Habitat-of-origin predicts degree of adaptation in urban tolerant birds

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Abstract

Urban exploiters and adapters are often coalesced under a term of convenience as 'urban tolerant'. This useful but simplistic characterisation masks a more nuanced interplay between and within assemblages of birds that are more or less well adapted to a range of urban habitats. Furthermore, cues are generally sought in behavioural ecology and physiology for the degree to which particular bird species are predisposed to urban living. The data in this paper are focused on two assemblages characterised as urban exploiters and suburban adapters from Melbourne, Australia. This study departs from the approach taken in many others of similar kind in that urban bird assemblages that form the basis of the work were identified at the landscape scale and from direct data analyses rather than indirect inference. Further, this paper employs a paired, partitioned analysis of exploiter and adapter preferences for points along the urban-rural gradient that seeks to decompose the overall trend into diagnosable parts for each assemblage. In the present paper I test the hypotheses that the distinct urban exploiter and suburban adapter assemblages within the broad urban tolerant grouping in Melbourne vary in their responses within the larger group to predictor variables, and that the most explanatory predictor variables vary between the two assemblages. Habitat-of-origin is found to predict degree of adaptation amongst urban tolerant birds.

Key words

Birds, urban adapter, urban exploiter, urban tolerance, urban-rural gradient, hierarchical Bayesian models, estimating habitat preference, habitat-of-origin

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Introduction

The community of ecologists studying urban bird ecology has to a large extent converged on Blair's (1996) typology of 'urban exploiters', 'urban avoiders' and 'suburban adapters', defined by the bird assemblages' biological and behavioural traits (Chace & Walsh 2006; González-Oreja *et al.* 2007; Kark *et al.* 2007; Croci *et al.* 2008). Such assemblages as described here are elsewhere sometimes characterised as 'response guilds' (Leveau 2013). Exploiters and adapters are often coalesced under a term of convenience as 'urban tolerant'. This useful but simplistic characterisation of the urban tolerant subset may mask a more nuanced interplay between and within groups of birds that are more or less well adapted to a range of urban habitats, ranging from the intensely urbanised 'down town' areas of the inner city, out through a fluctuating gradient of generally decreasing urbanisation intensity through the suburbs to the urban fringe. That there are identifiable 'exploiters' and 'adapters' in addition to the 'avoiders' suggests further targeted testing of the urban tolerant grouping may be fruitful in understanding some underlying processes in urban bird ecology.

When Kark *et al.* (2007) posed the question "*Can anyone become a urban exploiter*?" they attempted to find the answer in life history traits, phenotypic and behavioural characteristics of individual species. The result was inconclusive, with considerable variability evident in the traits of successful exploiters. They and others concluded that the answer lay in a suite of characters rather than any single factor (Kark *et al.* 2007; Evans *et al.* 2011; Møller 2014). Conole and Kirkpatrick (2011) took a landscape perspective (Snep *et al.* 2009), and found assemblage-specific patterns over a large urbanised landscape in foraging, nesting and mobility guilds that differentiated urban tolerant from urban avoider species, consistent with a number of other studies around the globe (summarised in Chace & Walsh 2006). White *et al.* (2005) identified the non-

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uniform nature of urban habitats in Melbourne, with species composition between native and exotic birds (within broadly urban tolerant groupings) varying according to habitat structure and floristics. Conole (2011) showed that exotic birds exhibited non-uniform responses to urbanisation in Melbourne in the same way as native birds. Fontana *et al.* (2011) showed that underlying environmental gradients can override the influence of human demographic gradients.

A humped distribution of bird species richness has been observed in a number of urban studies, with highest values recorded in the intermediate urbanisation intensity range on the rural-urban gradient (Tratalos *et al.* 2007; Luck & Smallbone 2010; Shanahan *et al.* 2014). This pattern has been shown to hold true for all species, but also for urban tolerant species as a subset (Shanahan *et al.* 2014). However, results of earlier data analyses by for this Melbourne study area suggest that the two assemblages within the urban tolerant bird grouping may not show a uniform response trend to urbanisation as has been shown for other cities (Conole 2011; Conole & Kirkpatrick 2011).

Gradient analysis has a moderately long history in the relatively young sub-discipline of urban bird ecology (Ruszczyk *et al.* 1987), has been broadly applied in urban ecological studies over the past two decades (McDonnell & Hahs 2008), and much longer in ecology more generally (Whittaker 1967). It is intuitively compatible with a landscape ecology perspective (Snep *et al.* 2009), and despite criticisms of the limitations of gradient analysis as an approach for studying urban ecology, (Catterall 2009; Ramalho & Hobbs 2012a), the potential remains for this approach to be the 'scaffolding' upon which deeper investigations are built (McDonnell *et al.* 2012; Ramalho & Hobbs 2012b).

In taking the assemblages identified through gradient analysis (Conole & Kirkpatrick 2011) as the basis for this study, I acknowledge the reality that the urban-rural gradient is not simplistically linear (Ramalho & Hobbs 2012a) or neatly concentric around the 'down town' centre (Catterall 2009), although in some city layouts it would be correct to assume simple linearity (Santos 2005). Also, these realities do not limit the usefulness of gradient analysis in understanding complexity and nuance in urban bird ecology. I also acknowledge the utility of the urban exploiter/adapter typology, but seek in this paper to deconstruct the concept of 'urban tolerance' for birds, and test a hypothesis which contends that 'urban tolerance' is not monolithic, but multifaceted.

The urban tolerance status of birds included in many published studies has been applied *a priori*, based on work of others in geographically related systems (such as Kark *et al.* 2007), or compiled from secondary or tertiary descriptive sources (such as Bonier *et al.* 2007), but see González-Oreja *et al.* (2007). An approach which separates the direct determination of urban tolerance status from the process of analysing species or assemblage responses to urban environmental factors runs the risk of weakening conclusions which may be drawn from such analyses (Conole & Kirkpatrick 2011).

