanotus			0 ± 0
Porphyrio porphyrio			0 ± 0
Zanda funerea			11.5 ± 0
Zosterops lateralis			13.0 ± 8.0

Table A6. The average height (m) at which species across the three environment types were found displaying each of the activities outlined in Appendix A: Table A1 (foraging, perching, flying over, flying through, etc.).

Species	Urban High			Urban Low			Urban Parkland		
	Fly Through	**Inter-Perch Flight**	**Perched**	**Fly Through**	**Inter-Perch Flight**	**Perched**	**Fly Through**	**Inter-Perch Flight**	**Perched**
Australasian Figbird	32.08	62.50	16.22	11.62	11.38	8.67	13.13	10.12	9.88
Australian Darter	37.50			11.50				5.50	
Australian Magpie	43.22	41.50	27.83	10.27	11.60	12.38	9.91	11.18	10.91
Australian White Ibis	45.79	39.33	38.13	16.77	0.50	9.50	12.46	4.86	8.15
Black-Faced Cuckoo		29.00		11.25	10.88	14.33	9.13	7.88	12.50
Blue-Faced Honeyeater	45.92	39.00	11.50	12.88	10.88	8.75	11.09	9.09	10.82
Brush Cuckoo	11.50			8.25	5.50	6.33	9.50	11.50	7.21
Bush Stone Curlew								3.25	0.00
Common Myna	15.17	38.88	35.10	12.90	10.60	6.65	5.50	7.75	9.50
Common Starling			37.50			7.71	3.75		5.39
Crested Pigeon			20.00	5.50	9.55	9.60		10.67	8.50
Domestic Pigeon	35.63	36.31	26.29	13.72	10.63	14.78	20.00	12.00	
Eastern Great Egret							32.67	2.67	
Fairy Martin		44.50					9.50	5.50	
Grey Butcherbird	11.50	36.25	28.86	8.43	13.45	10.76	20.00	8.88	10.82
Laughing Kookaburra			37.50	9.00	11.50	13.70			11.13
Little Corella	37.50		75.00	18.08	9.67	15.75	17.17	10.88	17.17
Magpie-Lark	68.75	36.10	26.13	13.42	13.71	7.36	4.75	6.27	7.55
Masked Lapwing	32.08	37.50		10.63	5.50	8.50	5.69	1.63	
Noisy Miner	16.24	15.53	15.34	8.88	9.03	8.17	8.70	9.42	7.71
Pied Butcherbird	75.00	54.06	40.53	11.10	8.28	8.69	7.60	10.00	8.91
Pied Currawong	40.50	37.50	44.38	9.78	11.33	16.00	10.68	11.34	10.21
Pink and Grey Galah			37.50	14.29	10.00	11.50	6.75	16.50	12.75
Rainbow Lorikeet	38.27	40.31	44.19	11.10	11.36	10.92	12.79	14.41	14.64
Raptor Spp	37.50	62.50	145.00	11.50	20.00	17.00			
Scale-Breasted Lorikeet	46.50	5.50		12.59	12.75	5.50	11.43	13.67	
Spotted Turtle Dove	5.50		37.50	9.18	9.64	8.66	9.50	8.50	7.90
Sulphur-Crested Cockatoo	37.50			10.00	9.00	9.50	13.25	16.00	12.93
Superb Fairy Wren		0.50		4.00	4.33	2.50	11.00	1.71	1.79
Torresian Crow	51.98	58.79	50.79	13.48	14.16	12.98	16.19	12.53	13.38
Welcome Swallow	24.00	71.63	26.29	22.00		10.30	7.25	1.25	8.50
White-Breasted Woodswallow				7.50	5.50	5.50	14.00	7.25	
Willy Wag Tail	11.50	29.00	23.71	5.50		6.13	4.75	2.25	4.44

Table A7. The average height (m) at which species across the three environment types were found portraying three activities, fighting, foraging, and nesting, which were deemed important to indicating environmental suitability.

