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Research Article

The role of invasion and urbanization gradients in shaping avian community composition

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Abstract

The extent to which native species utilize urban environments depends on species responses to multiple threatening processes. Here, we aimed to quantify changes in bird communities in response to changing habitat structure, invasive species and aggressive native species. We conducted surveys in two independently invaded regions with similar patterns of urban development. The study regions were New South Wales (NSW) and Queensland (QLD), Australia. We observed 127 species in NSW and 144 species in QLD. Most species (NSW 83 and QLD 84) are urban adapters making use of some or all urban sub-environments. Urban avoiders, species only found in remnant vegetation, were the second largest group (urban avoiders: NSW 23 and QLD 31). We found the lowest richness in the most urban sites (urban exploiters: NSW 10 and QLD 15). Using generalized linear mixed models, we found a non-significant relationship between species richness and the abundance of aggressive species like the common myna and noisy miners, *Manorina melanocephala*, but a significant positive correlation with the percentage of shrub cover at a site. As there is a gradual loss of species with increasing urbanization, retaining higher complexity in vegetation structure in urban areas will support large numbers of species and could help mitigate the potential impacts of aggressive urban-adapted species and habitat loss.

Key words: invasive species, habitat change, urban conservation, community ecology

INTRODUCTION

Species responses to urbanization can be divided into three categories: urban exploiters, urban adapters and urban avoiders (Blair 1996; Kark et al. 2007). Urban 'Exploiters' are species that can capitalize on the altered resources within urban environments and reach high densities in modified environments. Urban 'Adapters' are species that can make limited use of urban areas, or do well in lightly transformed environments. Urban 'Avoiders' are native species that are most sensitive to habitat change and prefer to occur in unmodified areas. However, urban environments are heterogeneous and individual species ability to use sub-environments within a city may differ depending on species-specific responses, size of the city, the patterns of urban development and the intensity of disturbance within urban habitat (Bolger et al. 1997; Sewell and Catterall 1998; Blair 2004; Fournier et al. 2020; Heggie-Gracie et al. 2020).

Factors such as habitat change, competition with invasive species and interactions with aggressive native urban adapted species are not uniform across urban environments (Garden et al. 2006, 2010), resulting in local and landscape-scale gradients of disturbance (Garaffa et al. 2009; Luck et al. 2013). The extent to which species use different parts of urban environments has important implications for conserving species in and around urban centres (Bolger et al. 1997). Understanding how urban communities vary within and among different cities can help identify important habitat features that promote urban biodiversity (Shwartz et al. 2008; Sushinsky et al. 2013).

In Australia, urban expansion over the last 200 years has occurred relatively recently (compared to places like Europe), and nearly 90% of the Australian population now live in cities (Australian Bureau of Statistics 2012). The changing Australian landscapes have driven significant changes in bird communities due to both species introductions and changes in native species distributions (Joyce et al. 2018). Around 60 species have been introduced to Australia, while 24 of these have established breeding populations (McKinney and Kark 2017); however, the impact of most of these established species on native bird species has not been studied. In addition to non-native species introductions, habitat modification associated with humans has facilitated the range expansion and spread of many native species (Major and Parsons 2010). Several of these native urban adapted birds are highly aggressive (Montague-Drake et al. 2011), further impacting urban birds in addition to the changes brought about by habitat change and introduced species (Haythorpe et al. 2014).

Two species associated with declines in native species richness and abundance are the native noisy miner (*Manorina melanocephala*) and the introduced common myna (*Acridotheres tristis*) (MacDonald and Kirkpatrick 2003; Tindall et al. 2007; Kath et al. 2009; Mac Nally et al. 2014). Evidence of significant impacts of the common myna in Australia is generally restricted to competition for nesting sites (Pell and Tidemann 1997a; Rogers et al. 2020), although they show aggressive behaviour around food resources and are associated with declines in native species (Grarock et al. 2014). Noisy miners are attributed to changing species composition and driving declines of small-bodied birds at both local and landscape scales (Montague-Drake et al. 2011; Mac Nally et al. 2014). The noisy miners achieve this through the aggressive exclusion of other birds from breeding territories (Maron et al. 2013; Haythorpe et al. 2014). Competition between myna, miners and other species show important differences across sites with varying levels of urbanization (Sol et al. 2012; Haythorpe et al. 2014) with both species being highly successful in sub-urban environments such as those created in city parks with scattered trees and large areas of open habitat (Pell and Tidemann 1997b; Grey et al. 1998).