It is also the case that many urban bird studies are largely descriptive or narrowly site-specific (Marzluff *et al.* 2001; McDonnell & Hahs 2013), lacking either a theoretical underpinning or focus (Scheiner 2013), and there have been calls to formulate research questions designed to develop a greater mechanistic understanding of the underlying ecological processes operating in urban landscapes (Shochat *et al.* 2006; McDonnell & Hahs 2013), and move towards generalizable concepts (Mac Nally 2000).

Part of the process of moving towards generalisable concepts in urban bird ecology involves gaining a better understanding of the extent to which the degree of adaptation to urban environments progresses from intolerance to the high level of adaptation that characterises exploiters. How similar are the responses of the adapters and exploiters to different aspects of the urban-rural gradient?

The data in this paper are focused on two assemblages characterised by the author as urban exploiters and suburban adapters from Melbourne, Australia (Figure S1) (Conole & Kirkpatrick 2011). The present study departs from the approach taken in many others of similar kind in that urban bird assemblages that form the basis of the work were identified at the landscape scale and from direct data analyses (Conole & Kirkpatrick 2011) rather than indirect inference or *a priori* assignment. Further, this paper attempts a paired, partitioned analysis of exploiter and adapter preferences for points along the urban-rural gradient which seeks to decompose the overall trend into diagnosable parts for each urban tolerant response guild, in a way not previously seen in the literature.

In the present paper I test the hypotheses that the distinct urban exploiter and suburban adapter assemblages within the broad urban tolerant grouping in Melbourne vary in their responses within the larger group to predictor variables, and that the most explanatory predictor variables vary between the two assemblages. I also test the hypothesis that habitat-of-origin has predictive utility in determining which urban tolerant birds become exploiters or adapters.

Materials & Methods

Detailed descriptions of the study area and methodology used to derive the urban bird assemblages can be found in (Conole & Kirkpatrick 2011).

Study area and data handling

The study area is metropolitan Melbourne; capital city of the State of Victoria in coastal south-eastern Australia, within a 50 km radius of its Central Business District (Figure S1) (37° 49' S and 144° 58' E). Approximately 220,000 records of birds were extracted from

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the Birds Australia 'New Atlas of Australian Birds' database (Barrett *et al.* 2003), and intersected with a 1 × 1 km grid (Hahs & McDonnell 2006) to produce a matrix of grid cells by species presence/absence. Species and sites were filtered out according to criteria for representativeness to arrive at a final list of 141 species and 390 cells (Conole & Kirkpatrick 2011).

Environmental and demographic indices

Spatial data on the degree of urbanisation of the study area employed in this study were developed at ARCUE and are discussed in detail by (Hahs & McDonnell 2006); a brief summary of the two selected factors follows. Frequency Greenspace (herafter greenspace) is the reciprocal of the average amount of impervious surface calculated at the sub-pixel level from the impervious surface fraction image created during the spectral mixture analysis of the 2000 Landsat ETM+ image (Hahs & McDonnell 2006). Combined index ($Index_{combined}$) is the average value of $Index_{image}$ and $Index_{census}$; where $Index_{image}$ is calculated from fraction images produced by the spectral mixture analysis of the 2000 Landsat ETM+ image, and $Index_{census}$ = the total number of people multiplied by the proportion of males employed in non-agricultural work, as enumerated in the 2001 census (Hahs & McDonnell 2006).

Data analysis

Statistical analyses were performed in R (R Core Team 2013) using core functions and procedures from the R-packages 'vegan' (Oksanen *et al.* 2013) and 'bayespref' (Fordyce *et al.* 2011). Figures were drawn using R core functions and R-packages 'vegan' and 'ggplot2' (Wickham 2009; Oksanen *et al.* 2013).

An earlier assemblage analysis (Conole & Kirkpatrick 2011) was the basis for partitioning the total bird data sets for this study; detailed methodology is described therein. Adapter and exploiter species were further partitioned into two new matrices for this study, and separate non-metric multidimensional scaling (NMDS) ordinations performed for each.

Species richness of exploiter and adapter species was enumerated for each of 390 grid cells (Conole & Kirkpatrick 2011), along with an index of urbanisation intensity ($Index_{Combined}$ – hereafter urbanisation index) and cover of vegetation (greenspace). Data were then modelled as hierarchical Bayesian models using R-package 'bayespref' (Fordyce *et al.* 2011) to test the preferences of exploiters and adapters for partitioned urban habitats. Model parameters were estimated using a Markov Chain Monte Carlo (MCMC) approach, with 10,000 MCMC steps following a burn-in of 1,000 generations. The parameters estimated in this way are intended to directly address the hypothesis (Fordyce *et al.* 2011), namely that adapter and exploiter bird assemblages show preferences for urban habitat characterised by differing levels of urbanisation intensity or vegetation cover. The hierarchical Bayesian approach has the advantage of directly estimating the parameter of interest (in this case preference for levels of urbanisation or green space by urban tolerant bird assemblages), and models the uncertainty around those parameters as well as allowing comparisons between *a priori* identified groups, in contrast to methods such as ANOVA or t-tests, which assess whether the mean difference is different from zero (Fordyce *et al.* 2011). The estimates are population-level preferences (Fordyce *et al.* 2011).

Adapter and exploiter species' habitats of origin were determined by reference to the literature (Marchant & Higgins 1993; Higgins & Davies 1996; Higgins 1999; Schodde & Mason 1999; Higgins *et al.* 2001; Higgins & Peter 2002; Higgins *et al.* 2006), shown in Table 1. The data for cluster analysis consisted of a standard 'r x c' array, with species as rows and habitats of origin as columns (forest, woodland, heath, scrub, urban, farm, air). A Bray-Curtis distance matrix was prepared, and groups of species were formed by hierarchical agglomerative clustering using Ward's algorithm performed on the distance matrix, using core R-function 'hclust' (R Core Team 2013).