Species	Urban High			Urban Low			Urban Parkland		
	Fighting	Foraging	Nesting	Fighting	Foraging	Nesting	Fighting	Foraging	Nesting
Australasian Figbird	37.50	20.00		11.50	9.38	13.50	8.50	7.17	
Australian Darter									
Australian Magpie	40.50			15.20	1.02		17.83	1.26	
Australian White Ibis		2.08			0.00			1.52	8.96
Black-Faced Cuckoo				20.00	9.50			11.50	
Blue-Faced Honeyeater		6.40		12.75	4.81	9.00	18.00	5.81	20.00
Brush Cuckoo							75.00	20.00	
Bush Stone Curlew								0.00	
Common Myna		0.10	46.75	8.00	2.93	7.61		0.80	
Common Starling					5.50				
Crested Pigeon		11.50		11.50	0.36			3.83	
Domestic Pigeon	50.00	7.17	37.50		4.25	5.50		0.00	11.50
Eastern Great Egret								0.13	
Fairy Martin		46.25	35.00		12.75			13.93	
Grey Butcherbird	29.00			15.75	5.68		11.50	4.63	
Laughing Kookaburra							4.50	8.67	
Little Corella				20.00				0.00	
Magpie-Lark		10.42		20.00	0.00	2.00	18.63	1.20	
Masked Lapwing					0.00			0.32	
Noisy Miner	21.22	7.67	20.00	10.91	5.95	6.58	10.56	5.47	5.50
Pied Butcherbird	5.50				7.38	9.00	4.00	3.50	
Pied Currawong	22.00	45.75		9.00	6.10		13.63	2.06	
Pink and Grey Galah					11.50		12.75	0.00	
Rainbow Lorikeet		22.93			10.84		15.75	13.53	15.14
Raptor Spp		120.63		5.50			62.50	11.50	
Scale-Breasted Lorikeet		16.50			9.79		20.00	11.90	17.17
Spotted Turtle Dove	5.50			11.50	0.00				
Sulphur-Crested Cockatoo	62.50			11.50	5.50		24.50	1.83	
Superb Fairy Wren					5.50			1.44	
Torresian Crow	16.00	46.00		18.90	2.00		22.70	2.80	
Welcome Swallow		74.75	64.74		16.00	21.54			
White-Breasted Woodswallow			65.63						29.00
Willy Wag Tail	19.75			5.00		2.00	1.21	16.71	11.50

Table A8. Coefficients for urban adapters' cumulative link mixed model with flexible variability between orders. The response variable is the observation heights of species activity, and this is explained by the environmental covariates below. Sub-sites are included as a random effect. Foliage Height Diversity (FHD) is incorporated as a defined metric. Levels of significance are displayed as an asterisk ($p <$ * 0.05, ** 0.01, *** 0.001).

Environmental Variables	Estimate	Std. Error	z Value	Pr (>∣z∣)
Mean building height (voxels)	0.05458	0.02714	2.011	0.04430 *
Building area	1.28905	0.23394	5.510	3.59×10^{-8} ***
FHD median	−1.31679	1.19626	−1.101	0.27100
Mean vegetation height (voxels)	0.40773	0.09104	4.479	7.51×10^{-6} ***
Vegetation area	−1.41265	0.58599	−2.411	0.01592 *
Interaction—mean building height: area	−0.04219	0.01554	−2.715	0.00664 **
Interaction—mean vegetation height: area	0.09860	0.06302	1.565	0.11766

Table A9. Coefficients for urban avoiders' cumulative link mixed model with flexible variability between orders. The response variable is the observation heights of species activity, and this is explained by the environmental covariates below. Sub-sites are included as a random effect. Foliage Height Diversity (FHD) is incorporated as a defined metric. Levels of significance are displayed as an asterisk (* $p < 0.05$, ***$p < 0.001$).