In Australia, the common myna is still expanding its geographic range, creating an invasion gradient as mynas spread from long invaded 'source' areas to the expanding invasion 'front' (Fogarty et al. 2011; Perkins 2012; Berthouly-Salazar et al. 2013). Source and front populations often have different impacts on local species (Urban et al. 2008; Tayleur 2010; Sullivan 2014), but the impacts of the common myna across its range have not been studied. The common myna is a member of the starling family (Sturnidae) and was introduced starting the 19th century into several locations across eastern Australia, and it has been gradually spreading across its potential range that includes the entire east coast of the continent (Martin 1996). The invasion gradient of the common myna also occurs along a landscape-scale gradient of urbanization, with larger cities generally having been invaded earlier and rural towns more recently. Previous studies on the myna have occurred in long invaded areas (Pell and Tidemann 1997a; Grarock et al. 2012), and it is unknown whether the reported impacts are consistent across its range.

Despite the impact of common myna and noisy miner on Australian bird communities having been demonstrated, most studies of impact have been derived from atlas data (at a very large spatial scale) or from single city field studies. Studies across multiple cities in Australia are lacking. As habitat quality is likely to vary within and between cities (Ferenc et al. 2014), conserving urban species in Australia requires understanding how species respond to variation in urbanization. Here we explore how bird richness changed along local urban gradients (sub-environments: urbanized, park and semi-natural edge habitats) and how vegetation structure, common myna presence and native noisy miner presence influenced species richness across urban sites. We followed up by asking how are bird species distributed across the urban exploiters, adapters and avoiders categories in two regions of Australia.

METHODS

Study area

In this study, we focused on south-east Queensland and central New South Wales, which have relatively similar patterns of urban development and independent invasion histories for the common myna (Fig. 1). Both regions are also within the native range of the noisy miner. We selected study sites in each region along an invasion gradient. Sites that had been invaded before 1970 ('source' sites) and those invaded after 1990 ('front sites'). We selected nine cities across the two regions representing five source locations and four front locations (Fig. 1). Within each city, we surveyed along an urbanization gradient, with one survey site in each of three different sub-environments; at the edge of remnant vegetation ('edge'), in an open park ('park') and a heavily urbanized area ('urban'). We chose areas within each city that contained the three sub-environments within 1 km of each other. Edge sites were areas adjacent to remnant native vegetation. Park sites were characterized by large amounts of mowed turf and few large trees. Urban sites were areas with high human activity, higher proportions of sealed surface (concrete or asphalt) and a large number of buildings and other artificial structures. Overall, we surveyed 27 sites, including 9 locations within the two regions (QLD, NSW) × 3 sub-environments (edge, park, urban) within each location (see Fig. 1).

In each study site, the study team and volunteers familiar with the local birds carried out monthly bird surveys between August 2014 and August 2016. Each survey consisted of a 10-min point count with an unlimited radius, during which we recorded the total number of birds that were seen and heard. For each observation, we recorded bird activity as flying overhead, flying through, walking, perched. We conducted bird surveys within 3 h of sunrise and did not survey on days with heavy rain or high winds. To minimize the effect of different observers, we pooled data over the 2 years for the analysis. We excluded birds observed only flying over a site, and not actively using a site from the analysis. For example, a raptor flying overhead but foraging would be included, but waterfowl flying high overhead would be excluded. To calculate the abundance, we used the total number of birds recorded within a 100 m radius of the point count, averaged over the 24 surveys for each site. We calculated common myna and noisy miner abundance by avearchivraging the total number of birds observed per survey, within 100 m of the survey point, over the 2 years.