Results and Discussion

Results

In an earlier ordination of all bird species from the Melbourne study, urban exploiters and adapters are shown as overlapping but distinct clusters in ordination space (Figure S2) (Conole & Kirkpatrick 2011). When the exploiters and adapters were partitioned from the avoiders and run as separate ordinations, different pictures of response to urban environmental factors became apparent (Figures 1 & 2).

For exploiters the observed species richness vector (S_{obs}) was orthogonal with both greenspace and the urbanisation index (Figure 2). The equivalent vector for adapters (Figure 1) was orthogonal with the urbanisation index, but almost aligned with that for greenspace (Figure 2). Greenspace and the urbanisation index were chosen as representative of structural and demographic aspects of urbanisation intensity even though other parameters were included in the initial analyses, and further analyses were limited to these two factors.

The same data plotted as binned boxplots showed that adapter species richness was positively associated with increasing greenspace, but exploiter species richness was flat across the range (Figure 3). Whilst broadly similar trends were evident for both groups as binned boxplots plotted against the urbanisation index (Figure 5), adapters trended to zero species richness at the highest levels, whilst 10 - 15 species of exploiters persisted at the same level. Peak species diversity of urban adapter birds occurred in the middle of

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the range of urbanisation intensity (Figure 5). Adapter richness peaked at approximately 0.8 frequency green-space; exploiters at around 0.55 (Figure 4).

The hierarchical Bayesian models for greenspace showed a relatively flat preference by urban exploiters across the range; though increasing preference by urban adapters for higher levels of greenspace (median = 0.46; credible intervals 0.424 – 0.494) almost match exploiter preference (0.54; 0.506 – 0.576) in the highest bin (Figure 4; Table S1). The preferences of urban exploiters and adapters did not overlap in any of the greenspace bins.

Hierarchical Bayesian models for the combined index showed a joint preference by urban adapters and exploiters in the middle of the range of the urbanisation index (20.0 – 29.9). Areas of low (0 – 19.9) and high (30.0 – 50.0) urbanisation index were strongly preferred by urban exploiters but not adapters (Figure 6; Table S2).

The cluster analysis of adapters and exploiters by habitat of origin returned a dendrogram showing two clear major clusters. All of the adapters clustered together in a woody vegetation habitat group, along with a group of exploiters; five indigenous nectarivores (Red Wattlebird *Anthochaera carunculata* (Shaw 1790), Little Wattlebird *A. chrysoptera* (Latham 1802), White-plumed Honeyeater *Lichenostomus penicillatus* (Gould 1837), Musk Lorikeet *Glossopsitta concinna* (Shaw 1791), Little Lorikeet *G. pusilla* (Shaw 1970)), two indigenous avivorous raptors (Australian Hobby *Falco longipennis* Swainson 1837, Brown Goshawk *Accipiter fasciatus* (Vigors and Horsfield, 1827)) and two exotic species which are not exclusively synanthropic (Common Blackbird *Turdus merula*, Linnaeus 1758, Common Starling *Sturnus vulgaris* Linnaeus 1758) (Conole 2011). The cluster of exclusively exploiter species were characterised by those originating from open grassy or urban habitats.

The boxplots (Figures 3 and 5) and the hierarchical Bayesian models (Figures 4 and 6) showed clear but distinct trends of urban habitat preference by urban exploiter and adapter bird assemblages against two these representative urban habitat measures. The landscape scale preferences of urban adapters and urban exploiters for levels of greenspace never overlap, though they come close tother at the highest values as exploiter preference declines and adapter preference increases. In contrast, landscape preferences for urbanisation intensity measured by the urbanisation index overlap strongly in the middle of the range but are strongly divergent at the lowest and highest values.

Discussion

The diversity of urban adapters on the gradient of urban intensity follows a humped distribution (Figure 5); the trend even more strongly humped when viewed as landscape scale preference (Figure 6). This is consistent with the trend seen for urban tolerant birds in other studies (Tratalos *et al.* 2007). The inverted, humped curve for exploiters is not consistent with the trends for urban tolerant bird species richness seen in other studies (Tratalos *et al.* 2007; Luck & Smallbone 2010; Shanahan *et al.* 2014).

This quadratic trend in diversity also resembles that described by the Intermediate Disturbance Hypothesis (IDH), where diversity peaks at a mid point along a gradient of disturbance (Catford *et al.* 2012; Fox 2013). The urban-rural gradient is however not a true analogue of a disturbance gradient. Suburban areas are more stable habitats than either the developing fringe or the intensely re-shaped core of the city, and so disturbance itself shows a quadratic distribution along the urban-rural gradient. Also implicit within IDH is a notion of competition/colonisation trade-off amongst species more or less adapted to disturbed environments, and at least for urban adapted birds it has been

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suggested that competition is not important (Mikami & Nagata 2013) except for specific cases such as the 'despotic' Noisy Miner (*Manorina melanocephala*) (Kath *et al.* 2009; Maron *et al.* 2013; Robertson *et al.* 2013).

The zone of overlap in habitat preference along the human demographic gradient accords broadly with the inner ring of suburbs in Melbourne; long established and heavily vegetated (Hahs & McDonnell 2006). At the extremes of this gradient lie the new suburbs/exurbia at the fringe, and the central business districts ('down town') at various central locations - either lightly vegetated or with largely treeless vegetation (lawns and pasture) (Hahs & McDonnell 2006). The overlap represents depressed preference by exploiters coincident with greatest preference shown by adapters.

The response of urban tolerant birds to increasing Frequency Greenspace is consistent with wider trends in other cities (Chace & Walsh 2006). The distinct responses between adapters and exploiters is also less marked with respect to greenspace than urbanisation intensity.

