Continental-scale urbanness predicts local-scale responses to urbanization

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Abstract

Understanding species-specific relationships with their environment is essential for ecology, biogeography, and conservation biology. Moreover, understanding how these relationships change with spatial scale is critical to mitigating potential threats to biodiversity. But methods which measure inter-specific variation in responses to environmental parameters, generalizable across multiple spatial scales, are lacking. We used broad-scale citizen science data, over a continental scale, integrated with remotely-sensed products, to produce a measure of response to urbanization for a given species at a continental-scale. We then compared these responses to modelled responses to urbanization at a local-scale, based on systematic sampling within a series of small cities. For 49 species which had sufficient data for modelling, we found a significant relationship (R^2= 0.51) between continental-scale urbanness and local-scale urbanness. Our results suggest that continental-scale responses are representative of small-scale responses to urbanization. We also found that relatively few citizen science observations (~250) are necessary for reliable estimates of continental-scale species-specific urban scores to predict local-scale response to urbanization. Our method of producing species-specific urban scores is robust and can be generalized to other taxa and other environmental variables with relative ease.

Keywords: citizen science; species-environment relationships; spatial scales; urbanization; urban ecology; eBird

Introduction

Understanding species-environment relationships (Mertes and Jetz 2018) is a critical and unifying goal in ecology (Hutchinson 1953, Levin 1992), biogeography (Currie and Paquin 1987, Hawkins et al. 2003), and conservation (Guisan et al. 2013, Duflot et al. 2018). A thorough and generalized understanding of how species respond to their environment should translate to an increased ability to mitigate potential threats, ultimately preserving biodiversity (Paterson et al. 2008, Tilman et al. 2017). Chief among these potential threats are anthropogenic changes (Tilman 1999, Hautier et al. 2015), such as climate change (Hampe and Petit 2005), species invasions (Ricciardi et al. 2017), and land use changes (Vandewalle et al. 2010). Yet the scale-dependence of species-environment relationships remains complex and unresolved (Mertes and Jetz 2018): for example, 10% of studies show biodiversity changes which switch directions across scales (Chase et al. 2018). Empirical analyses are desperately needed to inform understanding of the patterns and mechanisms relating to scale-dependence of species-environment relationships (Holland et al. 2004).

Our current understanding of spatial-scale dependence of biodiversity responses to land-use is commonly derived from aggregated biodiversity metrics (Gotelli and Colwell 2001), including: species richness (Whittaker et al. 2001, Weibull et al. 2003, Diniz-Filho and Bini 2005, McKinney 2008, Concepción et al. 2016, Zellweger et al. 2016), various measures of species diversity (He et al. 1996, Meynard et al. 2011, Morlon et al. 2011, Roeselers et al. 2015, Salazar et al. 2016), or other functional groupings (Devictor et al. 2008, Clavel et al. 2011, Gámez-Virués et al. 2015, Deguines et al. 2016). Even when assessing species-specific responses to environmental relationships, a general approach is to categorize species based on a priori knowledge in how they respond to a particular environmental parameter, or use a simple measure of abundance from a limited spatial scale (McKinney 2002, 2006, Bonier et al. 2007, Kark et al. 2007, Møller 2009, Pelletier et al. 2010, McDonnell and Hahs 2015, Geschke et al. 2018). While this approach is analytically and conceptually simple, it assumes that species within groups respond equally (Lepczyk et al. 2008, Evans et al. 2011), limiting our understanding of the complex mechanisms influencing how organisms respond to their environment. Characterizing how biodiversity responds to its environment should be species-specific (Cushman 2006, Ewers and Didham 2006, McGarigal et al. 2016, Yackulic and Ginsberg 2016, Vargas et al. 2017, Mertes and Jetz 2018).

This is particularly true for anthropogenic land use changes (Suárez-Seoane et al. 2002), such as urbanization (Gehrt and Chelsvig 2004, Russo and Ancillotto 2015). By accounting for species-specific responses relative to one another, environmental planners can accordingly mitigate urbanization responses for the least urban-tolerant species. By 2030, 10% of the earth's landmass is projected to be urbanized (Elmqvist et al. 2013), making increasing urbanization — and its associated habitat loss, fragmentation, and degradation — a significant anthropogenic threat to the world's biodiversity (Elmqvist et al. 2016, Sanderson et al. 2018). Much research has informed our understanding of the negative impacts of urbanization on biodiversity (McKinney 2002, McDonald et al. 2008, Vimal et al. 2012, Huang et al. 2018), but this understanding is still lacking unified theories across spatial scales, with repeatable and robust methods.

A traditional hurdle in providing species-specific responses to their environment at various spatial scales has been the cost of data collection: it is expensive to collect voluminous amounts of data at the necessary spatial and temporal scales for generalizable inferences. This hurdle necessarily limits the spatial scale of a particular study as well as the number of species being investigated. Unsurprisingly, then, the majority of studies have been conducted at somewhat localized scales — predominantly characterizing intra-city responses (Dickman 1987, Cornelis and Hermy 2004, e.g., Parsons et al. 2006, Bickford et al. 2010, Hedblom and Söderström 2010, Bates et al. 2011, Fontana et al. 2011, Lizée et al. 2012, Concepción et al. 2016). This local understanding is directly applicable for greenspace management within cities, aimed at maintaining high levels of biodiversity (Borgström et al. 2006, Perring et al. 2015, Aronson et al. 2017). But local-scale data is rarely available within a specific city, limiting environmental planners' ability to make informed decisions. And a wide variety of studies investigate different spatial extents and grains (Forman and Gordon 1986, Turner et al. 1989), with little unifying theory for informed decisions and generalizable patterns. Fortunately, we now have access to broad-scale empirical datasets numbering millions of observations — generally collected through citizen science programs (e.g., Sullivan et al. 2009, Prudic et al. 2017, Van Horn et al. 2018) — revolutionizing ecological and conservation research (Cooper et al. 2007, Silvertown 2009, Pocock et al. 2018). Simultaneously, the field of remote sensing is rapidly advancing (Kwok 2018), with increasing numbers of sensors, targeted missions for ecology (Wikelski et al. 2007, Bioucas-Dias et al. 2013, Jetz et al. 2016), freely available data, and improved access to data analysis pipelines (Gorelick et al. 2017, Murray et al. 2018). These biodiversity data, combined with remotely sensed data, are increasing our understanding of biodiversity responses to environmental change (Pettorelli et al. 2014a, 2014b, 2016), especially at macro-ecological scales (Hochachka and Fink 2012, La Sorte et al. 2014, Horton et al. 2018). But in regards to urbanization, how well do macro-ecological responses correspond with local-scale responses? If species-specific responses at broad spatial scales sufficiently predict local-scale responses, then environmental planners can make predictions for their local fauna, based on continental generalizations.

We assessed how bird species respond to urbanization across spatial scales, testing whether species-specific responses (i.e., changes in abundance relative to urbanization levels) to urbanization at a continental scale predict species-specific responses to urbanization at local scales. To do so, we integrated two disparate datasets with different spatial extent and grain (Turner et al. 1989): (1) continental-scale species-specific responses to urbanization based on globally available remotely-sensed data and (2) local-scale modelled responses to urbanization, derived from systematic sampling. The former relies on novel methods to assign species-specific continental urbanization responses, integrating broad-scale biodiversity data — collected through one particularly successful citizen science project: eBird (Sullivan et al. 2009, 2014, Wood et al. 2011) — with remotely-sensed landcover maps of continuous measures of urbanization. These data are then tested against local-level bird surveys within small cities.

Methods

Continental species-specific responses to urbanization

eBird (Sullivan et al. 2009, 2014, Wood et al. 2011, Callaghan and Gawlik 2015), launched in 2002 by the Cornell Lab of Ornithology, has > 600 million global observations and formed the data basis of the continental-scale species-specific responses. eBird works by enlisting volunteer birdwatchers who submit bird observations in the form of ‘checklists’ — defined as a list of birds seen or heard in a specified area. An extensive network of regional volunteers (Gilfedder et al.

2018) use their local expertise to provide filters for the submissions, limiting observations based on unexpected species or abundances of species. If an observation trips a filter then it is reviewed before inclusion in the database. More detailed information on eBird protocols are provided in (Sullivan et al. 2014).

Species-specific scores

We used continental eBird data to assign species-specific urban scores for each species in the analysis. This approach borrows from the longstanding theory behind urban adapters, avoiders, and exploiters (McDonnell and Hahs 2015, e.g., Geschke et al. 2018), and works theoretically by assessing how a species responds to a continuous level of urbanization (Fig. 1). For example, an urban avoider would have a predicted distribution of observations with very few in or near high levels of urbanization (Fig. 1).

