RESEARCH PAPER

Cities are hotspots for threatened species

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ABSTRACT

Aim Although urbanization impacts many species, there is little information on the patterns of occurrences of threatened species in urban relative to non-urban areas. By assessing the extent of the distribution of threatened species across all Australian cities, we aim to investigate the currently under-utilized opportunity that cities present for national biodiversity conservation.

Location Australian mainland, Tasmania and offshore islands.

Methods Distributions of Australia’s 1643 legally protected terrestrial species (hereafter ‘threatened species’) were compiled. We assessed the extent to which they overlapped with 99 cities (of more than 10,000 people), with all non-urban areas, and with simulated ‘dummy’ cities which covered the same area and bioregion as the true cities but were non-urban. We analysed differences between animals and plants, and examined variability within these groups using species accumulation modelling. Threatened species richness of true versus dummy cities was analysed using generalized linear mixed-effects models.

Results Australian cities support substantially more nationally threatened animal and plant species than all other non-urban areas on a unit-area basis. Thirty per cent of threatened species were found to occur in cities. Distribution patterns differed between plants and animals: individual threatened plant species were generally found in fewer cities than threatened animal species, yet plants were more likely to have a greater proportion of their distribution in urban areas than animals. Individual cities tended to contain unique suites of threatened species, especially threatened plants. The analysis of true versus dummy cities demonstrated that, even after accounting for factors such as net primary productivity and distance to the coast, cities still consistently supported a greater number of threatened species.

Main conclusions This research highlights that Australian cities are important for the conservation of threatened species, and that the species assemblages of individual cities are relatively distinct. National conservation policy should recognize that cities play an integral role when planning for and managing threatened species.

Keywords

Australia, biodiversity, conservation policy, species distributions, threatened species, urbanization.

INTRODUCTION

Threatened species can be found in cities all over the world. Twenty-two per cent of the known occurrences of endangered plants in the USA fall within the 40 largest cities (Schwartz et al., 2002), and in an analysis of 54 cities Aronson et al. (2014) found that nearly a third are known to contain globally threatened birds. Indeed, the probability of a species being listed on the
urbanized (McDonald et al., 2008). The reasons for this are becoming well understood: cities are often located in areas of high biological diversity (Luck, 2007), and urbanization is a significant and expanding land-use change that leads to habitat loss and fragmentation (Seto et al., 2012). While the impacts of urbanization on biodiversity are undeniable, this may also make cities especially important for achieving conservation outcomes. However, little is known about the relative importance of cities for conserving different kinds of organisms.

Urban areas occupy less than 0.5% of the Earth’s total land area (Schneider et al., 2009), yet some threatened species are highly reliant on urban environments. For example, in the UK, the song thrush Turdus philomelos, a declining species of national conservation concern, occurs at densities more than three times higher in urban habitats than in the surrounding rural environment (Mason, 2000). The endangered Nielsen Park she-oak Allocasuarina portuensis also occurs exclusively within the metropolitan area of greater Sydney. Despite examples such as these, the designation of protected areas remote from human disturbance remains the dominant conservation paradigm world-wide (Miller & Hobbs, 2002). We have known for a long time that such wilderness thinking does not reflect ecological reality (Williams, 1980; Cronon, 1995). Yet conservation decision-making continues to implicitly, and sometimes explicitly, exclude urban environments from conservation investment (e.g. Sanderson et al., 2002; Mittermeier et al., 2003), as the negative pressures associated with urban development are seen to render urban habitats as ‘lost causes’ from a biodiversity perspective (Cavin, 2013). By ignoring urban areas, important conservation opportunities are potentially missed.