The responses of the two assemblages to two simple measures of urban habitat character were divergent, consistent with the study's main hypothesis. Though the larger group of urban tolerant bird species may occasionally be treated as one entity, it is clear from this study and others (Croci *et al.* 2008; Catterall 2009; Conole 2011; Conole & Kirkpatrick 2011) that the two groups within it are sufficiently distinct in their responses to urbanisation to caution against using pooled data for urban tolerant species in future studies.

The response of urban adapter species to the urbanisation index is consistent with what we broadly understand them to be; adapted to suburbanisation (Blair & Johnson 2008). Greenspace typically increases in old suburbs versus the exurban fringe or downtown

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areas (Hahs & McDonnell 2006). The strong depression in exploiter preference for mid-range urbanisation intensity (versus the extremes) is less expected. At least with the Melbourne data, there is not a single generalised urban tolerant group of birds. The adapters and exploiters share ecological traits with each other but also with avoiders (Conole & Kirkpatrick 2011).

In part the contemporary avifauna of an urbanised area is a legacy of the species present in the former landscape, rather than solely being the product of invasion or colonisation (*sensu* Møller *et al*. 2012). As urban areas progressively come to resemble woodland, structurally if not floristically (Kirkpatrick *et al.* 2007), it makes sense that the urban tolerant bird species are likely to include legacy woodland adapted species. Despite the findings of Blair and Johnson (2008) in North American urban areas, it does not appear that suburban areas within a previously forested landscape in Melbourne are *loci* for indigenous woodland bird extirpation or exotic bird invasion (Conole & Kirkpatrick 2011). Instead the reverse seems to be true, and they are sites for colonisation and expansion of some indigenous woodland birds (adapters) and where exotic exploiters are less abundant.

Exploiters are mostly indigenous species derived from open environments such as grassland and grassy open-woodland (Møller *et al.* 2012), with a small cohort of synanthropic exotic species and indigenous dietary specialists (avivorous raptors, nectarivores) more typical of forest/woodland habitats (Table 1; Figure 7) (Conole & Kirkpatrick 2011). Adapters as a group are all indigenous species of forest, woodland and riparian scrub origins (Table 1; Figure 7), and they have closer affinities with the riparian and bush remnant urban avoiders than the exploiters (Conole & Kirkpatrick 2011). It is therefore remnants of the former indigenous avifauna of wooded parts of Melbourne that are the source of the emerging group of urban adapted species, though none are yet as successful as the aptly named urban exploiters. The adapters are essentially the vanguard of a group of semi-specialised bird species that utilise particular niches within urban matrix habitats, but are not yet ubiquitous across the matrix in the way that exploiters are.

The responses observed here of each group to both degree of urbanisation and greenspace are largely explained by their ecological histories. The exploiters are able to use disturbed habitats across the matrix analogous to their original habitats, and many of them were established in Melbourne during the early stages of urban expansion and consolidation of the city. As suburban parts of the city became more heavily vegetated and less open, a group of species from analogous riparian/forest habitats became increasingly well established in parts of the city proximate to their source natural habitats. Many parts of the urban matrix are now at or close to the point of saturation with members of the exploiter assemblage due to their ubiquity, but the number of adapter species contributing to bird species richness at points across the matrix is likely to increase on a site by site basis as the process of afforestation of the older suburbs continues. It follows then that the distribution of exploiter species may decline in more established suburban parts of the city over time, though expanding in range and continuing to dominate in developing areas of the city at or near the fringe.

The broad linear trends documented by Blair and Johnson (2008) for overall indigenous woodland bird richness falling as urban tolerant bird richness increases holds for this study area too (Conole & Kirkpatrick 2011). However, the partitioning of adapters and exploiters within the urban tolerant grouping in this study reveals the fallacy of assuming uniformity of response of all 'urban tolerant' species, thereby overlooking a key to understanding how habitat origins may be important for understanding how species adapt to urban environments. Other workers have examined the importance of a variable suite of physiological and behavioural traits that may predispose birds to urban adaptability (e.g. Kark *et al.* 2007; Møller 2009; Evans *et al.* 2011). This study has examined the higher order habitat filtering mechanism that may be influential in this regard, and more broadly generalisable as a conceptual model at the scale of the landscape and the assemblage.

Conclusion

In a similar way to that in which time since establishment has been found to be related to high urban densities of some bird species (Møller *et al.* 2012), spatial or habitat origins of members of bird assemblages influence the degree to which they become urban tolerant; ranging from not at all through to ubiquitous. Bird species that classify as urban tolerant will further classify as either exploiters or adapters according to their habitats of origin.

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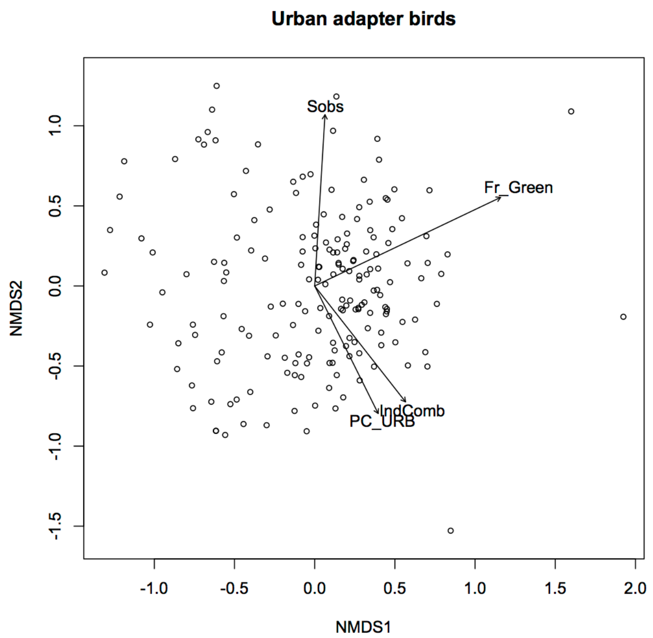

Figure 1: NMDS ordination, urban adapters – fitted vectors for which $p \leq 0.01$.