We first filtered all eBird data to the best quality lists, removing potential outliers, (e.g., La Sorte et al. 2014, Callaghan et al. 2017). This was done by including only complete eBird checklists — where the observer recorded all birds heard and/or seen — from mainland Australia, which followed the travelling, random, stationary, area, or BirdLife Australia protocols. We then filtered these checklists to checklists which recorded birds between 5-240 minutes and travelled less than 5 km or less than 500 Ha area searches (La Sorte et al. 2014, Callaghan et al. 2017, 2019b, Johnston et al. 2018), minimizing the chance that outliers would be included in the analyses. All checklists shared among multiple observers were randomly subsampled, and all seabirds were omitted from the potential suite of species. Only species with a minimum of 100 observations were considered for this analysis. Following filtering, each eBird checklist was assigned a measure of urbanization — on a continuous scale. This was done by taking the average radiance of night-time lights within a 5 km buffer of each checklist. A buffer was used to minimize any bias in eBird sampling protocols (e.g., mis-placement of eBird checklists by participants) and the size of the buffer has no discernible influence on the urban-score differences among species (Callaghan et al. 2019a). We used the VIIRS night-time lights (Elvidge et al. 2017) as a proxy for urbanization (Pandey et al. 2013, Zhang and Seto 2013, e.g., Stathakis et al. 2015) because of its global availability and ease of use with Google Earth Engine (Gorelick et al. 2017). And this approach shows strong agreements with other measures of urbanization such as human population density (Callaghan et al. 2019a, 2019b). Each species was then assigned a measure of their response to urbanization, which was defined as the median of a species' distributional response to urbanization. For more methodological details, and a published list of species-specific urban scores, see (Callaghan et al. 2019a, 2019b). Note that exotic species were excluded from Callaghan et al. 2019, but were included in this analysis.

Local-scale species-specific responses to urbanization

We conducted bird-surveys within the Greater Blue Mountains World Heritage Area (GBWHA), which is ~ 10,000 km^2 and lies about 180 km from Sydney, New South Wales, Australia. Within a strip of linear conurbation, we designed transects through each of four cities within this conurbation (Fig. S1). Points were spaced ~ 500 m apart on each transect. Woodford, Lawson, and Hazelbrook had 5 points each, while Katoomba (the largest city) had 9 points (Fig. S1). Between August 2017 and August 2018, transects were visited twice per month (N=576), and 5-min point-counts were conducted at each point, with all birds heard or seen counted. Surveys were conducted only conducted on days with fine weather (i.e., no rain and minimal wind), and surveys were completed between sunrise and 5 hrs after sunrise. Transects, as well as order of transects were randomized so that the same transect was not being conducted first every month. We visually estimated the degree of urbanization at each point as the percent impervious surface within a 250-m radius buffer surrounding that point, using recent aerial photography from Google Earth Pro (*sensu* Blair 1996; Fig. S2). The percent impervious surface was chosen as it is a direct measure of urbanization, and generally readily available at local-scales for urban planners, whereas VIIRS night-time lights is at 500-m resolution, not generally applicable at a small-scale. Hence, we are comparing different spatial grains, albeit measuring the same environmental response.

In order to extract species-specific responses to urbanization at a local scale, we modelled the number of observations of a species against the percent impervious area at each survey point, summed across all visits. We fitted Generalized Linear Mixed Models (GLMMs; Bolker et al. 2009) with a Poisson distribution, where the random effect was transect (i.e., city). This model was separately fitted to each species, and the regression coefficient for the impervious surface area predictor for a given species was taken as the species-specific response to urbanization at a local scale. Only species with a minimum of 10 nonzero observations were considered for the GLMMs, ensuring that models would converge. Although species in the study region can show some seasonal movement, this was not included in our models to minimize over-fitting, given the sample size of the number of points. Additionally, many of the seasonal species were excluded from analyses based on our cut-off for minimum of nonzero observations. Our initial exploration considered negative binomial model distributions, but AIC was consistently lower for poission than negative binomial, and more species failed to converge due to differing theta parameter estimations (i.e., only 44 species would have bene included in final comparisons). Thus, we specified our models with poission distributions to maximize the number of species which could be compared with continental-scale species-specific urban scores. But the results were similar when comparing the modelling approaches. Models were fit using the ‘glmer’ function from the lme4 package (Bates et al. 2015).

Regression of continental and local-scale urban measures

We observed a total of 94 species on our local-scale bird surveys (Appendix S1). Fifty-one species had > 10 nonzero observations (Appendix S1) and were thus considered for GLMMs. After initial modelling, two species were further eliminated from analyses as their estimates from the GLMM were outliers when compared with the rest of the dataset (Pilotbird and White-eared Honeyeater; Appendix S2). Thus, 49 species were regressed against their log-transformed continental-scale species-specific urban scores, using the ‘lm’ function in R.

Assessing necessary number of citizen science observations for reliable estimates

We re-ran our linear model, multiple times, calculated with different numbers of samples used to calculate continental-scale species-specific urban scores (i.e., the median of the distributional response to night-time lights), in order to assess the number of citizen science observations necessary for reliable estimates. We re-calculated the urban scores based on the use of 10 to 1000 randomly sampled eBird observations, by increments of 10. For each of these different sets of urban scores (N=100), we again regressed the log-transformed variables against the static local-scale responses.

Results

A total of 94 species were observed on our local-level transects (Appendix S1). The species that was most likely to be associated with urbanization at the local-scale was Rock Pigeon (parameter estimate: 0.14), while the species least likely to be associated with urbanization at a local-scale was Rufous Whistler (parameter estimate: -0.88; Fig. S3). Similarly, Rock Pigeon had the highest continental-scale species-specific urban score (12.49) while Red-capped Robin had the lowest continental-scale species-specific urban score (0.047). Of the 49 species included in analyses, the mean urban score was 2.37 Â± 2.81 (Fig. S4). Thus, Rock Pigeon had both the highest local-urban score and continental-urban species-specific score, while Superb Lyrebird had the lowest local-urban score and the second lowest continental-urban species-specific score (cf. Fig. S5 and Fig. S6).

Continental species-specific urban scores significantly predicted ($t=6.95$, $df=47$, $p < 0.001$) the localized urban scores with an R^2 of 0.51, and the relationship was even stronger ($t=8.93$, $df=47$, $p < 0.001$, $R^{2=}0.63$) when the model was weighted by the standard error of the local-scale urban scores' parameter estimates, to reduce distortion by species with small sample sizes. Even without this correction, the relationship appears to be robust to the number of underlying samples per species used to calculate the continental urban score. Indeed, of 100 different models, based on sample sizes from 10 to 1000 there was little differentiation in the underlying relationship (Fig. 2a), and the R^2 for these models quickly leveled off after ~ 250 observations (Fig. 2b).

Discussion

Urbanization will continue to impact biodiversity in a multitude of ways (Elmqvist et al. 2016), and understanding species-specific responses to urbanization (Gehrt and Chelsvig 2004) is essential to understand how to best mitigate the threats to native fauna (Møller 2010), especially those most at-risk. Indeed, much research has investigated which biological and ecological traits are associated with urban-adapted birds in an attempt to identify those species most at-risk (Kark et al. 2007, Croci et al. 2008, Evans et al. 2011, Callaghan et al. 2019b). We provide significant methodological enhancements to these approaches, serving as a foundation for future studies to investigate the ecological and conservation validity of how biodiversity responds to urbanization. This method moves past the traditional notion of characterizing species based on known responses to urbanization (Kark et al. 2007, Geschke et al. 2018), instead relying on continuous measures of inter-specific variation, although we note that species can indeed be clustered into those which respond to urbanization positively, negatively, and show mixed responses (e.g., Fig. 1). The difference, however, is that these characterizations are informed, incorporating the inter-specific variation which exists. We integrated two disparate datasets: semi-structured citizen science data and systematic bird-sampling at a local scale, demonstrating that continental-scale responses to urbanization sufficiently predict local-scale responses to urbanization. Furthermore, we found that a relatively small number of observations (~250) are needed to provide reasonable estimates of local-scale responses to urbanization, highlighting the potential applications of broad-scale citizen science data.