More than 1600 species on the Australian continent are considered to be threatened with extinction (Walsh et al., 2013). Australian environmental policies and legislation are similar to those of other jurisdictions in that they tend to prioritize existing natural environments over disturbed or human-modified areas for biodiversity conservation or investment. Indeed, the second principle underpinning Australia’s Biodiversity Conservation Strategy is that ‘biodiversity is best conserved by protecting existing natural environments’ (Natural Resource Management Ministerial Council, 2010, p. 16). Under the Environment Protection and Biodiversity Conservation Act 1999 (EPBC Act), threats to listed species of conservation concern occurring in areas of highly modified or degraded habitat within city boundaries may be less likely to be deemed significant. This is because decision-makers need to consider, among other factors, the ‘sensitivity of the environment which will be impacted’, as well as whether the action will lead to a long-term decrease in the size of a population (Department of the Environment, 2013, p. 5). Consequently, certain projects within cities may not trigger impact assessment and approval requirements because the long-term viability of the population or habitat is assessed as having already been compromised. This set of circumstances, particularly in the case of small-scale urban expansion, has the potential to lead to death by a thousand cuts, whereby incremental habitat destruction can lead to significant landscape-scale biodiversity loss (Dales, 2011; McAuley et al., 2013).

The aim of this study is to assess the extent to which threatened species are reliant on conservation within cities. To explore this we use the continent of Australia, which has very high endemic biodiversity (Chapman, 2009), as a case example, and investigate how the geographic distributions of species of national conservation concern overlap with urban areas. Specifically we measure how restricted the geographic ranges of threatened species are to cities, and whether this is different for plants and animals. Finally, we explore the potential contribution that individual cities can make to biodiversity conservation by examining how the composition of threatened species varies in different cities across the continent.

METHODS

Threatened species and city data

All 1643 species (1215 plants and 428 animals) that are considered to be of ‘national environmental significance’ under Australia’s EPBC Act were included in our analyses. This includes nationally listed threatened species, native migratory species listed under international conventions or agreements and marine species that use terrestrial areas for nesting (Commonwealth of Australia, 2014a). We hereafter refer to all of these species as ‘threatened species’. The listing criteria and categories used under the EPBC Act are adapted from those used to list species under the IUCN Red List of Threatened Species (Walsh et al., 2013), with the main difference being the absence of a ‘near threatened’ category from the EPBC Act, making the list more conservative (Commonwealth of Australia, 2014a). The majority of these species were from the flowering plant class Magnoliopsida (857 species) followed by lilies (Liliopsida, 289 species), birds (181 species), mammals (84 species) and reptiles (50 species).

Polygons representing the modelled distribution of each species were sourced from the Australian Department of the Environment’s ‘Environment Resources Information Network’ (Commonwealth of Australia, 2014b). The Australian government uses these data to inform management and policy decisions and to undertake preliminary assessments of whether proposed developments or land-use changes trigger targeted assessment and approval under the EPBC Act. The polygons were modelled from observation records, ecological data and information provided from a range of Australian government, industry and non-governmental organizations, in addition to national-scale environmental data. For migratory species, distributions refer only to breeding sites, sites of significance or known locations rather than the entire range of the species. The polygons are not intended to be definitive maps of species occurrence, and generalizations made in the modelling process preclude detailed analyses of species distributions at fine scales. However, a reasonable level of spatial certainty is possible because polygons were classified by the likelihood of species occurrence. For our analyses, only polygons where

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species are ‘known to occur’ (restricted to preferred habitat near observation records) and ‘likely to occur’ (preferred habitat within a species’ range) were used. Polygons indicating where species ‘may occur’ (areas within the environmental envelope or geographic region) were excluded. Polygons were projected to the Geocentric Datum of Australia 1994 Australian Albers, and clipped to a shapefile representing terrestrial areas (the Australian mainland, Tasmania and offshore territorial islands).

A layer representing the urban areas of Australia was derived from Australian Bureau of Statistics data (Section of State Ranges classification based on Statistical Area 1 polygons; Australian Bureau of Statistics, 2011a). This is a standard categorization of land in Australia, used by governmental and non-governmental agencies. According to the dataset, land was classified as ‘urban character’ if: (1) the urban ‘mesh block’ (the smallest census unit) population was ≥ 45% of the total population of the Statistical Area 1 polygon and dwelling density ≥ 45 dwellings km⁻²; or (2) the population density was ≥ 100 persons km⁻² and dwelling density ≥ 50 dwellings km⁻²; or (3) the population density was ≥ 200 persons km⁻² (Australian Bureau of Statistics, 2011b, p. 19). Only urban polygons with populations of over 10,000 were selected (hereafter referred to as ‘cities’ for simplicity), thereby excluding the smallest settlements. Following our criteria, the 99 cities in Australia cover 17,420 km² (0.23% of the terrestrial land mass), and range in size from 10.5 km² for Nelson Bay, New South Wales, to 2597.4 km² for Melbourne, Victoria (mean = 175.3 km², median = 50.0 km², SD = 420.2 km²). Although designated as ‘urban’ in character, the scale at which these areas were classified meant that they contained a range of land covers including both built and natural lands.