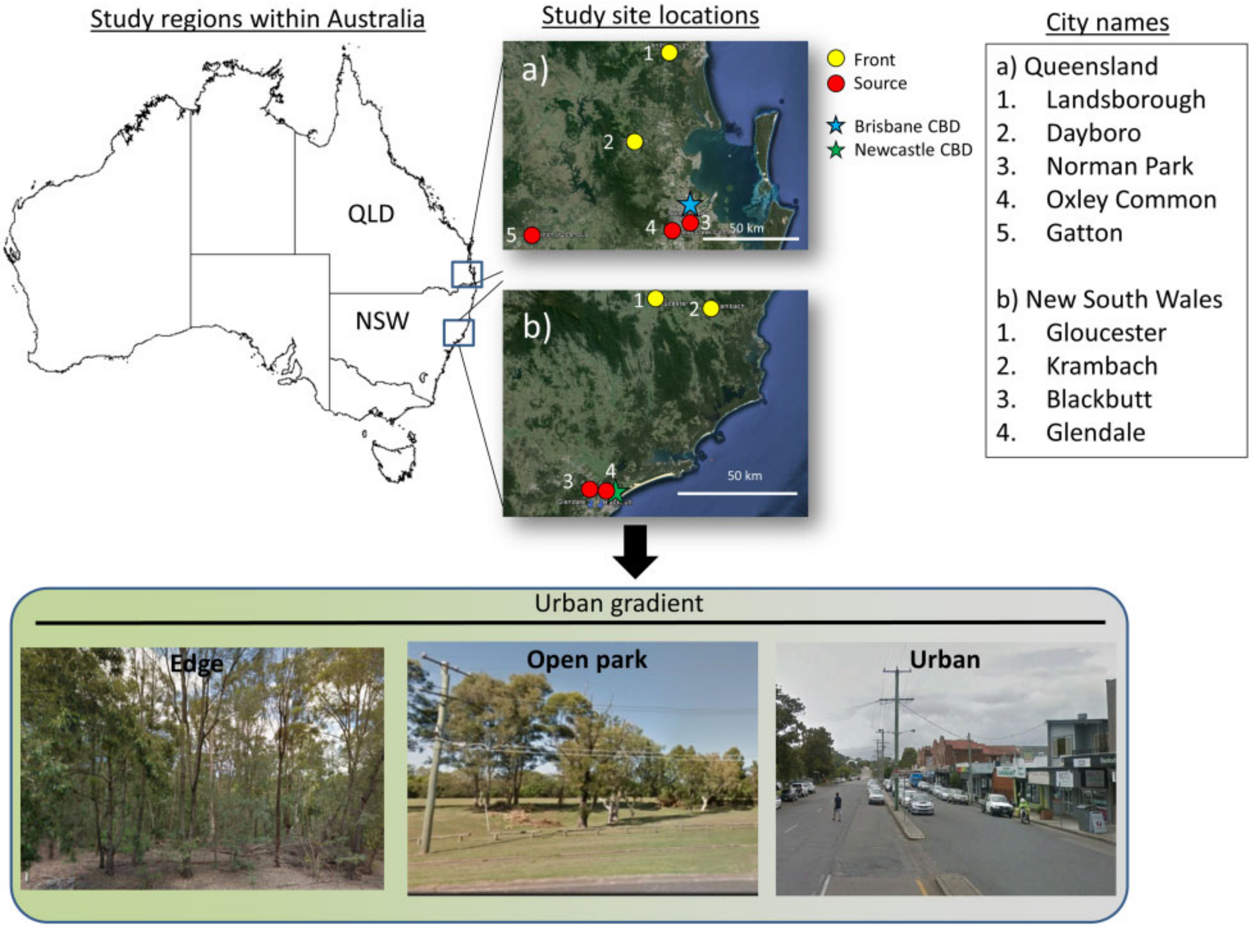

Figure 1: Study sites were located within nine cities across the states of Queensland (QLD) and New South Wales (NSW). Study sites were located along an invasion gradient (front, source) and within each city (edge, park, urban) representing the urban gradients within each city.

We calculated species richness using data pooled across the 2 years of surveys. Species abundance was calculated using all birds observed utilizing a site during surveys but excluding birds flying over. We calculated average survey richness with the 'specnumber' function in the 'biodiversityR' package (Oksanen et al. 2018) in the program R (R Core Team 2015). We calculated total site richness using the SJack2 species richness estimator as it makes no assumptions about underlying species distributions and has been shown to be robust even when calculating richness with small sample sizes (Hellmann and Fowler 1999; Magurran 2004).

To quantify changes in vegetation across sites, we used several approaches. The native vegetation at our sites would have historically been open eucalypt woodland characterized by 50–80% crown cover (Australia's state of the forests report 2018). To quantify variation in the vegetation cover surrounding the study sites, we used remotely sensed data of the normalized difference vegetation index (NDVI; Supplementary materials, Table S1) *sensu* Bino et al. (2008). We used NDVI data from NASA's LandSat satellite, which produces images with a 30 m × 30 m pixel resolution. We downloaded NDVI images for all sites for the years 2009 –2014. We evaluated each image for cloud cover, and only images that had less than 10% cloud cover were used. We found 14 cloud-free images to include in the analysis. For each survey site, we calculated NDVI by averaging the NDVI value for pixels in a 100 m^2 area centred on each survey site.