There is the temptation to ‘think big’, and address macroecological questions, given we are in the midst of a ‘big-data’ revolution in ecology (Hampton et al. 2013, Soranno and Schimel 2014). Simultaneously, advances in sensor-based data collection (e.g., satellite remote sensing) are increasing environmental monitoring efforts, and an increased commitment to collating and sharing spatially explicit biodiversity records (i.e., point observation data) (Turner et al. 2015) for a range of taxa are increasing our understanding of biodiversity at spatial scales unimaginable mere decades ago. We acknowledge that these data are rapidly expanding our ability to monitor biodiversity at global scales (Chandler et al. 2017, McKinley et al. 2017, Vihervaara et al. 2017). But many policy-relevant decisions happen at local scales, and the utility of these data needs to be empirically grounded in local-relevance (e.g., Callaghan and Gawlik 2015, Sullivan et al. 2017). Adaptive governance systems, supporting practical management at local-scales are necessary for environmental planners to sufficiently mitigate the impacts of urbanization on biodiversity (Borgström et al. 2006). At the same time, local-decisions should be grounded at several spatial scales (Borgström et al. 2006), accounting for the diverse biodiversity responses. Often, however, such data are unavailable for environmental planners. Our results provide empirical evidence that continental-scale data reflects local-scale relevance, albeit within one localized study site. Although we investigated local-impacts at a small-scale (i.e., small cities), similar patterns would likely emerge for medium and large-sized cities, because we would expect the most significant differences between continental-scale responses to urbanization and smaller-scale responses would be most discernible when comparing small-scale cities, as opposed to medium and large-sized cities.

This methodological approach is in its infancy, and we highlight here some potential opportunities for future research. First, and foremost, this approach is applicable across taxa, reliant mainly on spatial coordinates of a large number of sightings. Although our analysis is focused on species-specific responses to urbanization, we highlight that these procedures can be repeated with other environmental factors (e.g., tree-cover, water-cover). These data have the ability to move beyond species-specific measures to community-level measures of response to urbanization (Callaghan et al. 2019a). Although we focused on measuring inter-specific variation, this approach may be able to be used to measure intra-specific variation, informing how local populations are adapting to anthropogenic change (e.g., González-Oreja 2011). We currently use large amounts of data to provide a 'snapshot' of how birds are currently responding to urbanization. But many species change their responses through time, showing localized adaptations (Evans et al. 2009, Martin et al. 2010, Yackulic and Ginsberg 2016). In time, this approach should be able to confidently measure species-specific responses to urbanization through time. Last, this approach should be adopted to regions where the fauna have differing migration strategies, thereby assessing species-specific responses to urbanization intra-annually.

Citizen science data is radically shaping the spatial and temporal scale with which ecological questions are being answered (Dickinson et al. 2012, Kobori et al. 2016), and this is particularly true within urban areas (Cooper et al. 2007, Callaghan et al. 2018). We do not suggest that systematic sampling should be replaced with citizen science data, but rather, that they can compliment one another to provide a more generalized understanding (Bayraktarov et al. 2019). Nevertheless, methods such as the one we validated here will be essential to track biodiversity responses to urbanization into the Anthropocene.

Data accessibility

Code and data necessary to reproduce these analyses have been uploaded as supplementary material alongside this manuscript, and will be made available as a permanently archived Zenodo repository upon acceptance of the manuscript.

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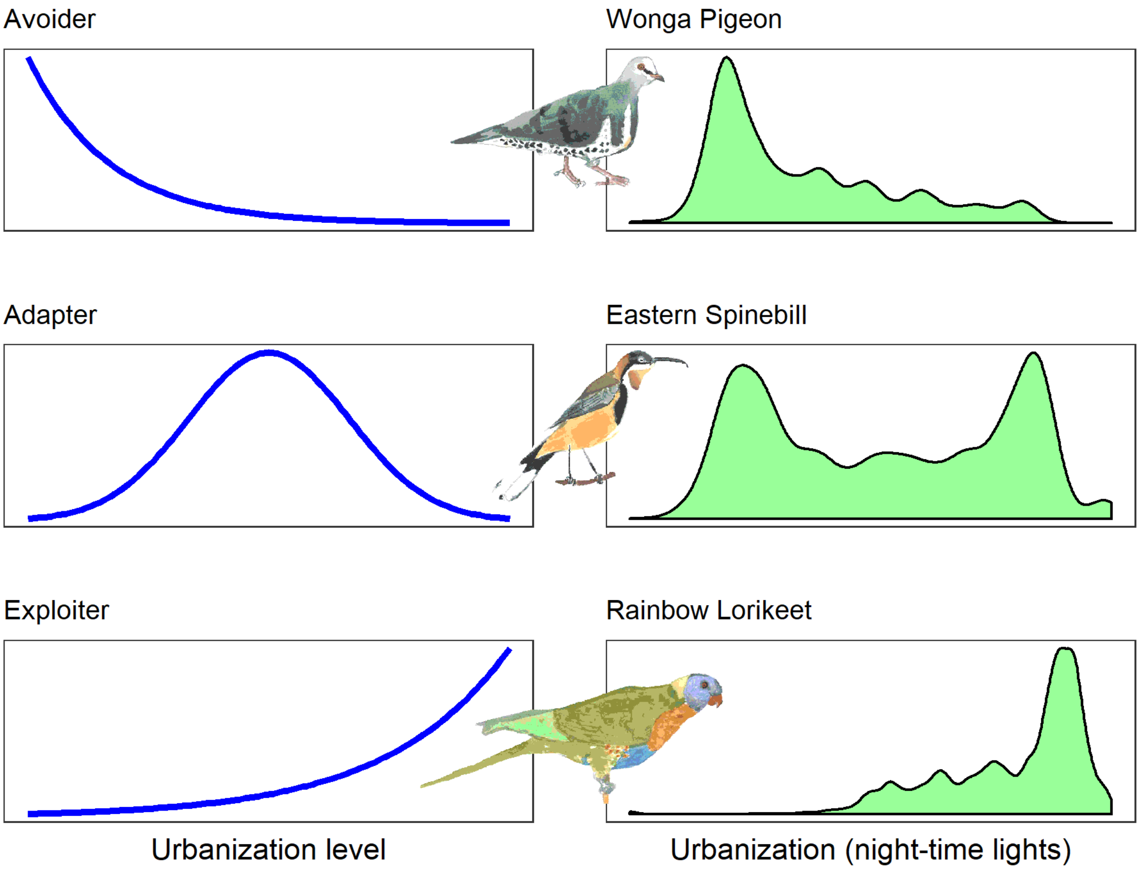
Figure Legends

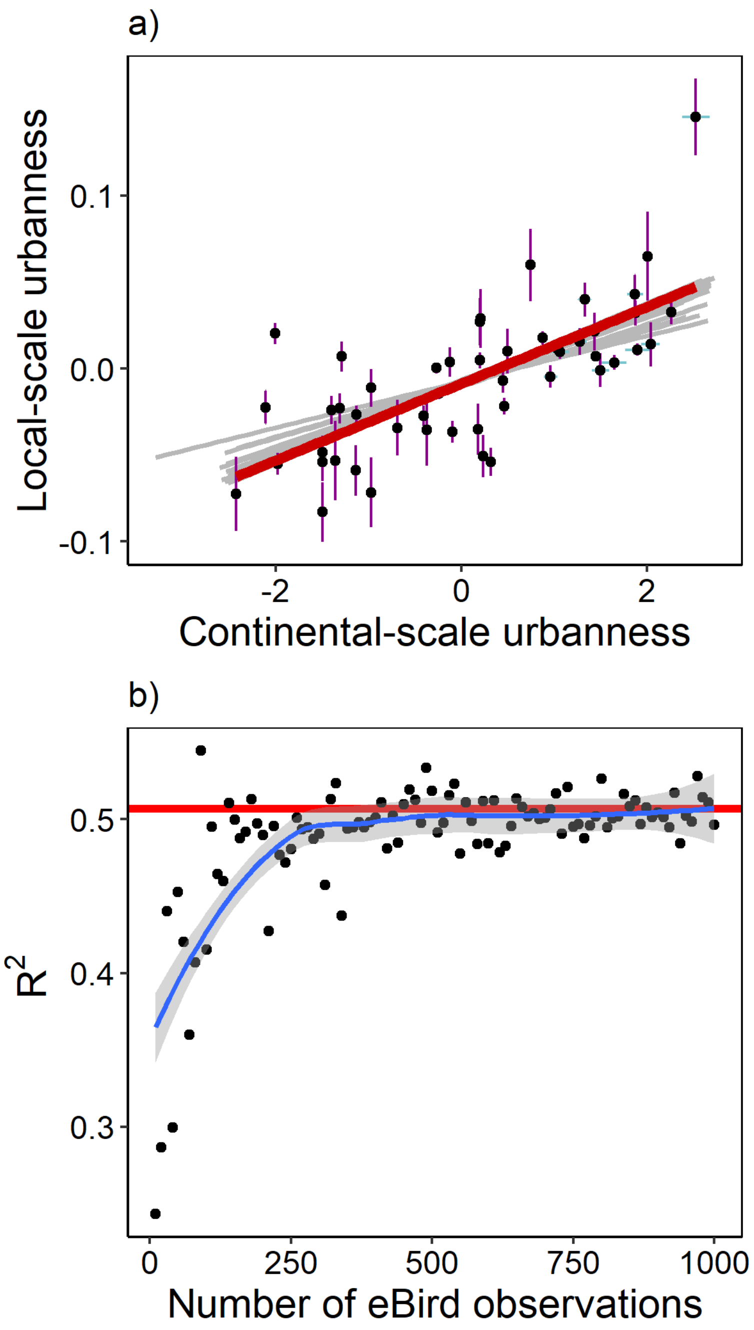
Figure 1. The theoretical expected distributions for the three types of commonly assigned responses to urbanization: urban avoider, urban adapter, and urban exploiter. Also, showing three species' distributions in response to night-time lights based on their eBird data observations, demonstrating an 'example' species for each of these theoretical distributions. The y-axis represents the density of observations that occur along the urbanization level. The real data was based on responses to VIIRS night-time lights, where radiance is on the x-axis, but this urbanization level could be a number of other metrics.