Environmental Variables	Estimate	Std. Error	Z Value	Pr (>∣z∣)
Mean building height (voxels)	−0.03033	0.06607	−0.459	0.646209
Building area	1.21017	0.32660	3.705	0.000211 ***
FHD median	−1.68733	1.04298	−1.618	0.105707
Mean vegetation height (voxels)	0.19116	0.12048	1.587	0.112589
Vegetation area	1.99544	0.85056	2.346	0.018974 *
Interaction—mean building height: area	−0.01392	0.03739	−0.372	0.709607
Interaction—mean vegetation height: area	−0.20336	0.08818	−2.306	0.021095 *

Table A10. Coefficients for urban exploiters' cumulative link mixed model with flexible variability between orders. The response variable is the observation heights of species activity, and this is explained by the environmental covariates below. Sub-sites are included as a random effect. Foliage Height Diversity (FHD) is incorporated as a defined metric. Levels of significance are displayed as an asterisk ('.' $p < 0.1$, * 0.05, ** $p < 0.01$).

Environmental Variables	Estimate	Std. Error	z Value	Pr (>∣z∣)
Mean building height (voxels)	0.03944	0.01502	2.625	0.00867 **
Building area	0.55317	0.20201	2.738	0.00618 **
FHD median	−0.75610	0.93818	−0.806	0.42029
Mean vegetation height (voxels)	0.13368	0.07202	1.856	0.06345 .
Vegetation area	−0.78963	0.55657	−1.419	0.15598
Interaction—mean building height: area	−0.02382	0.01155	−2.063	0.03908 *
Interaction—mean vegetation height: area	0.03384	0.05984	0.565	0.57175

Table A11. Coefficients for arboreal high/aerial feeders' cumulative link mixed model with flexible variability between orders. The response variable is the observation heights of species activity, and this is explained by the environmental covariates below. Sub-sites are included as a random effect. Foliage Height Diversity (FHD) is incorporated as a defined metric. Levels of significance are displayed as an asterisk (* $p < 0.05$, *** $p < 0.001$).

Environmental Variables	Estimate	Std. Error	z value	Pr(>∣z∣)
Mean building height (voxels)	0.06675	0.01778	3.755	0.000174 ***
Building area	1.27745	0.21662	5.897	3.70×10^{-9} ***
FHD median	−1.05698	1.01467	−1.042	0.297553
Mean vegetation height (voxels)	0.38246	0.07830	4.885	1.04×10^{-6} ***
Vegetation area	−1.29992	0.55901	−2.325	0.020050 *
Interaction—mean building height: area	−0.05246	0.01292	−4.060	4.91×10^{-5} ***
Interaction—mean vegetation height: area	0.07957	0.06036	1.318	0.187401

Table A12. Coefficients for ground/arboreal low feeders' cumulative link mixed model with flexible variability between orders. The response variable is the observation heights of species activity, and this is explained by the environmental covariates below. Sub-sites are included as a random effect. Foliage Height Diversity (FHD) is incorporated as a defined metric. Levels of significance are displayed as an asterisk ('.' $p < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

Environmental Variables	Estimate	Std. Error	z Value	Pr (>∣z∣)
Mean building height (voxels)	0.04509	0.01704	2.645	0.00816 **
Building area	0.78027	0.19851	3.931	8.48×10^{-5} ***
FHD median	−0.63178	0.93211	−0.678	0.49790

Table A12. *Cont.*

Environmental Variables	Estimate	Std. Error	z Value	Pr (>|z|)
Mean vegetation height (voxels)	0.02673	0.07095	0.377	0.70632
Vegetation area	−1.02455	0.50972	−2.010	0.04443 *
Interaction—mean building height: area	−0.02214	0.01170	−1.892	0.05851 .
Interaction—mean vegetation height: area	0.07837	0.05487	1.428	0.15316

Table A13. Coefficients for arboreal all/all feeders' cumulative link mixed model with flexible variability between orders. The response variable is the observation heights of species activity, and this is explained by the environmental covariates below. Sub-sites are included as a random effect. Foliage Height Diversity (FHD) is incorporated as a defined metric. Levels of significance are displayed as an asterisk ('.' $p < 0.1$, *** $p < 0.001$).