We quantified local habitat structure and the cover around each survey point using eight circular vegetation plots with a diameter of 30 m. We selected points for the vegetation plots by generating a random distance (within 100 m) and the direction of the centre of site. If that point was not accessible (a building or other structure was in the way), the nearest accessible point to the selected point was used. Because tree density is an important habitat factor for both common myna and noisy miners (Grarock et al. 2014; Haythorpe et al. 2014), we counted the number of trees within each plot and where possible identified to a genus for individual trees over 5 cm in diameter. Additionally, within each plot, we estimated the percent ground cover of shrub (woody vegetation between 5 cm and 3 m in height), turf, and sealed ground (i.e. asphalt and concrete).

The relationship between habitat characteristics, the abundance of aggressive species, and species richness at each site was explored using Generalized Linear Mixed Models (Zuur et al. 2009) using the package 'lme4' (De Boeck et al. 2011) and 'lmerTest' (Kuznetsova et al. 2015). We used the SJack2 richness estimate for each site as the dependent variable. Explanatory variables include common myna abundance, noisy miner abundance, average tree density, average percent shrub ground cover and average NDVI. To account for the nested nature of the study design, we included the city as a random factor. We tested for collinearity between explanatory variables and included variables in the final model if they had a variance inflation factor of less than four (Crawley 2007). The percent ground cover of shrub, turf and sealed ground showed high collinearity. Both percent ground cover shrubs and sealed surface showed the largest differences between sub-environments (Supplementary materials, Fig. S2), so we selected used shrub cover in the GLMMs to help distinguish between sites. In Australia, areas with higher shrub cover have been shown to support greater bird richness in Australia (see Archibald et al. 2017). The correlation between explanatory variables in the final model, along with the full model results are included in supplementary materials (Supplementary materials, Table S2).

RESULTS

Bird surveys

In total, we conducted 648 surveys (24 for each of the 27 sites) and recorded 168 species across all study locations. Regionally, we found 132 species in our 15 Queensland sites and 117 species in the 12 New South Wales (NSW) sites. Across all sites, we found 129 native and five invasive species (Supplementary materials, Table S3). The introduced bird species in the QLD sites were the common myna, common starling (*Sturnus vulgaris*) and the rock dove (*Columba livia*). In NSW introduced species included the common myna, common starling, common blackbird (*Turdus merula*), European goldfinch (*Carduelis carduelis*) and rock dove. Species richness along the urbanization gradient showed that edge sites contained the most species, followed by the park then urban sites (Fig. 2). The pattern of decreasing richness with increasing levels of urbanization was consistent after pooling the data for each region, and front vs. sources locations (Fig. 2). Total bird abundance was highly variable across sites and showed no consistent pattern between regions (Fig. 2). The abundance of the common myna and noisy miner showed high variation along the urban gradient between regions and across front/source locations (Fig. 3). However, noisy miners were similarly or more abundant compared to the common myna. Across the invasion gradient, the common myna was more abundant in source sites on average but these differences are not significant (Fig. 3).

Urban exploiters, adapters and avoiders

Based on species rank abundance across all urban sub-environments in each region (Supplementary materials, Table S3), we found a gradual loss of species with the increasing urbanization of sub-environments at local scales (Fig. 4). We categorized urban adapters as species that occurred in some, but not all of the urban and park sites. Adapters were the largest group, with 83 species in QLD and 84 species in NSW. Urban adapters, therefore, represent 60–70% of the urban bird assemblages in our study regions. Urban avoiders, species found only the edge sites, were the next largest group with 35 species in NSW and 42 species in QLD that occurred in the least developed sites. We found that urban exploiters were the group with the smallest number of species with 10 birds in NSW and 16 in QLD. These species accounted for 8.5% and 11.6% of the total species pool in NSW and QLD but accounted for 42% and 52% of all individuals birds observed in the respective regions. The two study regions shared six of the ten most abundant urban exploiters including the Australian magpie (*Gymnorhina tibicen*), laughing kookaburra (*Dacelo novaeguineae*) and magpie-lark (*Grallina*