Figure 2. a) Regression of log-transformed continental-scale urbanness versus local-scale urbanness for 49 species. Standard error is shown for local-scale urbanness as the standard error retreived from each Generalized Linear Model, whereas standard error for the continental-scale urbanness are boot-strapped standard error estimates for the median of a species' response to urbanization. Each gray model fit shows a model fit for 100 different models, each with 10-1000 data points (by 10) used to calculate the continental-scale urbanness. The red line of best fit shows the linear model results, using all available observations for each species. b) R^2 for each of the 100 different linear models fitted, using 10-1000 data points to calculate the continental-scale urban scores.



Avoider
Wonga Pigeon
Adapter
Eastern Spinebill
Exploiter
Rainbow Lorikeet
Urbanization level
Urbanization (night-time lights)

Figure 1.



a)
Local-scale urbanness
0.1
0.0
-0.1
-2
0
2
Continental-scale urbanness
b)
R^2
0.5
0.4
0.3
0
250
500
750
1000
Number of eBird observations

Figure 2.

Appendix S1. A table of the 94 species observed in the Blue Mountains and the total number of observations for each species. Also included is the number of continental observations, from eBird, used to assign continental-scale urban scores. Only species with > 10 local records were considered for analysis, and 2 were removed as outliers (Appendix S2).

Species	Number of local observations	Number of continental observations	Included in regression
Eastern Spinebill	412	27990	Yes
Red Wattlebird	390	84046	Yes
Sulphur-crested Cockatoo	383	80030	Yes
Pied Currawong	291	65858	Yes
Crimson Rosella	269	45991	Yes
Australian Magpie	229	158615	Yes
Yellow-faced Honeyeater	210	35557	Yes
White-throated Treecreeper	179	28238	Yes
Spotted Pardalote	117	36944	Yes
Rainbow Lorikeet	111	117290	Yes
Brown Thornbill	108	48114	Yes
Satin Bowerbird	108	12580	Yes
Gray Butcherbird	104	59384	Yes
Australian King-Parrot	103	22845	Yes
New Holland Honeyeater	96	39402	Yes
Gray Fantail	93	77707	Yes
Common Myna	74	62497	Yes
Silver-eye	70	58159	Yes
Rock Pigeon	66	29618	Yes
Australian Raven	65	53001	Yes
Rufous Whistler	59	38256	Yes
Eastern Yellow Robin	52	35185	Yes
Gray Shrikethrush	49	50951	Yes
Eurasian Blackbird	48	43878	Yes

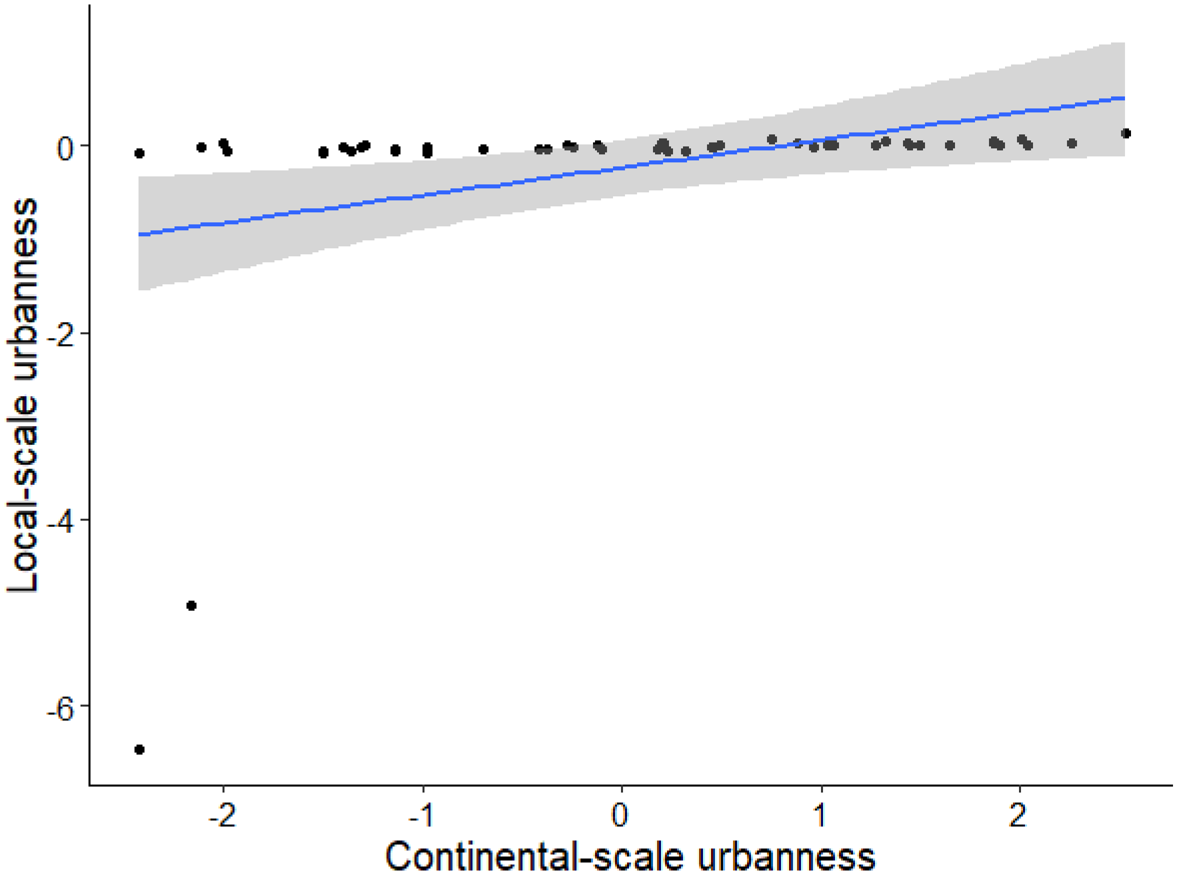
White-naped Honeyeater	48	9612	Yes
Striated Thornbill	44	11878	Yes
Eastern Whipbird	42	29452	Yes
Laughing Kookaburra	41	70107	Yes
White-browed Scrubwren	40	43541	Yes
Fan-tailed Cuckoo	38	15908	Yes
Pacific Koel	36	15357	Yes
House Sparrow	35	36193	Yes
Superb Lyrebird	34	4247	Yes
Lewin's Honeyeater	33	35617	Yes
Yellow-tailed Black-Cockatoo	33	13862	Yes
Golden Whistler	29	31744	Yes
Little Wattlebird	23	28734	Yes
Black-faced Cuckooshrike	19	55254	Yes
Galah	19	80009	Yes
Crested Pigeon	18	69964	Yes
Superb Fairywren	17	86836	Yes
Noisy Miner	16	89821	Yes
Welcome Swallow	15	109006	Yes
Magpie-lark	14	131621	Yes
White-eared Honeyeater	14	9179	No
Noisy Friarbird	13	25532	Yes
Red-whiskered Bulbul	13	4524	Yes
Scarlet Myzomela	13	14387	Yes
Masked Lapwing	12	80029	Yes
Mistletoebird	11	25640	Yes
Pilotbird	11	749	No
Channel-billed Cuckoo	10	9686	Yes