The importance of cities for threatened species

Using ArcMap (v.10.2, ESRI, Redlands, CA, USA), we identified areas where the city polygons intersected with threatened species distribution polygons. From this, we calculated the proportion of each species’ distribution that was urban and created a threatened species list for each city. To analyse the unique contribution of each city to the total assemblage of species located in urban areas, presence/absence species accumulation curves were generated using the ‘specaccum’ function in the ‘vegan’ package in R (R Core Team, 2014, v.3.1.0). We also generated a pairwise Jaccard dissimilarity matrix for the presence and absence of plant and animal species per city and carried out a hierarchical cluster analysis (using the ‘average’ linkage method and the ‘hclust’ function) to assess differences in community composition between cities. We then mapped mean dissimilarity values for each of the cities to help visualize patterns of beta diversity across the continent.

We converted the polygons representing threatened species to 1-km² resolution binary rasters using the ‘rasterize’ function in R’s ‘raster’ package (v.2.2–31). Raster cells were given a value of one if the centre of the cell overlapped with the associated polygon or zero if there was no overlap. We calculated the number of threatened species that were known or likely to occur in each cell by summing the values across all of the threatened species rasters.

As a conservative comparative analysis, we repeated the processes outlined above using only those polygons that represented where species were ‘known’ to occur. As the difference between these analyses was minimal (see Appendix S1 in Supporting Information) we consequently present only the results from the combined ‘known’ and ‘likely’ distributions here, as this includes the larger complement of species.

Mixed-effects models to account for potentially confounding factors

To account for potentially confounding environmental variables that might influence the threatened species richness of a city irrespective of urbanization, for each of our 99 ‘true’ cities we generated a paired ‘dummy’ city of equivalent area which was randomly positioned within the same bioregion (of which there are 89 across Australia). We then calculated both total threatened species richness of each true and dummy city and the mean richness of the raster cells that comprised them. Both total and mean threatened species richness were analysed using mixed-effects regression models in the ‘lme4’ package in R. Total threatened species richness was fitted as a generalized linear mixed-effects model against a Poisson distribution using a log link with the ‘glmer’ function, and mean threatened species richness as a linear mixed-effects model with the ‘lmer’ function. The models were fitted with five fixed predictor variables: (1) categorical city type (i.e. true versus dummy), (2) mean net primary productivity [NPP; calculated as the mean across the months of 2014 and downloaded as a 0.1” raster from NASA Earth Observations (2015)], (3) city area, (4) distance from the coast (measured from the nearest city edge), and (5) latitude. Continuous variables were centred and scaled prior to the analysis. The bioregion in which the true or dummy city occurred was fitted as a random effect in both models. We also noted that protected areas made up a substantially smaller proportion of the land mass in the true cities (mean = 0.03 ± 0.17 SD) than the dummy cities (mean = 0.12 ± 0.33 SD), but because this was strongly correlated with city type it was not included in the models.

RESULTS

The distribution of threatened species in cities versus non-urban areas

Of the 1643 threatened species in our analysis, 503 (30%) had distributions that intersected with cities. This proportion differed for plants and animals, with 25% of listed plants and 46% of listed animals having at least part of their distributions located in cities. Species distribution area varied considerably (many species had relatively small distributions and only a small number had very large distributions) but distribution area was not strongly correlated with the proportion of a species’ distribution located in cities (Spearman’s ρ = 0.33). The distributions
of animals (mean = 4,500,000 ha, median = 63,743 ha) tended to be much larger than those of plants (mean = 240,000 ha, median = 13,463 ha). Threatened species richness was higher in coastal areas and around the edges of cities (Fig. 1).