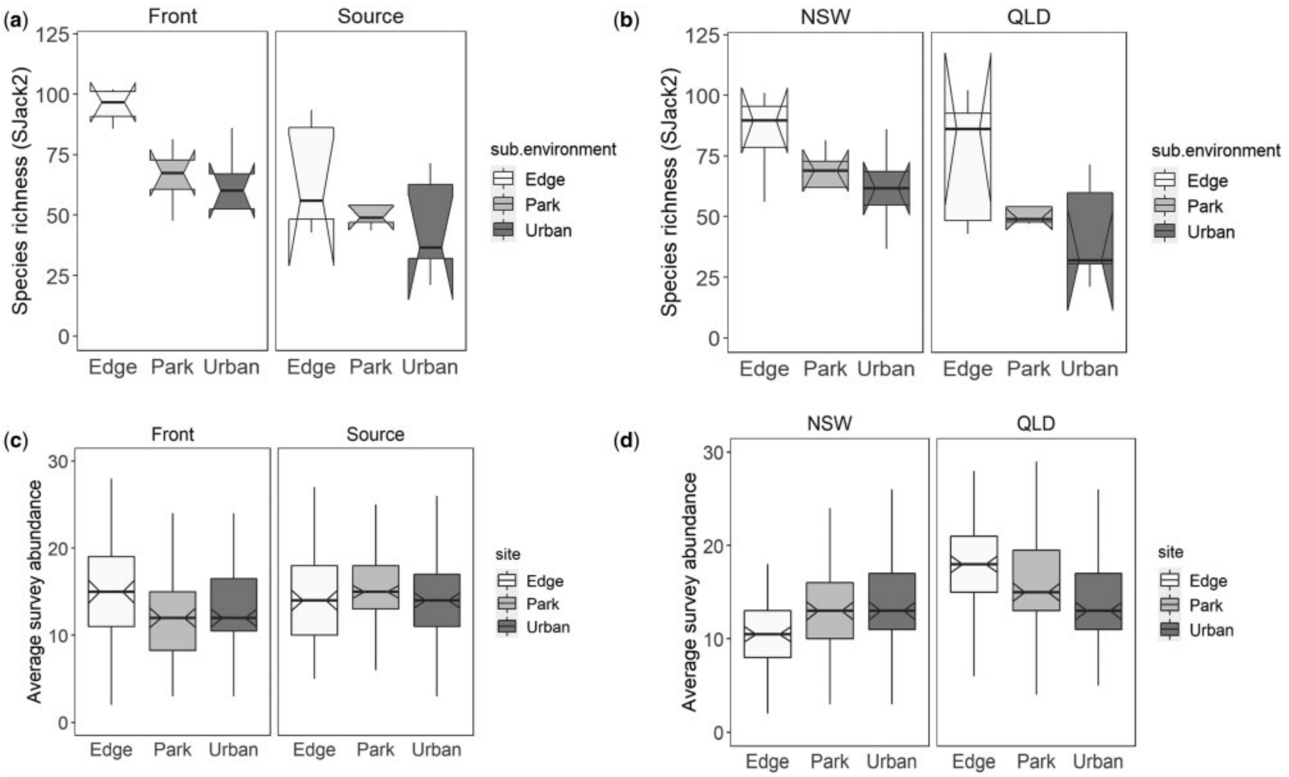

Figure 2: Avian species richness (SJack2) and abundance calculated for each sub-environment (edge, park, urban) representing the invasion gradient within the front and source locations of the two regions (QLD and NSW) combined (**a**, **c**), and the two regions with front and source locations combined (**b, d**). Horizontal lines in the boxes represent median values, and box boundaries indicate 25th and 75th percentiles. Whiskers span two standard deviations of the mean. Non-overlapping notches indicate significant differences between medians.