Environmental Variables	Estimate	Std. Error	z Value	Pr (>|z|)
Mean building height (voxels)	0.0244583	0.0226925	1.078	0.281117
Building area	0.7925588	0.2323020	3.412	0.000645 ***
FHD median	−2.2718179	1.1688072	−1.944	0.051931 .
Mean vegetation height (voxels)	0.2837988	0.0854167	3.323	0.000892 ***
Vegetation area	−0.3795495	0.6396224	−0.593	0.552916
Interaction—mean building height: area	−0.0217013	0.0139549	−1.555	0.119922
Interaction—mean vegetation height: area	0.0004077	0.0687609	0.006	0.995269

References

1. Yang, G.; Xu, J.; Wang, Y.; Wang, X.; Pei, E.; Yuan, X.; Wang, Z. Evaluation of microhabitats for wild birds in a Shanghai urban area park. *Urban For. Urban Green.* **2015**, *14*, 246–254. [CrossRef]
2. Zuñiga-Palacios, J.; Zuria, I.; Moreno, C.E.; Almazán-Núñez, R.C.; González-Ledesma, M. Can small vacant lots become important reservoirs for birds in urban areas? A case study for a Latin American city. *Urban For. Urban Green.* **2020**, *47*, 126551. [CrossRef]
3. Xie, S.; Han, B.; Zhou, W.; Xian, C.; Ouyang, Z. Spatio-Temporal Variation in Bird Assemblages in a Subtropical Urban Ecosystem. *Diversity* **2022**, *14*, 341. [CrossRef]
4. Anderies, J.M.; Katti, M.; Shochat, E. Living in the city: Resource availability, predation, and bird population dynamics in urban areas. *J. Theor. Biol.* **2007**, *247*, 36–49. [CrossRef] [PubMed]
5. Frey, D.; Vega, K.; Zellweger, F.; Ghazoul, J.; Hansen, D.; Moretti, M. Predation risk shaped by habitat and landscape complexity in urban environments. *J. Appl. Ecol.* **2018**, *55*, 2343–2353. [CrossRef]
6. Schlesinger, M.D.; Manley, P.N.; Holyoak, M. Distinguishing stressors acting on land bird communities in an urbanizing environment. *Ecology* **2008**, *89*, 2302–2314. [CrossRef]
7. Seymour, C.L.; Dean, W.R.J. The influence of changes in habitat structure on the species composition of bird assemblages in the southern Kalahari. *Austral Ecol.* **2010**, *35*, 581–592. [CrossRef]
8. Kim, J.Y.; Lee, S.; Shin, M.S.; Lee, C.H.; Seo, C.; Eo, S.H. Altitudinal patterns in breeding bird species richness and density in relation to climate, habitat heterogeneity, and migration influence in a temperate montane forest (South Korea). *PeerJ* **2018**, *6*, e4857. [CrossRef]
9. White, J.G.; Antos, M.J.; Fitzsimons, J.A.; Palmer, G.C. Non-uniform bird assemblages in urban environments: The influence of streetscape vegetation. *Landsc. Urban Plan.* **2005**, *71*, 123–135. [CrossRef]
10. Caula, S.A.; Sirami, C.; Marty, P.; Martin, J.L. Value of an urban habitat for the native Mediterranean avifauna. *Urban Ecosyst.* **2010**, *13*, 73–89. [CrossRef]
11. Melles, S.; Glenn, S.; Martin, K. Urban bird diversity and landscape complexity: Species–environment associations along a multiscale habitat gradient. *Conserv. Ecol.* **2003**, *7*, 5. [CrossRef]
12. Ehlers Smith, Y.C.; Ehlers Smith, D.A.; Seymour, C.L.; Thébault, E.; van Veen, F.F. Response of avian diversity to habitat modification can be predicted from life-history traits and ecological attributes. *Landsc. Ecol.* **2015**, *30*, 1225–1239. [CrossRef]
13. Reynolds, J.S.; Ibáñez-Álamo, J.D.; Sumasgutner, P.; Mainwaring, M.C. Urbanisation and nest building in birds: A review of threats and opportunities. *J. Ornithol.* **2019**, *160*, 841–860. [CrossRef]
14. Sohil, A.; Sharma, N. Bird diversity and distribution in mosaic landscapes around Jammu, Jammu & Kashmir. *Acta Ecol. Sin.* **2020**, *40*, 323–338. [CrossRef]
15. Stagoll, K.; Manning, A.D.; Knight, E.; Fischer, J.; Lindenmayer, D.B. Using bird–habitat relationships to inform urban planning. *Landsc. Urban Plan.* **2010**, *98*, 13–25. [CrossRef]