There was substantial variation in the degree to which the distributions of threatened species included cities. Species that were at least partially urban were found in an average of six cities (±11.8 SD). While some species were found in many cities (e.g. the eastern great egret *Ardea modesta* was found in 90 urban settlements), 258 threatened species (51%) occurred in one urban settlement only (Fig. 2a). The distributions of eight threatened species (all plants) entirely overlapped with cities, while 51 (10%) of the 503 threatened species found in cities had over 30% of their distribution in urban areas (Fig. 2b). Patterns were quite different for threatened plants and animals. Plants tended to be found in fewer cities (mean = 1.95 ± 2.34 SD) than animals (mean = 12.57 ± 16.63 SD) and were thus more spatially restricted, but had a larger proportion of their distribution contained within cities (plant mean = 0.16 ± 0.26 SD, animal mean = 0.04 ± 0.08 SD; Fig. 2).

**The importance of cities for threatened species**

All 99 cities were known to or likely to contain threatened animal species, and 88 cities (89%) contained threatened plant species or appropriate habitat (see Appendix S2 for city-specific details). Cities coincided with the distributions of substantially more threatened species than all other non-urban areas on a per-unit-area basis (Fig. 3). This was true for both animals and plants, with a very high proportion of non-urban cells containing no threatened plant species. The mean threatened species...
Figure 2 Plots of (a) species ranked according to the number of cities in which they occur and (b) the proportion of their distributions that fall in cities. Species are ordered on the x-axes by their rank, with species occurring in the most cities, or with the greatest proportion of their distribution as urban, assigned the rank of 1.

Figure 3 The proportion of 1-km² cells in Australia classified as either urban (white) or non-urban (grey) which support different numbers of threatened species. Data are presented for (a) all threatened species, (b) animals and (c) plants. Urban cells typically contain more threatened species than non-urban cells, as shown by the spread of the white bars to the right of the grey bars for all plots. Across Australia a small number of cells contained from 19 up to 32 threatened species, but the plot has been truncated at 18 along the x-axis because bars were not visible when the proportion was < 0.005.
richness for 1-km² city cells was 10.04 (± 3.79 SD), and 2.72 (± 2.88 SD) for non-urban cells.

On average, cities contained 32 threatened species (± 25.5 SD). Sydney contained the most threatened species (124 species), but only a few (large) cities contained a high diversity of threatened species (Fig. 4a). This was especially pronounced for plants, with only 12% of cities containing more than 10 threatened plant species (see Fig. 4a).

Individual cities contained distinct sets of threatened species, and contributed unique species to the total urban assemblage, with no evidence of an asymptote in the threatened species accumulation curves (Fig. 4b). This differentiation among cities was driven primarily by threatened plants. Hierarchical cluster analysis supported this result, demonstrating that few cities had a similar threatened species composition (Figs S3.1 & S3.2 in Appendix S3). The mean Jaccard dissimilarity score between cities for animals was 26.94 (± 3.63 SD), with Kalgoorlie-Boulder supporting the most unique animal assemblage and Port Macquarie the least (Fig. S3.3 in Appendix S3). Plant communities were even more dissimilar between cities, with a mean Jaccard dissimilarity score of 26.76 (± 3.76 SD); Kempsey supported the most unique plant assemblage while Taree’s assemblage was most similar to other cities (Fig. S3.4 in Appendix S3).

Our comparison of true versus non-urban dummy cities reinforced the findings of our broader analysis. As noted above, total threatened species richness ranged from 2 to 124 for true cities (mean = 31.49 ± 25.39 SD), and for dummies this range was 1 to 61 (mean = 12.12 ± 11.07 SD). The mean threatened species richness of cells was 0.19–18.36 for true cities (mean = 9.04 ± 3.78 SD) and 0.02–14.07 for dummies (mean = 7.26 ± 3.88 SD).

Regression modelling demonstrated that non-urban dummy cities had consistently lower total threatened species richness (coefficient estimate −0.84 ± 0.05 SE) and mean 1-km² cell threatened species richness (−1.67 ± 0.42 SE) than the true cities, even once potentially confounding factors had been accounted for (Fig. 5; see Appendix S4 for all coefficient estimates). Other factors which appeared to have strong effects on threatened species richness included NPP, which was positively associated with mean cell richness (1.15 ± 0.34 SE), and distance from the coast, which had a negative effect on both mean cell richness (−1.21 ± 0.38 SE) and total richness (−0.72 ± 0.09 SE; Fig. 5).