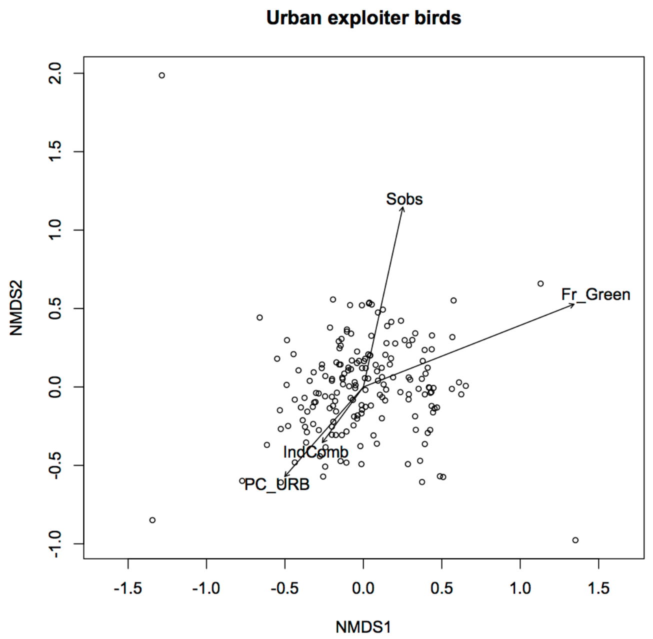

Figure 2: NMDS ordination, urban exploiters – fitted vectors for which $p \leq 0.01$.

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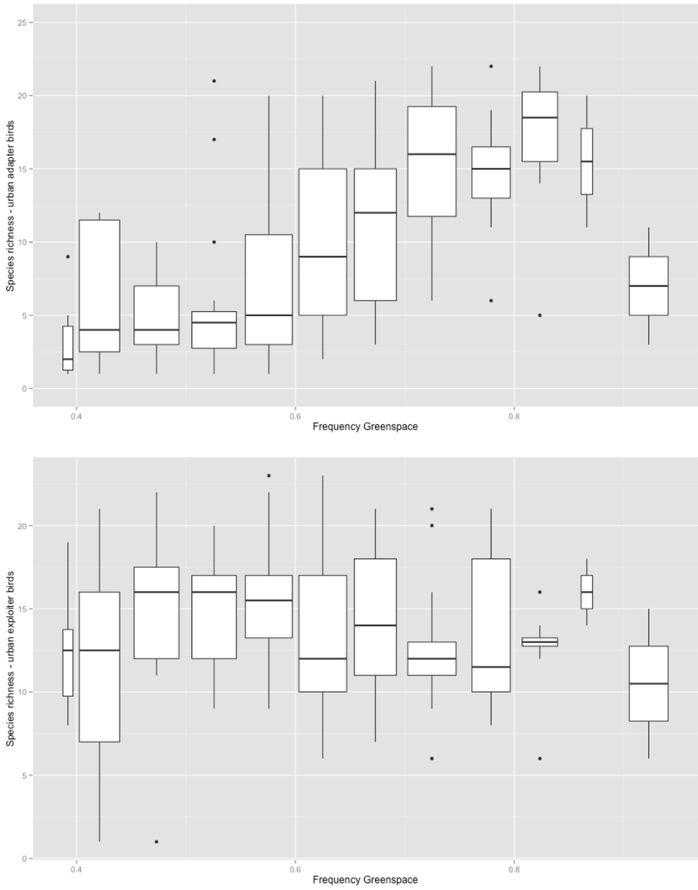

Figure 3: Species richness of (a) urban adapter and (b) urban exploiter bird species as a function of the proportion of green space at urbanised sites.

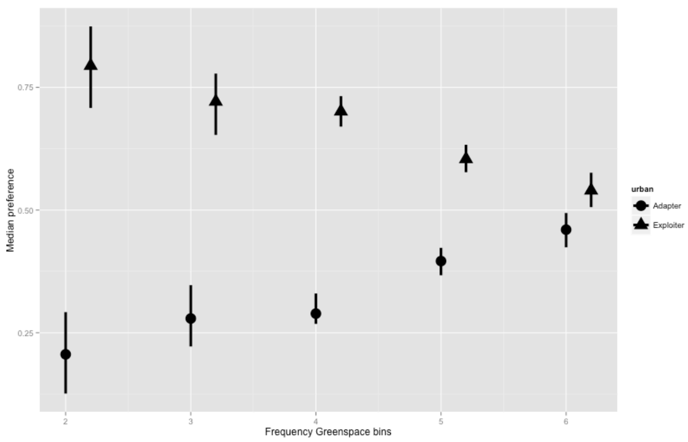

Figure 4: Posterior density for landscape-scale preferences of urban adapter and exploiter bird assemblages (median preference and 95% credible intervals) binned by Frequency Greenspace at urbanised sites. Posterior densities estimated from 10,000 MCMC steps following a burn-in of 1,000 generations.