16. Belaire, J.A.; Whelan, C.J.; Minor, E.S. Having our yards and sharing them too: The collective effects of yards on native bird species in an urban landscape. *Ecol. Appl.* **2014**, *24*, 2132–2143. [CrossRef]
17. DeGraaf, R.M.; Wentworth, J.M. Avian guild structure and habitat associations in suburban bird communities. *Urban Ecol.* **1986**, *9*, 399–412. [CrossRef]
18. Rutz, C. The establishment of an urban bird population. *J. Anim. Ecol.* **2008**, *77*, 1008–1019. [CrossRef]
19. Sasaki, T.; Imanishi, J.; Fukui, W.; Morimoto, Y. Fine-scale characterization of bird habitat using airborne LiDAR in an urban park in Japan. *Urban For. Urban Green.* **2016**, *17*, 16–22. [CrossRef]
20. Maas, B.; Putra, D.D.; Waltert, M.; Clough, Y.; Tscharntke, T.; Schulze, C.H. Six years of habitat modification in a tropical rainforest margin of Indonesia do not affect bird diversity but endemic forest species. *Biol. Conserv.* **2009**, *142*, 2665–2671. [CrossRef]
21. Hu, Y.; Cardoso, G.C. Which birds adjust the frequency of vocalizations in urban noise? *Anim. Behav.* **2010**, *79*, 863–867. [CrossRef]
22. D'Amico, M.; Catry, I.; Martins, R.C.; Ascensão, F.; Barrientos, R.; Moreira, F. Bird on the wire: Landscape planning considering costs and benefits for bird populations coexisting with power lines. *Ambio* **2018**, *47*, 650–656. [CrossRef] [PubMed]
23. Van Doren, B.M.; Willard, D.E.; Hennen, M.; Horton, K.G.; Stuber, E.F.; Sheldon, D.; Winger, B.M. Drivers of fatal bird collisions in an urban center. *Proc. Natl. Acad. Sci. USA* **2021**, *118*, e2101666118. [CrossRef] [PubMed]
24. Davis, R.A.; Wilcox, J.A. Adapting to suburbia: Bird ecology on an urban-bushland interface in Perth, Western Australia. *Pac. Conserv. Biol.* **2013**, *19*, 110–120. [CrossRef]
25. Ruaux, G.; Lumineau, S.; de Margerie, E. The development of flight behaviours in birds. *Proc. R. Soc. B* **2020**, *287*, 20200668. [CrossRef]
26. Barton, C.M.; Riding, C.S.; Loss, S.R. Magnitude and correlates of bird collisions at glass bus shelters in an urban landscape. *PLoS ONE* **2017**, *12*, e0178667. [CrossRef]
27. Betleja, J.; Jankowiak, Ł.; Sparks, T.H.; Tryjanowski, P. Birds crossing over roads: Species, flight heights and infrastructure use. *Eur. J. Ecol.* **2020**, *6*. [CrossRef]
28. Lill, A.; Muscat, I. Importance of inherent suitability, behavioural flexibility and competitiveness in occupancy of urban parks by an endemic honeyeater. *Avian Biol. Res.* **2015**, *8*, 227–236. [CrossRef]
29. Fontana, S.; Sattler, T.; Bontadina, F.; Moretti, M. How to manage the urban green to improve bird diversity and community structure. *Landsc. Urban Plan.* **2011**, *101*, 278–285. [CrossRef]
30. Dickson, J.G. *The Role of Insectivorous Birds in Forest Ecosystems*; Elsevier: Amsterdam, The Netherlands, 2012.