DISCUSSION

The importance of cities for conservation

This is the first study to demonstrate at a continental scale that cities contain more threatened species per unit area than non-urban areas. Our analyses have shown that all Australian cities harbour or are likely to harbour threatened species, and 30% of Australia’s threatened species occur, or are likely to occur, in cities that cover only 0.23% of the total land area. The elevated importance of cities for threatened species richness remained evident even when accounting for other biogeographic factors that may affect species richness, such as primary productivity, distance from the coast and latitude. This extends the findings of Schwartz et al. (2002), who revealed that 22% of the occurrences of endangered US plant populations were located in the 40 largest metropolitan areas (comprising 8.4% of the land area). We note, however, that these findings may be influenced by the fact that both Australian and US cities are relatively young on a global scale, and may be carrying extinction debts (Hahs et al., 2009). Further, it is likely that the regions defined as ‘urban’ in the present study contain a more heterogeneous composition of land covers than other studies in the literature. We therefore reaffirm the need for clear definitions of urbanization to be reported in urban biodiversity research, as has been called for by other scholars (McDonnell & Hahs, 2013).
The greater richness of threatened species in cities compared with equivalent non-urban dummy cities was more pronounced for total threatened species richness than for mean cell threatened species richness (Fig. 5). This suggests that the assemblages of threatened species in cities vary more greatly across their area than equivalent non-urban areas. Cities are known to have high levels of landscape heterogeneity (Alberti, 2005), with patches of remnant habitat commonly interspersed with highly disturbed areas. This landscape configuration may favour a wider variety of threatened species, thus increasing beta diversity and contributing to the higher total threatened species richness observed in cities. This is plausible in Australia where native ecosystems commonly remain within and around cities and adjacent to other land uses (Newton et al., 2001; Bekessy et al., 2012).

**Spatial patterning of species distributions**

The composition of threatened species varies among cities (Fig. 4b, Appendix S3). This suggests that the pattern identified by Aronson et al. (2014), whereby city biotas reflect regional species pools, extends to threatened species. This trend may be especially pronounced in Australia given that the cities included in our study cover a vast spatial area with huge variation in environmental conditions. Patterns were different for plants and animals. Unique sets of threatened plants were found in individual cities, while threatened animals tended to be found in multiple cities (Fig. 4b). These results strongly suggest that all cities ought to be considered carefully with regard to threatened species conservation and management.

We found that a small subset of threatened species were highly restricted to cities, and that this pattern was more pronounced for plants than it was for animals. Individual plant species were usually found within few cities; however a large proportion of their distribution was contained within those cities. In contrast, few animal species had a substantial share of their distributions located in cities (Fig. 2b). Most threatened plants in our dataset have relatively small distributions, and would be considered local endemics that are unique to certain bioclimatic regions of Australia. For example, the fringed spider-orchid Caladenia thysanochila is an endangered species with a small distribution, found entirely within a rapidly urbanizing region of Melbourne, Victoria (Department of the Environment, 2014). In contrast, some animals had very large distributions, occurring in 30 or more cities (Fig. 2a). This pattern of distribution for plants probably contributes to our finding of higher total threatened species richness per city than mean cell threatened species richness. Our finding that some threatened plants are found exclusively in urban environments is similar to that for North American floras (Schwartz et al., 2002) and highlights that cities can be important for the conservation of rare and unique plants.