Gang-gang Cockatoo	9	5248	No
Leaden Flycatcher	9	13615	No
Tree Martin	8	18471	No
Variegated Fairywren	8	15152	No
Wonga Pigeon	8	7094	No
Red-browed Treecreeper	7	1286	No
Sacred Kingfisher	7	25194	No
Brown-headed Honeyeater	6	7435	No
Little Corella	6	30860	No
Shining Bronze-Cuckoo	6	9331	No
Brown Cuckoo-Dove	5	10589	No
Red-browed Firetail	5	33456	No
Brown Gerygone	4	9410	No
Common Cicadabird	4	6728	No
Maned Duck	4	56221	No
Scarlet Robin	4	7211	No
Crescent Honeyeater	3	3293	No
Crested Shrike-tit	3	3933	No
Olive-backed Oriole	3	22539	No
Striated Pardalote	3	44295	No
Wedge-tailed Eagle	3	11006	No
Australian Owlet-nightjar	2	2836	No
Black-faced Monarch	2	6181	No
European Starling	2	53070	No
Long-billed Corella	2	10453	No
White-throated Needletail	2	3515	No
Beautiful Firetail	1	906	No
Brown Goshawk	1	9918	No

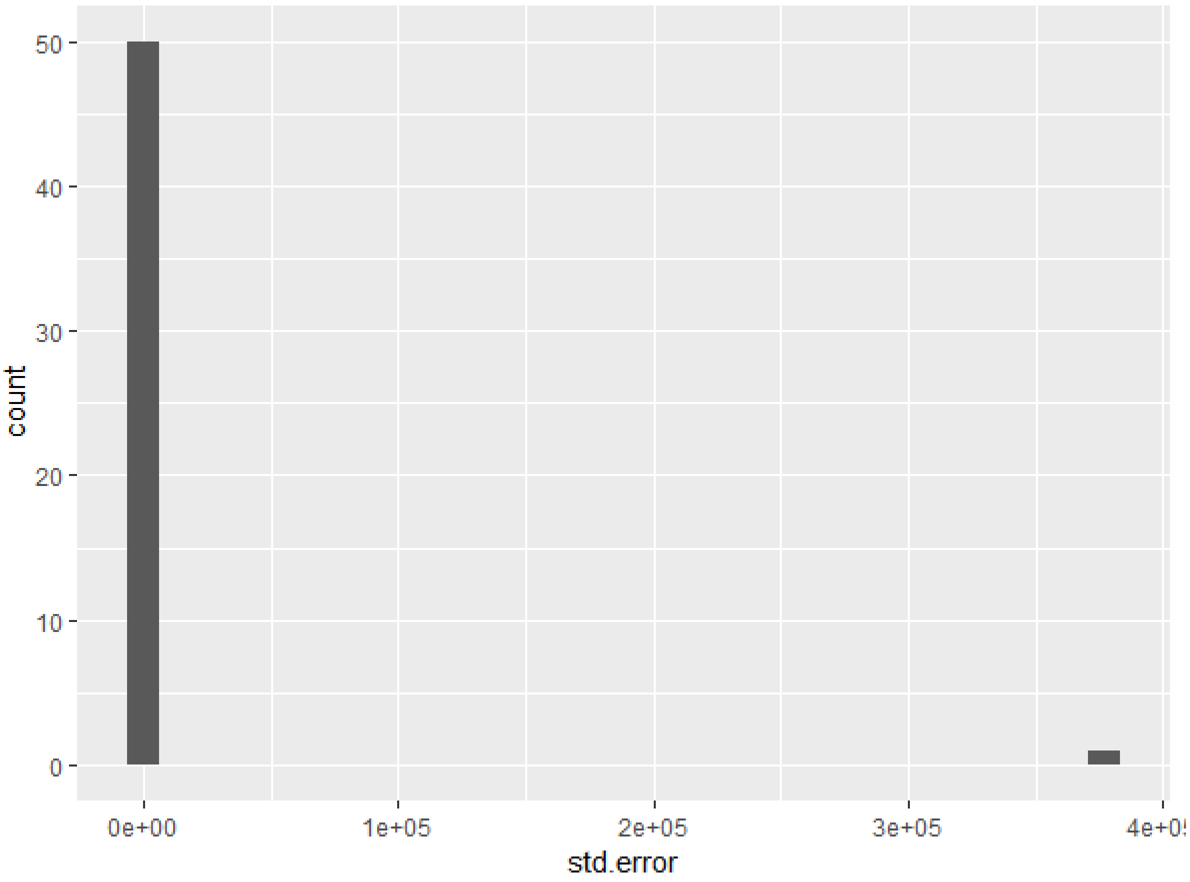
Buff-rumped Thornbill	1	7033	No
Collared Sparrowhawk	1	4270	No
Common Bronzewing	1	15076	No
Fuscous Honeyeater	1	4085	No
Horsfield's Bronze-Cuckoo	1	8035	No
Little Lorikeet	1	4865	No
Peregrine Falcon	1	2960	No
Red-capped Robin	1	4299	No
Rufous Fantail	1	10113	No
Spotted Quail-thrush	1	423	No
Varied Sittella	1	4854	No
White-headed Pigeon	1	4069	No
Willie-wagtail	1	106114	No
Yellow Thornbill	1	12237	No

Appendix S2. Methods used to identify and eliminate outliers from analyses. Outliers were for species which had poor model-fit at the local-scale, and only considered species at the local-scale, based on GLMM model fits.

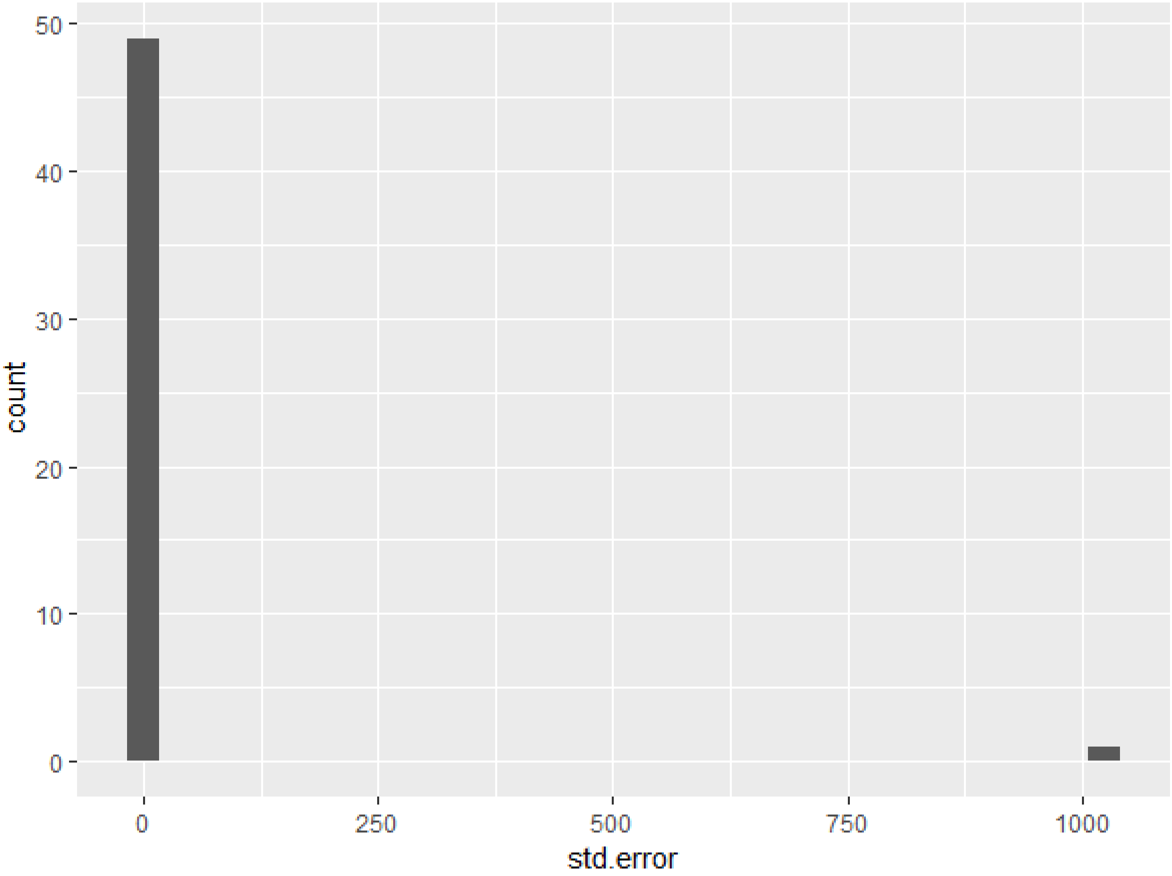
1.) Investigated relationship between all 51 species' parameter estimates and their continental-scores – 51 species had > 10 observations, meeting our a priori cut-off for modelling consideration.