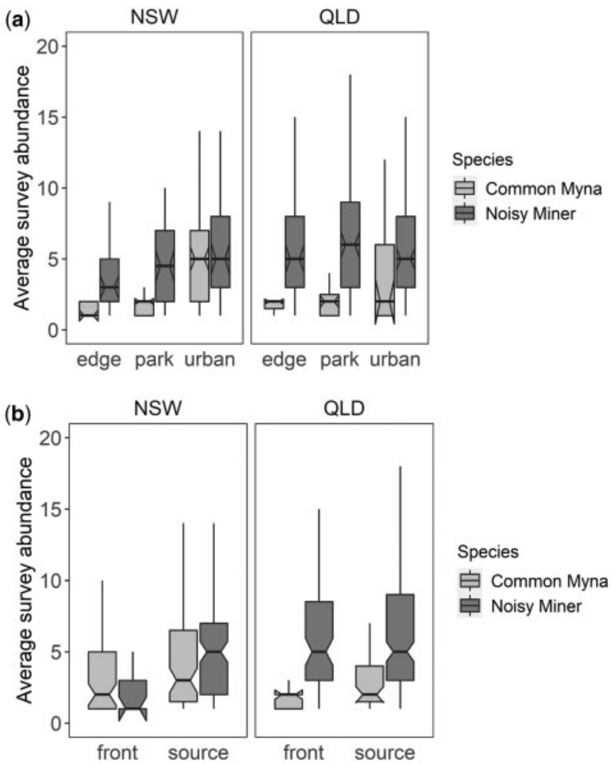

Figure 3: The mean observed abundance of the common myna and the noisy miner in Queensland and New South Wales across the (**a**) urban gradient and (**b**) front-source locations. Horizontal lines in the boxes represent median values, and box boundaries indicate 25th and 75th percentiles. Whiskers span two standard deviations of the mean. Non-overlapping notches indicate significant differences between medians.

cyanoleuca), the galah (*Eolophus roseicapilla*) and the noisy miner and rainbow lorikeet (*Trichoglossus moluccanus*).

Species richness and sources of disturbance

We found that across all 27 survey sites, species richness was positively correlated with per cent shrub ground cover (estimate $= 0.52$, df $= 15.68$, $P < 0.00$). A non-significant negative correlation was found between common myna abundance and noisy miner abundance with species richness and remnant vegetation (Supplementary materials, Fig. S1), and we found no significant relationships in the generalized linear mixed models.

DISCUSSION

Bird communities across disturbance gradients

In this study, we were interested in how urban bird communities respond to habitat modification, invasive species and aggressive native species across multiple Australian cities. We found consistent patterns of species loss and increasing biotic homogenization with increasing urbanization across our invasion gradients, and across the two study regions, a result found across many urban environments (Blair 1996; Kark et al. 2007; Fontana et al. 2011, Heggie-Gracie et al. 2020). However, the majority of bird species across our study sites were urban adapters, making some use of some but not all urban sub-environments. Sub-environments that had more complex habitat structure (shrub ground cover); a finding that lends further support to the importance of urban green space with complex vegetation structure (Bolger et al. 1997; Chace and Walsh 2006; Shwartz et al. 2008; Shanahan and Possingham 2009; Archibald et al. 2017). Importantly, the high numbers of urban adapters highlight the need for conservation in modified environments and the benefit of retaining green space for native wildlife (Edwards et al. 2011; Ives et al. 2016).

We found weak support for the impact of common myna and noisy miners on avian community richness and more support for the importance of habitat structure. Earlier work (Grarock et al. 2014a) investigating common myna impacts along an urban gradient in Canberra found that the common myna in combination with habitat change was a driver of changes in bird communities, but that work did not report the impact of noisy miners. The low abundance of mynas we observed across some sites, especially in Queensland, relative to other parts of its range (Grarock et al. 2013), highlights important variation in the common myna's success across the continent. Nevertheless, the higher average abundance of noisy miners compared to common mynas across our urban gradients means that the baseline levels of aggression by native noisy miners need to be taken into account when assessing impacts of non-native species (Mac Nally et al. 2012; Haythorpe et al. 2014). Both species showed a non-significant but negative correlation with shrub cover, such that increasing the structural diversity of habitat fragments may deter these species from increasing the value of such habitat to other birds.

In both study regions, total species richness was lower in larger urban areas (sites in the greater Brisbane and greater Newcastle areas) compared to our more rural study sites. This pattern may be due to shorter distances from our rural sites to intact forests, allowing more species to filter into urban sub-environments (Fontana et al. 2011; MacGregor-Fors et al. 2011). However, the same pattern of species loss with increasing urbanization intensity in both large and small cities suggests that maintaining remnant habitat as cities grow will have significant conservation benefits for many birds (Shanahan and Possingham 2009; Rayner et al. 2015; Archibald et al. 2017). An important finding is that of higher bird diversity in edge sites across local gradients of urbanization (within 1 km), such that even small patches of habitat with complex vegetation structure are likely to support more diverse bird assemblages in urban environments (Shwartz et al. 2008).