31. Holmes, R.T.; Bonney, R.E., Jr.; Pacala, S.W. Guild structure of the Hubbard Brook bird community: A multivariate approach. *Ecology* **1979**, *60*, 512–520. [CrossRef]
32. Crome, F.H.J. Foraging ecology of an assemblage of birds in lowland rainforest in northern Queensland. *Aust. J. Ecol.* **1978**, *3*, 195–212. [CrossRef]
33. Keast, A.; Recher, H.F. The adaptive zone of the genus Gerygone (Acanthizidae) as shown by morphology and feeding habits. *Emu* **1997**, *97*, 1–17. [CrossRef]
34. Klein, J.; Haverkamp, P.J.; Lindberg, E.; Griesser, M.; Eggers, S. Remotely sensed forest understory density and nest predator occurrence interact to predict suitable breeding habitat and the occurrence of a resident boreal bird species. *Ecol. Evol.* **2020**, *10*, 2238–2252. [CrossRef]
35. Hinsley, S.A.; Hill, R.A.; Gaveau, D.L.A.; Bellamy, P.E. Quantifying woodland structure and habitat quality for birds using airborne laser scanning. *Funct. Ecol.* **2002**, *16*, 851–857. [CrossRef]
36. Goetz, S.; Steinberg, D.; Dubayah, R.; Blair, B. Laser remote sensing of canopy habitat heterogeneity as a predictor of bird species richness in an eastern temperate forest, USA. *Remote Sens. Environ.* **2007**, *108*, 254–263. [CrossRef]
37. Hao, Z.; Wang, C.; Sun, Z.; van den Bosch, C.K.; Zhao, D.; Sun, B.; Pei, N. Soundscape mapping for spatial-temporal estimate on bird activities in urban forests. *Urban For. Urban Green.* **2021**, *57*, 126822. [CrossRef]
38. Huang, Q.; Swatantran, A.; Dubayah, R.; Goetz, S.J. The influence of vegetation height heterogeneity on forest and woodland bird species richness across the United States. *PLoS ONE* **2014**, *9*, e103236. [CrossRef]
39. Zurita, G.A.; Bellocq, M.I. Bird Assemblages in Anthropogenic Habitats: Identifying a Suitability Gradient for Native Species in the Atlantic Forest. *Biotropica* **2012**, *44*, 412–419. [CrossRef]
40. Fijn, R.C.; Collier, M.C. Distribution and flight heights of Sandwich Terns Thalasseus sandvicensis during different behaviours near wind farms in the Netherlands. *Bird Study* **2022**, *69*, 53–58. [CrossRef]
41. Driscoll, P.V. Comparison of Bird Counts from Pine Forest and Indigenous Vegetation. *Wildl. Res.* **1977**, *4*, 281–288. [CrossRef]
42. Kutt, A.S.; Martin, T.G. Bird foraging height predicts bird species response to woody vegetation change. *Biodivers. Conserv.* **2010**, *19*, 2247–2262. [CrossRef]
43. Fortin, D.; Liechti, F.; Bruderer, B. Variation in the nocturnal flight behaviour of migratory birds along the northwest coast of the Mediterranean Sea. *Ibis* **1999**, *141*, 480–488. [CrossRef]
44. Liu, Z.; Huang, Q.; Tang, G. Identification of urban flight corridors for migratory birds in the coastal regions of Shenzhen city based on three-dimensional landscapes. *Landsc. Ecol.* **2021**, *36*, 2043–2057. [CrossRef]