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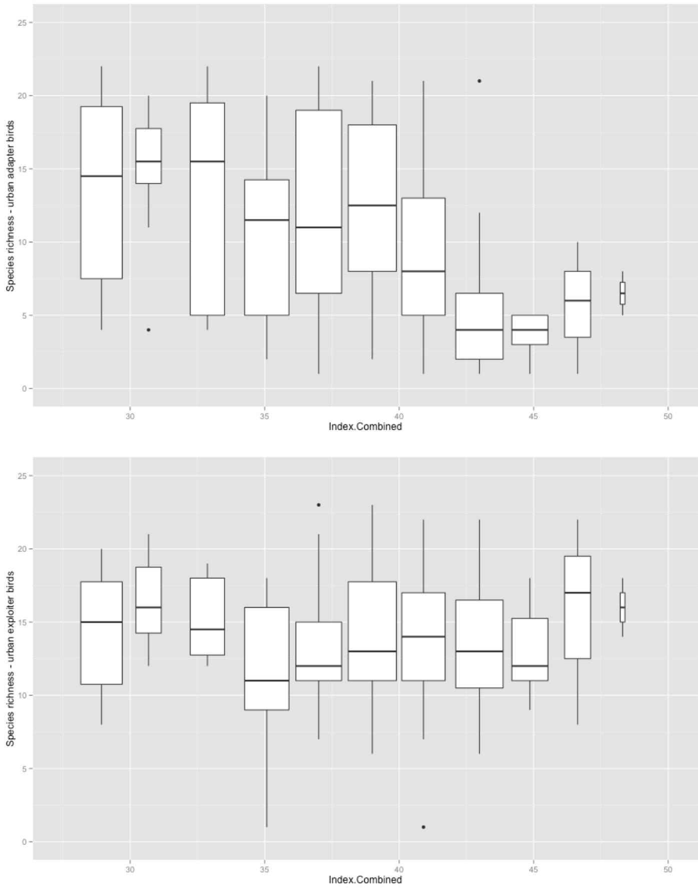

Figure 5: Species richness of (a) urban adapter and (b) urban exploiter bird species as a function of urbanisation intensity ($Index_{Combined}$) at urbanised sites.

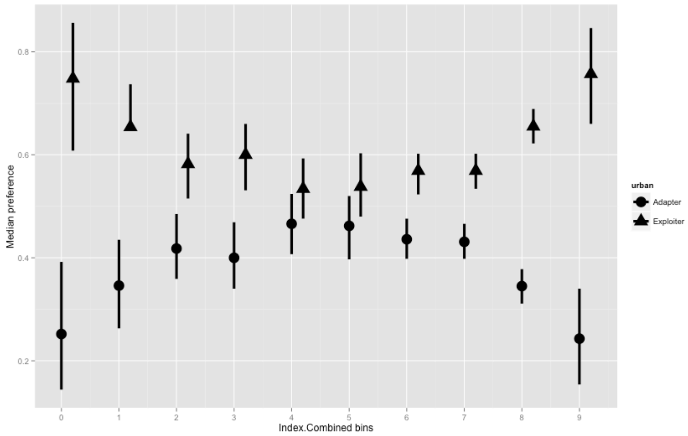

Figure 6: Posterior density for landscape-scale preferences of urban adapter and exploiter bird assemblages (median preference and 95% credible intervals) binned by urbanisation intensity (as $Index_{Combined}$) at urbanised sites. Posterior densities estimated from 10,000 MCMC steps following a burn-in of 1,000 generations.

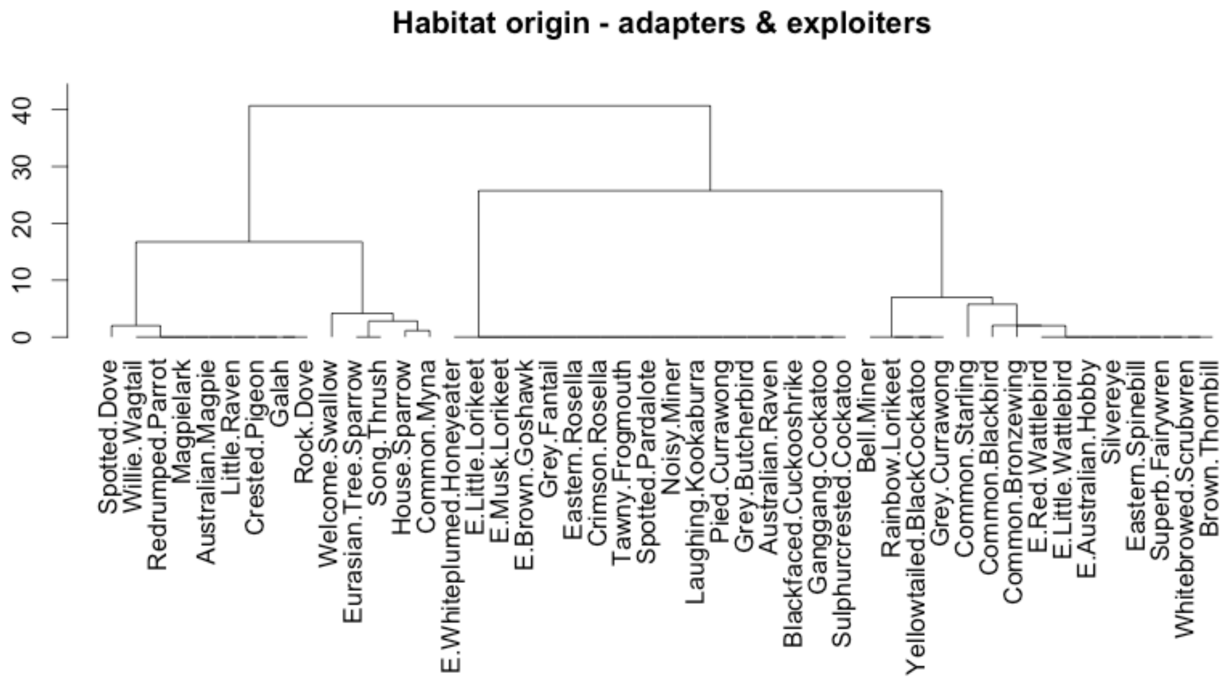

Figure 7: Cluster dendrogram (Ward method) of adapters and exploiters by habitats of origin. Exploiters that cluster within the adapters are prefixed with the letter "E".