Individual species tolerance to urbanization contributed to a pattern of gradual species loss across urban environments (Blair 1996; Joyce et al. 2018). Conservation efforts to support the urban adapters, therefore, stand to benefit between 60% and 70% of birds that are found in urban environments. Conservation efforts targeting these urban adapters should be a priority as Joyce et al. (2018) found the long-term population trends of many common birds in SE Queensland are declining. The relatively recent establishment of Australian cities, within the last 200 years, and may mean that there remains an extinction debt in more rural–urban areas (Szabo et al. 2011; Hanski 2013; Soga and Koike 2013). Mitigating the loss of species from urban environments will require better incentives and policies to protect and improve the remaining fragments for birds and other wildlife (Bolger et al. 1997; Rodewald and Shustack 2008; Dale 2018).

Patterns of urban habitat use by alien and despotic species

Beyond changes in habitat, interactions between species can also drive changes in community composition (Tindall et al. 2007; Kath et al. 2009; McClure et al. 2011; Maron et al. 2013),

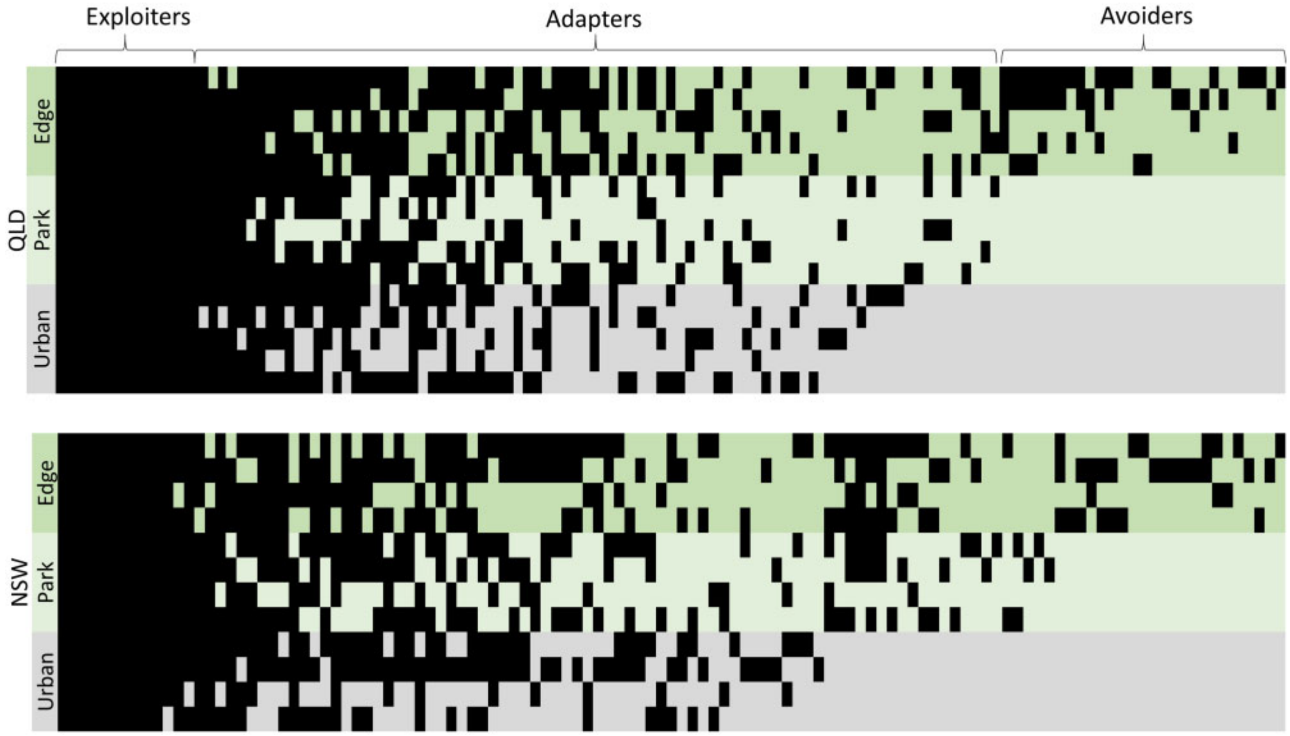

Figure 4: Presence and absence (black squares are present) for species (each column) in each sub-environment, for Queensland (QLD) New South Wales (NSW). Sites are grouped and coloured by sub-site with an edge, park and urban being green, light green and grey, respectfully. Urban exploiters (species that occurred at all sites) are 8.5% and 11.6% of the regional species pool (10 NSW; 15 QLD). Many more species are urban adapters and occurred in some but not all the sites (84 NSW; 83 QLD) representing 71.7% and 62.8% of NSW and QLD species, respectfully. Urban avoiders, species found only in edge sites were the second largest group (23 NSW; 31 QLD). The urban exploiters (species recorded at all sites) made up 42% and 52% of the total individuals recorded in NSW and QLD, respectfully.