**Implications for conservation policy and practice**

The disproportionate representation of threatened species in Australian cities identified in this study suggests that practitioners should seek to identify and act upon conservation opportunities in urban environments. It is important to note, though, that cities contain both opportunities for and threats to biodiversity conservation. The animals in our dataset included several nationally migrant and nomadic species, such as the grey-headed flying-fox, Pteropus poliocephalus (Eby & Collins, 1999), and swift parrot, Lathamus discolor (Swift Parrot Recovery Team, 2001), that move across large areas as food resources (e.g. nectar, fruit or blossoms) become seasonally available. Often these resources are found in non-remnant, human-modified habitats. Indeed, Carnaby’s black cockatoo, Calyptorhynchus latirostris, relies on an introduced pine plantation within the city of Perth for food, despite the fact that this represents a comparatively small proportion of its range (Valentine et al., 2014).
Cities may be especially valuable to these kinds of species, as they can provide more stable resources throughout the year as a result of human planting selection and supplementary watering (Parris & Hazell, 2005; Williams et al., 2006). In contrast, other species rely on remnant patches of vegetation for their survival, many of which are under threat or in a degraded condition. The fringed spider-orchid, for example, is unlikely to persist if its remaining historical habitat is developed for housing, and its occurrence may even represent an extinction debt given the amount of habitat remaining. Irrespective of whether threatened species are threatened by urbanization or supported by urban conditions, this study highlights the need for conservation action in cities. Depending on the nature of conservation threats and opportunities, a suite of conservation tools should be employed, such as spatial planning of urban development (e.g. Bekessy et al., 2012), focused recovery planning and active management, restoration and improvement of habitats (Hahs et al., 2009; Standish et al., 2012).

Caveats and future research opportunities

As with any spatial data compiled from multiple sources over a period of time, our species data may contain mapping errors. The most pertinent errors are those of commission and omission as a result of incomplete and unequal sampling effort. Few systematic biodiversity surveys have been conducted in Australia, yet those that have been done have often excluded urban areas (e.g. the regional forest agreement process; Slee, 2001). On the other hand, it is possible that ad hoc databases may have an over-representation of urban records, as survey effort will arguably be greater in more populous areas. Ultimately, despite any inaccuracies, the results presented here are noteworthy since the datasets are those used by decision-makers when assessing development applications and generating species recovery plans. Nevertheless, while our conservative analysis indicated that modelling assumptions did not have a large impact on our inference relating to the distribution of threatened species in cities, future research could explore the role of possible sampling biases further.

Finally, we note that while the presence of a population in a location does not indicate its fitness or long-term viability in that location, it signals a potential conservation opportunity. In their multidisciplinary review of 787 urban biodiversity conservation studies, Shwartz et al. (2014) found only eight papers that reported similar or improved levels of population viability of species of conservation significance in urban areas compared with nearby greener environments. Yet the authors also note that only three studies specifically set out to test this condition of viability, all of which reported in the affirmative. From these results Shwartz et al. (2014) concluded that ‘the importance of urban areas for general conservation is not convincingly supported by scientific research’ (p. 43). Nevertheless, we argue that even if threatened species experience lower levels of population viability in urban environments, their over-representation in these areas makes cities even more important for conservation management and planning, noting too that doing nothing may reduce viability even further. We echo the call of Shwartz et al. (2014) for further research into the population dynamics of significant species in cities as a way of shedding light on ecological mechanisms that influence species persistence, as it can help determine the specific conservation actions that are required.

CONCLUSION

Using Australia as a case example, this study is the first to demonstrate at a continental scale that cities contain disproportionately more threatened species than equivalent non-urban areas. Some species (particularly plants) have a much greater proportion of their distribution within urban areas than others, and all Australian cities are home to different suites of threatened species. These findings highlight and reinforce the global importance of planning and managing urban landscapes to conserve biodiversity (Secretariat of the Convention on Biological Diversity, 2012). We recommend that practitioners consider seriously the contribution that urban environments could make to national biodiversity conservation, and incorporate this information into species recovery planning.

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**SUPPORTING INFORMATION**

Additional Supporting Information may be found in the online version of this article:

**Appendix S1**  Comparative analysis between known and known and/or likely to occur distributions

**Appendix S2**  List of Australian cities, with human population size and total, animal and plant threatened species richness.

**Appendix S3**  Analysis of differences in threatened species composition between cities including hierarchical cluster analysis of (1) animals and (2) plants, and maps of mean threatened species community similarity across Australia for (3) animals and (4) plants.

**Appendix S4**  Models of (1) total city threatened species richness and (2) mean 1-km² cell threatened species richness for true cities versus dummy cities (non-urban controls).

**BIOSKETCH**

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