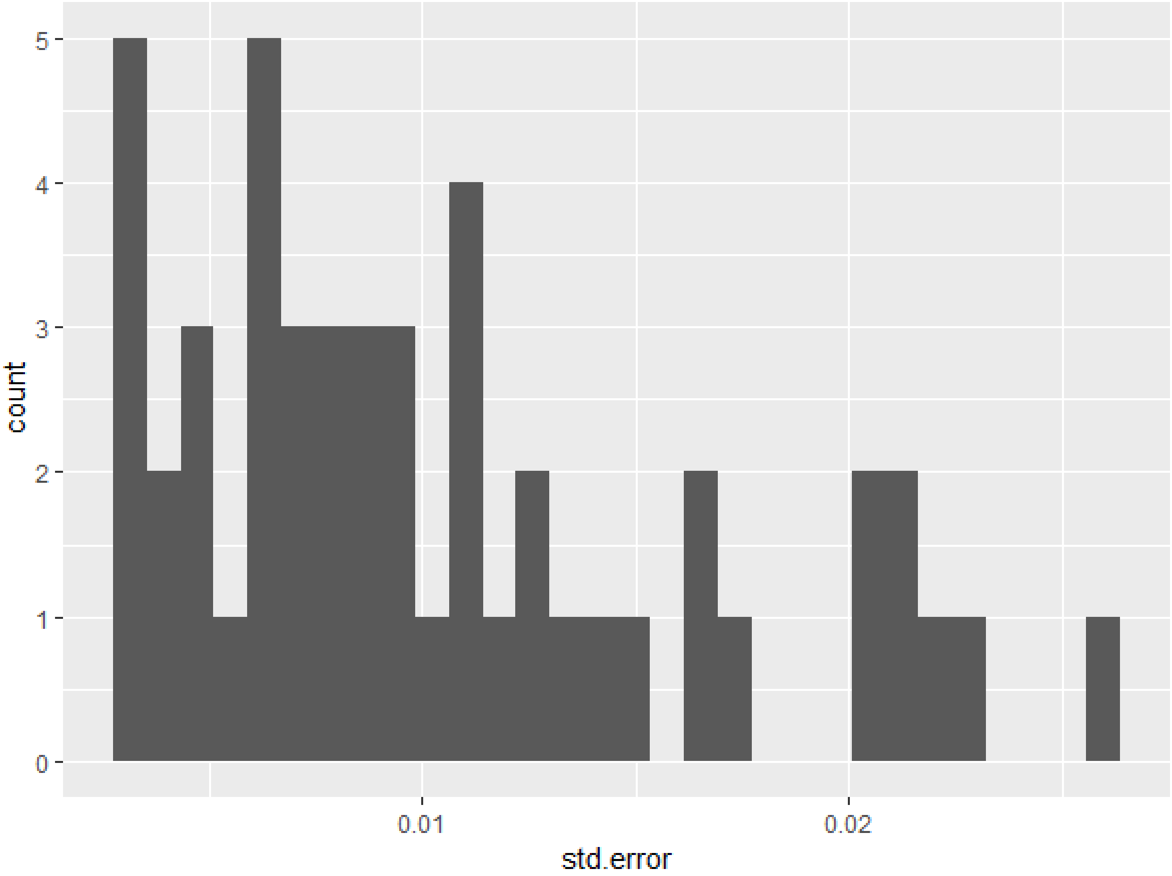
2.) Then investigated the outliers, using a histogram of their standard error for the 51 species included in the analysis.



3.) Then identified any species which were greater than 0.95 outlier, using the ‘scores’ function from the outliers package in R. This identified one species which was an outlier – Pilotbird. We then re-plotted the histrogram.



4.) We repeated step 3 and found that there was one individual outlier still present, obvious from the histogram. Thus, we removed White-eared Honeyeater from the analysis. We were then satisfied with the statistical spread of standard errors associated with GLMMs.



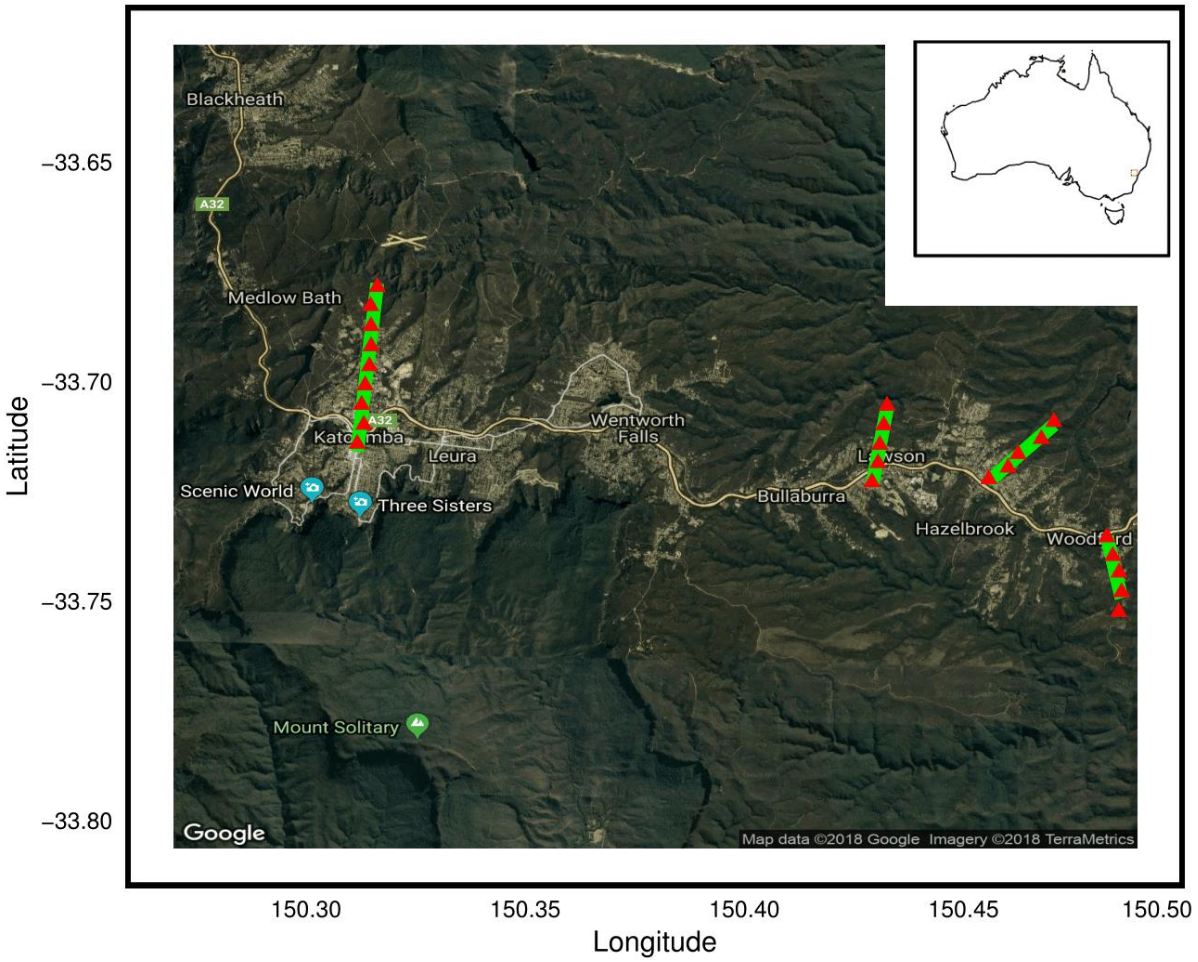


Figure S1. A map of the study area, located in the Blue Mountain World Heritage area, ~ 180 km west of Sydney, New South Wales, Australia.