45. Roussel, J.R.; Auty, D.; Coops, N.C.; Tompalski, P.; Goodbody, T.R.; Meador, A.S.; Achim, A. lidR: An R package for analysis of Airborne Laser Scanning (ALS) data. *Remote Sens. Environ.* **2020**, *251*, 112061. [CrossRef]
46. Marchant, S.; Ambrose, S.J.; Steele, W.K. *Handbook of Australian, New Zealand & Antarctic Birds*; Oxford University Press: Oxford, UK, 2006; Volumes 1–7.
47. Shanahan, D.F.; Miller, C.; Possingham, H.P.; Fuller, R.A. The influence of patch area and connectivity on avian communities in urban revegetation. *Biol. Conserv.* **2011**, *144*, 722–729. [CrossRef]
48. Sol, D.; González-Lagos, C.; Moreira, D.; Maspons, J. Measuring Tolerance to Urbanization for Comparative Analyses. *Ardeola* **2013**, *60*, 3–13. [CrossRef]
49. Beissinger, S.R.; Osborne, D.R. Effects of urbanization on avian community organization. *Condor* **1982**, *84*, 75–83. [CrossRef]
50. Emlen, J.T. An urban bird community in Tucson, Arizona: Derivation, structure, regulation. *Condor* **1974**, *76*, 184–197. [CrossRef]
51. Bonier, F.; Martin, P.R.; Wingfield, J.C. Urban birds have broader environmental tolerance. *Biol. Lett.* **2007**, *3*, 670–673. [CrossRef]
52. Calviño-Cancela, M. Time-activity budgets and behaviour of the Amazilia hummingbird, Amazilia amazilia (Apodiformes: Trochilidae) in an urban environment. *Rev. Biol. Trop.* **2006**, *54*, 873–878. [CrossRef]
53. Chiquet, C.; Dover, J.W.; Mitchell, P. Birds and the urban environment: The value of green walls. *Urban Ecosyst.* **2013**, *16*, 453–462. [CrossRef]
54. Fernández Cañero, R.; González Redondo, P. Green roofs as a habitat for birds: A review. *J. Anim. Vet. Adv.* **2010**, *9*, 2041–2052.
55. Mayrand, F.; Clergeau, P. Green roofs and green walls for biodiversity conservation: A contribution to urban connectivity? *Sustainability* **2018**, *10*, 985. [CrossRef]
56. Shepard, E.L.; Williamson, C.; Windsor, S.P. Fine-scale flight strategies of gulls in urban airflows indicate risk and reward in city living. *Philos. Trans. R. Soc. B Biol. Sci.* **2016**, *371*, 20150394. [CrossRef] [PubMed]
57. Posa, M.R.C.; Sodhi, N.S. Effects of anthropogenic land use on forest birds and butterflies in Subic Bay, Philippines. *Biol. Conserv.* **2006**, *129*, 256–270. [CrossRef]
58. Walther, B.A. Vertical stratification and use of vegetation and light habitats by Neotropical forest birds. *J. Für Ornithol.* **2002**, *143*, 64–81. [CrossRef]
59. Merola-Zwartjes, M.; DeLong, J.P. Avian species assemblages on New Mexico golf courses: Surrogate riparian habitat for birds? *Wildl. Soc. Bull.* **2005**, *33*, 435–447. [CrossRef]
60. Leston, L.F.; Rodewald, A.D. Are urban forests ecological traps for understory birds? An examination using Northern cardinals. *Biol. Conserv.* **2006**, *131*, 566–574. [CrossRef]
61. Møller, A.P. Successful city dwellers: A comparative study of the ecological characteristics of urban birds in the Western Palearctic. *Oecologia* **2009**, *159*, 849–858. [CrossRef]
62. Champlin, T.B.; Kilgo, J.C.; Moorman, C.E. Food abundance does not determine bird use of early-successional habitat. *Ecology* **2009**, *90*, 1586–1594. [CrossRef]
63. Culbert, P.D.; Radeloff, V.C.; Flather, C.H.; Kellndorfer, J.M.; Rittenhouse, C.D.; Pidgeon, A.M. The influence of vertical and horizontal habitat structure on nationwide patterns of avian biodiversity. *Auk* **2013**, *130*, 656–665. [CrossRef]
64. Clergeau, P.; Savard, J.P.L.; Mennechez, G.; Falardeau, G. Bird abundance and diversity along an urban-rural gradient: A comparative study between two cities on different continents. *Condor* **1998**, *100*, 413–425. [CrossRef]