Table 1: Generalized linear model residuals for testing the relationship between species richness and local habitat structure and the presence of aggressive urban-adapted species (the common myna and noisy miner). Models used a negative binomial error distribution and a log link

	Estimate	Std. error	df	p
(Intercept)	18.872	19.42	17.015	0.345
NDVI	41.488	32.767	17.803	0.222
Common myna abundance	5.685	3.216	14.71	0.098
Noisy miner abundance	−0.304	4.033	20.532	0.941
Percent ground cover: shrubs	0.525	0.141	15.681	0.002
Total number of trees	−0.018	0.038	15.185	0.637

creating additional challenges for conservation management in urban areas (Grarock et al. 2014). Of the two aggressive species we focused on here, the common myna and noisy miner, the later was more abundant at all spatial scales of the study except in urban sites in NSW. Noisy miners aggression can influence bird community composition at large spatial scales (Grey et al. 1998; Montague-Drake et al. 2011). In contrast, the common myna in experimental studies quantifying aggressive interactions around food sources has shown that mynas are less aggressive than many urban adapted native species (Sol et al. 2012). Most of the impact of common myna is restricted to competition for natural tree hollows (Pell and Tidemann 1997a; Grarock et al. 2013). Regardless of the relative impact of each species on bird communities, both mynas and miners show preferences for more open habitats so efforts to maintain or restore habitat should mitigate the impact of these two species.

Patterns of common myna abundance were highly variable across source-front gradients. The pattern of increasing common myna abundance with increasing urbanization is consistent with other studies from across its range (Sol et al. 2012; Grarock et al. 2013). Common myna can reach high densities in cities, and in some parts of its invasive range, it is one of the most common urban birds (Grarock et al. 2012). The variation of common myna abundance at landscape scales remains a key gap in our understanding of common myna invasion dynamics in Australia. The impact of the introduced common myna on local bird assemblages has been largely inferred from patterns of increasing myna density and decreasing bird abundance (Tindall et al. 2007; Grarock et al. 2012). This poor understanding of the drivers of myna abundance in different regions limits what conclusions can be made about common myna impacts across its introduced range (Newson et al. 2011; Baker 2017).

Importantly, both the noisy miner and common myna prefer areas of habitat with an open understory, represented in our sites by areas of grass or sealed surfaces (concrete or asphalt). We did not find a significant correlation between these species and shrubs in our study (likely due to the small habitat patch sizes we were working in); however, the pattern of lower myna and miner abundance in areas with more shrubs is supported by previous work (Pell and Tidemann 1997b; Grey et al. 1998). While the amount of shrub cover at our bird survey locations was inversely correlated with grass cover and amount of sealed surface (concrete and asphalt), we did not explicitly test the relationship between grass/sealed surfaces with myna and miner abundance. Identifying thresholds in species tolerance to habitat change by identifying exactly how much area of grass or sealed surface is needed to encourage urban species (and conversely how much shrub deters them) will greatly aid urban habitat management.

Conserving birds urban in urban environments

Australia is a mega-diverse country with cities occurring across many diverse climatic and environmental gradients. Here we showed that significant differences in species richness do occur at small spatial scales within urban and peri-urban environments, with remnant habitat supporting many more species than more urban habitat. Significantly, conserving urban habitat patches that have high structural complexity has the potential to support more species while also deterring highly competitive urban exploiter species such as noisy miners and common mynas (Parsons et al. 2003).

Supplementary data

Supplementary data are available at *JUECOL* online.

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Conflict of interest statement. None declared.

Ethics approval (include appropriate approvals or waivers)

University of Queensland Animal Ethics approval number 454/13.

Consent for publication

All authors gave final approval for publication.

Data availability

All data used in the analysis are included in the supplementary data

Code availability

All software to conduct analysis used open source software and packages.

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