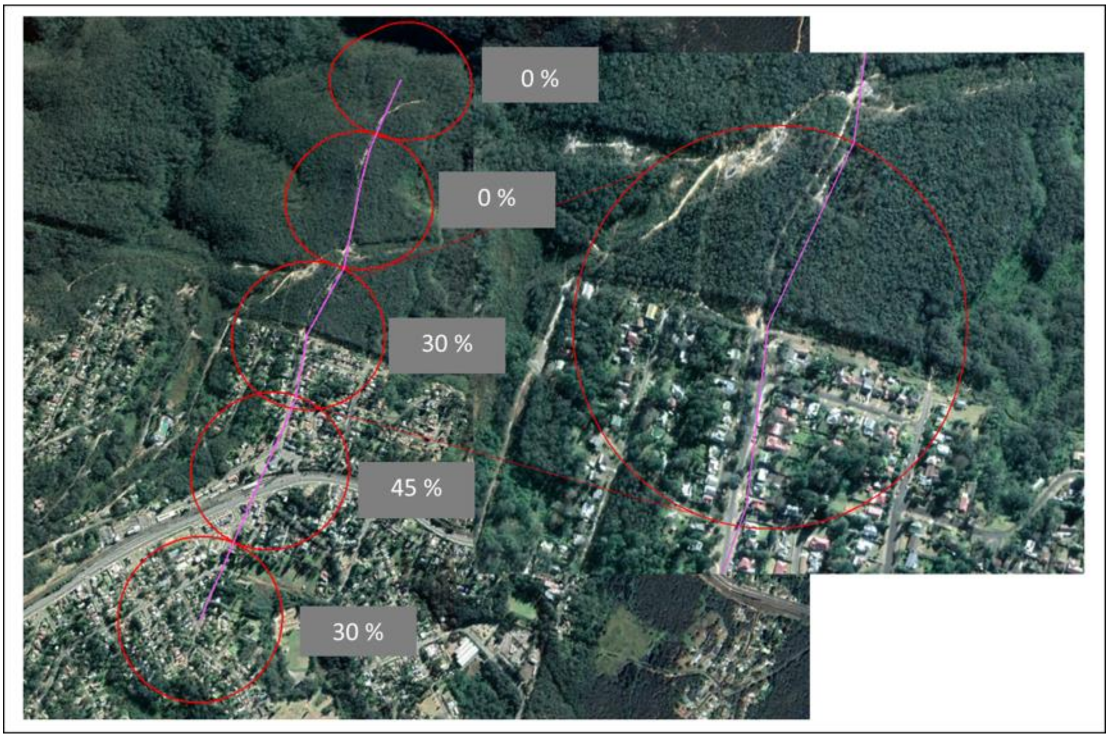


Figure S2. An example of how urbanization was calculated at a given point, showing the Lawson transect. The percent impervious surface was estimated within a 250 m buffer, and is shown in the gray boxes for each of the transect points. The circle on the right is an enlarged version of point C from the Lawson Transect.

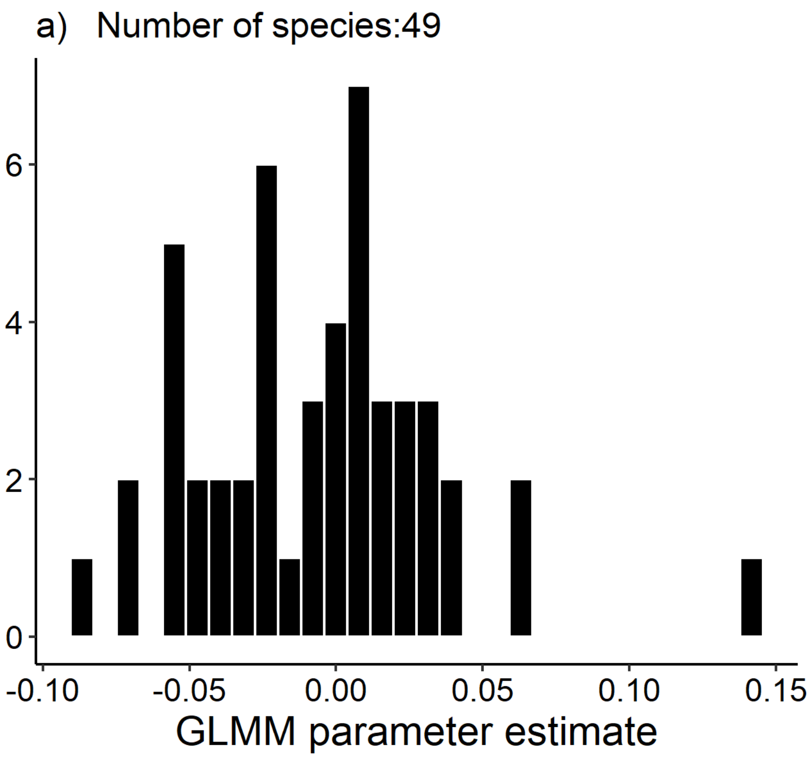
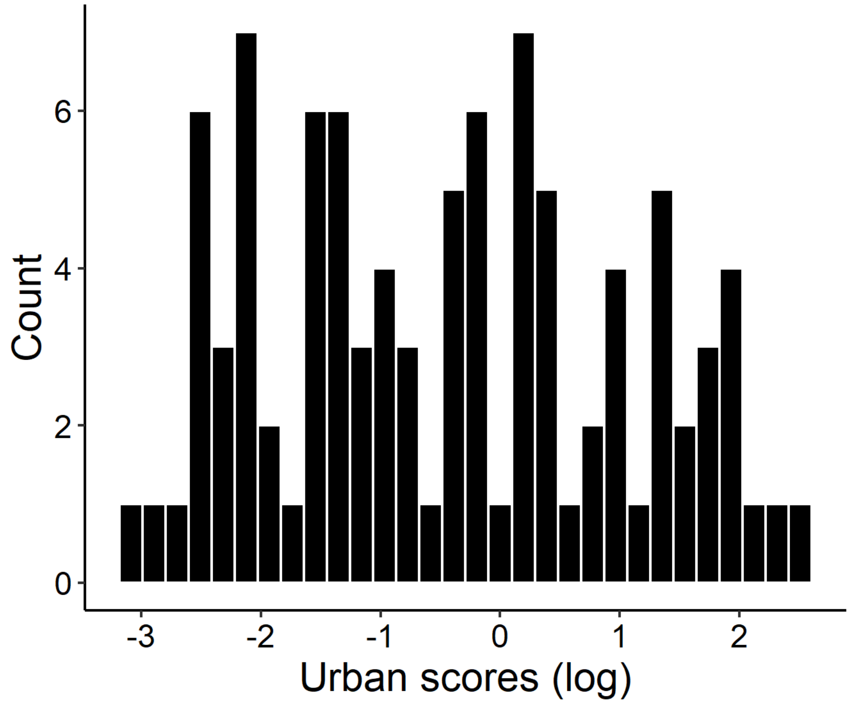


Figure S3. Histogram of the parameter estimates from Generalized Linear Models fitted for each species, representing the local-scale response to urbanization. Species with a parameter estimate > 0 are responding positively to urbanization, while species with a parameter estimate < 0 are responding negatively to urbanization.

a) Number of species:94



b) Number of species:49

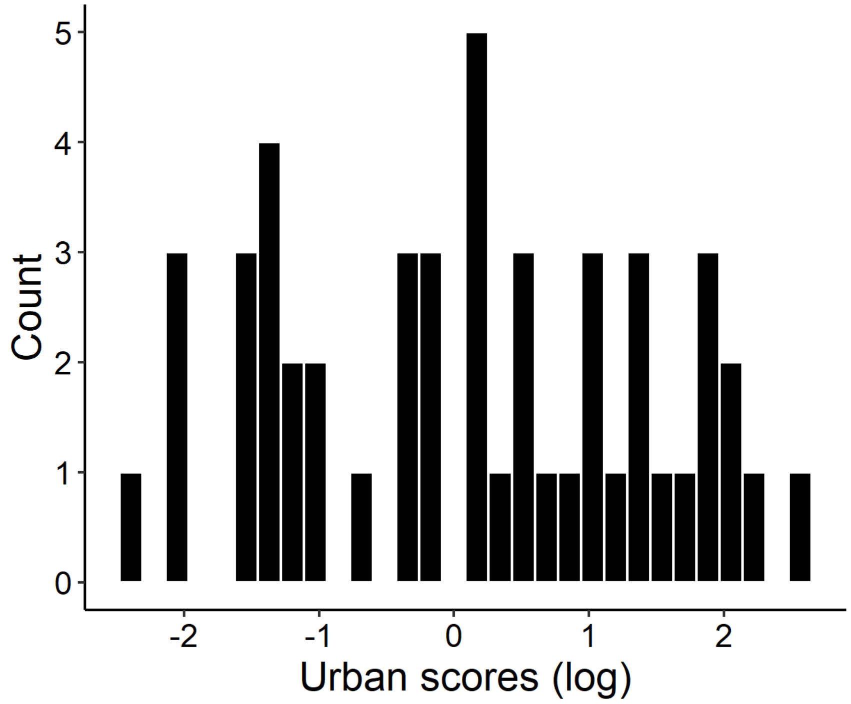


Figure S4. Histogram of the continental-urban scores for the 94 species (a) and for the 49 species included in the analysis (b). The urban-scores are measures of a species-specific distributional response to VIIRS night-time lights, gleaned from eBird data (Callaghan et al. 2019).