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Table 1: List of bird species analysed in this study

Urban status	**Common name**	**Scientific name**	**Family**	**Feral**	**Original habitat**
Adapter	White-browed Scrubwren	Sericornis frontalis	Acanthizidae		Forest, woodland, heath, scrub
Adapter	Brown Thornbill	Acanthiza pusilla	Acanthizidae		Forest, woodland, heath, scrub
Adapter	Yellow-tailed Black-Cockatoo	Calyptorhynchus funereus	Cacatuidae		Forest, woodland, heath
Adapter	Gang-gang Cockatoo	Callocephalon fimbriatum	Cacatuidae		Forest, woodland
Adapter	Sulphur-crested Cockatoo	Cacatua galerita	Cacatuidae		Forest, woodland
Adapter	Black-faced Cuckoo-shrike	Coracina novaehollandiae	Campephagidae		Forest, woodland
Adapter	Common Bronzewing	Phaps chalcoptera	Columbidae		Forest, woodland, scrub
Adapter	Australian Raven	Corvus coronoides	Corvidae		Forest, woodland
Adapter	Grey Butcherbird	Cracticus torquatus	Artamidae		Forest, woodland
Adapter	Pied Currawong	Strepera graculina	Artamidae		Forest, woodland
Adapter	Grey Currawong	Strepera versicolor	Artamidae		Forest, woodland, heath
Adapter	Laughing Kookaburra	Dacelo novaeguineae	Halcyonidae		Forest, woodland
Adapter	Rainbow Lorikeet	Trichoglossus haematodus	Loriidae		Forest, woodland, heath
Adapter	Superb Fairy-wren	Malurus cyaneus	Maluridae		Forest, woodland, heath, scrub
Adapter	Eastern Spinebill	Acanthorhynchus tenuirostris	Meliphagidae		Forest, woodland, heath, scrub
Adapter	Bell Miner	Manorina melanophrys	Meliphagidae		Forest, woodland, scrub
Adapter	Noisy Miner	Manorina melanocephala	Meliphagidae		Forest, woodland
Adapter	Spotted Pardalote	Pardalotus punctatus	Pardalotidae		Forest, woodland
Adapter	Tawny Frogmouth	Podargus strigoides	Podargidae		Forest, woodland
Adapter	Crimson Rosella	Platycercus elegans	Psittacidae		Forest, woodland
Adapter	Eastern Rosella	Platycercus eximius	Psittacidae		Forest, woodland
Adapter	Grey Fantail	Rhipidura albiscapa	Rhipiduridae		Forest, woodland
Adapter	Silvereye	Zosterops lateralis	Timaliidae		Forest, woodland, heath, scrub
Exploiter	Brown Goshawk	Accipiter fasciatus	Accipitridae		Forest, woodland
Exploiter	Galah	Eolophus roseicapillus	Cacatuidae		Woodland, grassland
Exploiter	Rock Dove	Columba livia	Columbidae	Y	Grassland
Exploiter	Spotted Dove	Streptopelia chinensis	Columbidae	Y	Forest, woodland

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Urban status	**Common name**	**Scientific name**	**Family**	**Feral**	**Original habitat**
Exploiter	Crested Pigeon	Ocyphaps lophotes	Columbidae		Woodland, grassland
Exploiter	Little Raven	Corvus mellori	Corvidae		Woodland, grassland
Exploiter	Australian Magpie	Cracticus tibicen	Artamidae		Woodland, grassland
Exploiter	Australian Hobby	Falco longipennis	Falconidae		Forest, woodland, heath, scrub
Exploiter	Welcome Swallow	Hirundo neoxena	Hirundinidae		Aerial
Exploiter	Musk Lorikeet	Glossopsitta concinna	Loriidae		Forest, woodland
Exploiter	Little Lorikeet	Glossopsitta pusilla	Loriidae		Forest, woodland
Exploiter	White-plumed Honeyeater	Lichenostomus penicillatus	Meliphagidae		Forest, woodland
Exploiter	Little Wattlebird	Anthochaera chrysoptera	Meliphagidae		Forest, woodland, heath, scrub
Exploiter	Red Wattlebird	Anthochaera carunculata	Meliphagidae		Forest, woodland, heath, scrub
Exploiter	Magpie-lark	Grallina cyanoleuca	Monarchidae		Woodland, grassland
Exploiter	House Sparrow	Passer domesticus	Passeridae	Y	Urban, farm
Exploiter	Eurasian Tree Sparrow	Passer montanus	Passeridae	Y	Urban
Exploiter	Red-rumped Parrot	Psephotus haematonotus	Psittacidae		Woodland, grassland
Exploiter	Willie Wagtail	Rhipidura leucophrys	Rhipiduridae		Woodland, grassland
Exploiter	Common Starling	Sturnus vulgaris	Sturnidae	Y	Urban,farm, woodland, heath, scrub
Exploiter	Common Myna	Sturnus tristis	Sturnidae	Y	Urban,farm, woodland
Exploiter	Common Blackbird	Turdus merula	Turdidae	Y	Forest, woodland, heath, scrub, urban
Exploiter	Song Thrush	Turdus philomelos	Turdidae	Y	Urban

Habitat data from (Marchant & Higgins 1993; Higgins & Davies 1996; Higgins 1999; Schodde & Mason 1999; Higgins et al. 2001; Higgins & Peter 2002; Higgins et al. 2006).