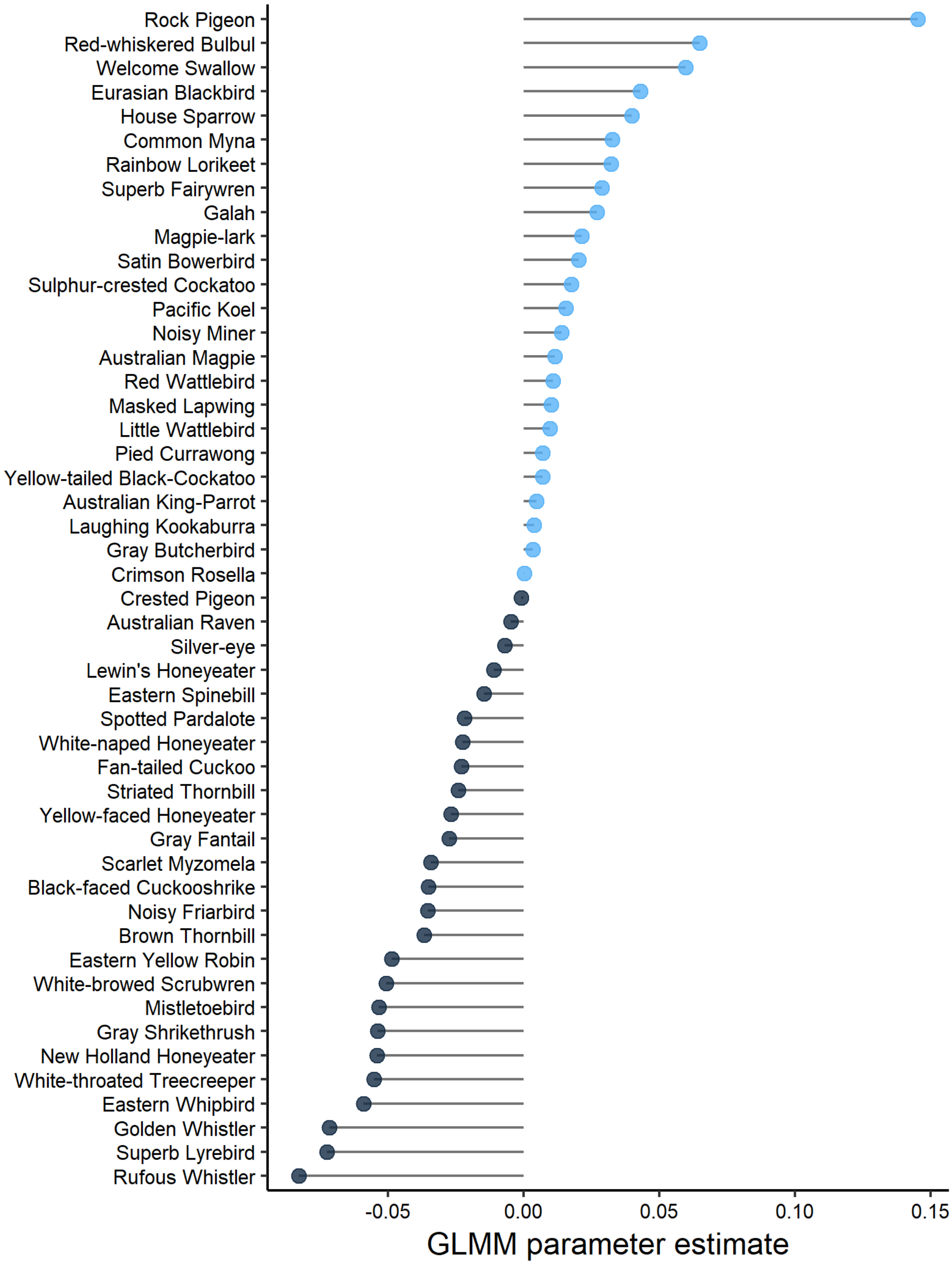


Figure S5. The 49 species included in the study, ranked by their local-scale urban score (i.e., GLMM parameter estimate). Values on the right (light blue) are positively associated with urbanization while values on the left (dark blue) are negatively associated with urbanization.

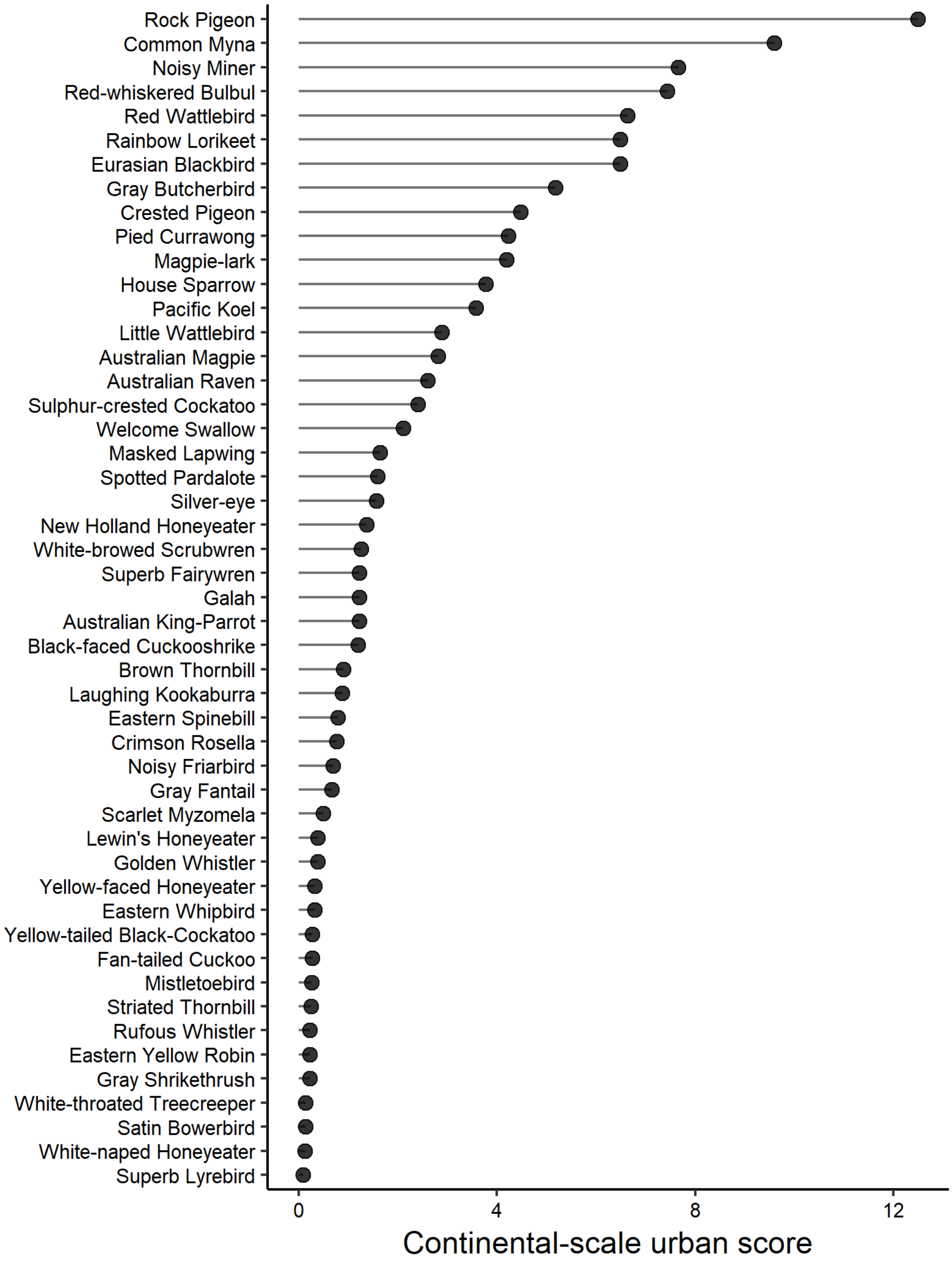


Figure S6. The 49 species included in the study, ranked by their continental-scale urban scores, showing the species most associated with urbanization (Rock Pigeon) to the least (Superb Lyrebird). Compare with Figure S5.