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SUPPLEMENTARY MATERIAL

Table S1: Posterior density for landscape-level preferences of urban adapter bird assemblages (species richness) in Frequency Greenspace bins

Frequency Greenspace		Urban adapter		Urban exploiter	
Bin name	**Range**	**Median preference**	**Credible intervals**	**Median preference**	**Credible intervals**
2	20 – 29.9	0.206	0.126, 0.292	0.794	0.708, 0.874
3	30 – 39.9	0.279	0.222, 0.347	0.721	0.653, 0.778
4	40 – 49.9	0.289	0.268, 0.33	0.701	0.67, 0.732
5	50 – 59.9	0.396	0.367, 0.423	0.604	0.577, 0.633
6	60 – 69.9	0.46	0.424, 0.494	0.54	0.506, 0.576

Table S2: Posterior density for landscape-level preferences of urban adapter bird assemblages (species richness) in $\text{Index}_{\text{Combined}}$ bins

$\text{Index}_{\text{Combined}}$		Urban adapter		Urban exploiter	
Bin name	**Range**	**Median preference**	**Credible intervals**	**Median preference**	**Credible intervals**
0	0 – 4.9	0.252	0.144, 0.392	0.748	0.608, 0.856
1	5.0 – 9.9	0.346	0.263, 0.435	0.654	0.565, 0.737
2	10 – 14.9	0.418	0.359, 0.485	0.582	0.515, 0.641
3	15 – 19.9	0.4	0.34, 0.469	0.6	0.531, 0.66
4	20 – 24.9	0.466	0.407, 0.524	0.534	0.476, 0.593
5	25 – 29.9	0.462	0.397, 0.52	0.538	0.48, 0.603
6	30 – 34.9	0.436	0.398, 0.476	0.569	0.523, 0.602
7	35 – 39.9	0.431	0.398, 0.466	0.569	0.534, 0.602
8	40 – 44.9	0.345	0.311, 0.378	0.655	0.622, 0.689
9	45 – 50	0.243	0.154, 0.34	0.757	0.66, 0.846

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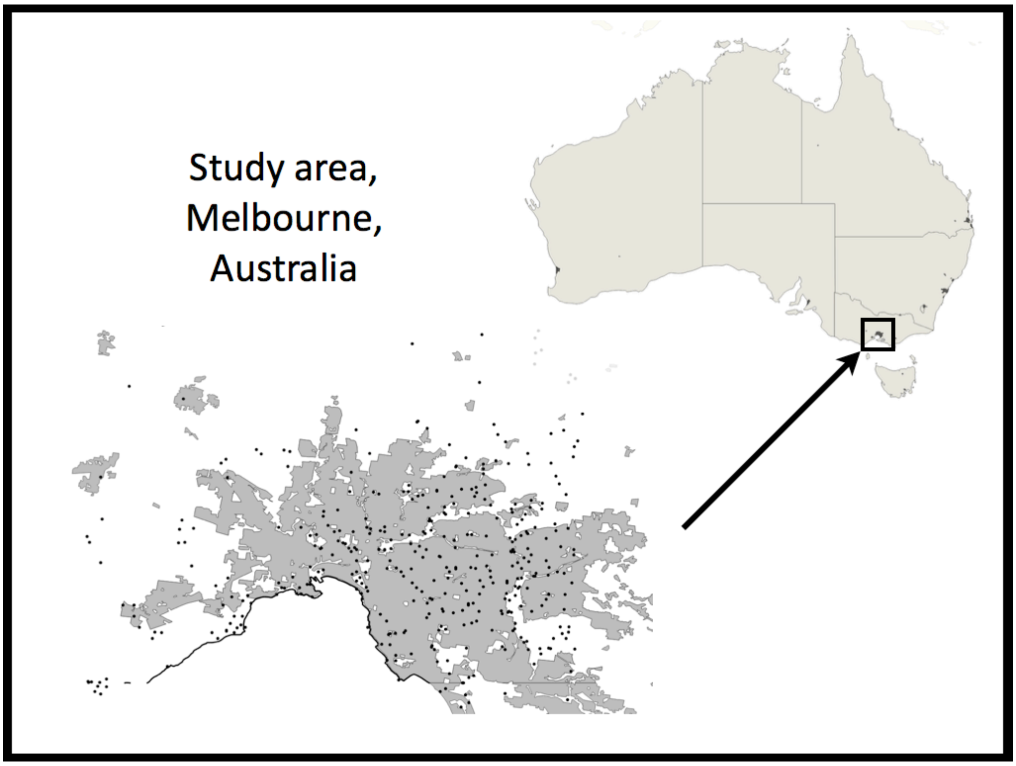

Figure S1: Map of Melbourne study area, Australia). Grey areas show built-up areas of Melbourne. Black circles are survey sites.

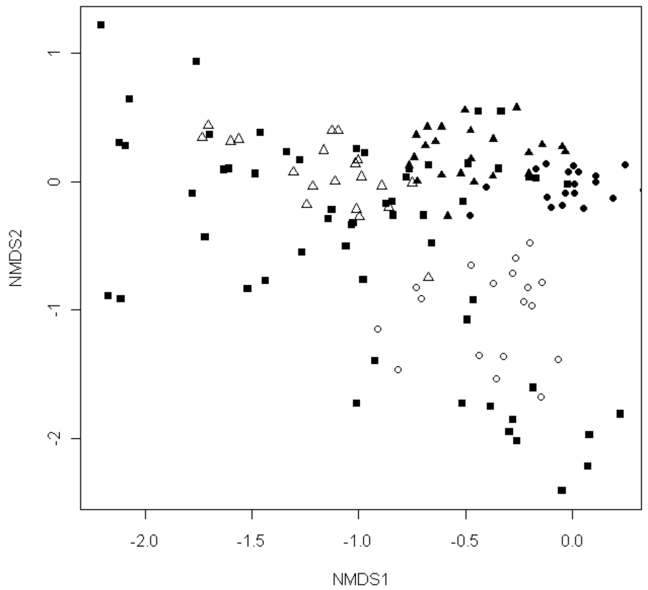

Figure S2: Plot of non-metric multidimensional scaling ordination results for species. Urban tolerant species: ▲= Urban adapters, ● = urban exploiters. Urban avoiders: ■ = Assemblage 4; ○ = Assemblage 3, Δ = Assemblage 1 (Conole and Kirkpatrick 2011).

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