A continental measure of urbanness predicts avian response to local urbanization

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Author contributions
CTC, WKC, JHW, and REM conceptualized the data processing to assign urban scores. CTC, MBL, and REM designed the study. CTC performed the data analysis with insight from WKC and AGBP. All authors contributed to drafting and editing the manuscript.

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.

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 response to environmental parameters that are also generalizable across multiple spatial scales are scarce. We used broad-scale avian citizen science data, over continental Australia, integrated with remotely-sensed products, to produce a measure of urban-tolerance for a given species at a continental-scale. We then compared these urban-tolerances to modelled responses to urbanization at a local-scale, based on systematic sampling within four 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. 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 approach demonstrates the applicability of broad-scale citizen science data, contrasting both the spatial grain and extent of standard point-count surveys generally only conducted at small spatial scales. Continental-scale responses in Australia are representative of small-scale responses to urbanization among four small cities in Australia, suggesting that our method of producing species-specific urban scores is robust and may be generalized to other locations lacking appropriate data.

Keywords: Australia; birds; 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 via urbanization (Vandewalle et al. 2010). Yet the scale-dependence of species-environment relationships remains complex and generally unresolved (Weins 1992, Pautasso 2007, 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 (Hostetler 2001, 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 thus 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).

Quantifying species-specific responses to environmental parameters is particularly important for anthropogenic land use changes (Suárez-Seoane et al. 2002), such as urbanization (Jokimäki 1999, Fernandez-Juricic and Jokimäki 2001, Gehrt and Chelsvig 2004, Russo and Ancillotto 2015). If environmental planners can appropriately identify and predict the species most at-risk of urbanization (i.e., the least urban-tolerant species), then environmental planners can attempt to mitigate the threats specific to these least-tolerant species (Hostetler 2001) – e.g., by installing nestboxes if hollow-nesting birds are most at-risk. Conversely, if environmental planners can appropriately identify the abundant (i.e., most urban-tolerant) species that may be harmful to other less urban-tolerant species, then steps can be taken to minimize the harm these species pose (e.g., by managing invasive species in urban environments). 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 the impacts of urbanization on biodiversity are inconsistent among cities and across spatial scales, sometimes with peaks of biodiversity at intermediate levels of urbanization (Chace and Walsh 2006, Batáry et al. 2018). Thus, understanding of biodiversity responses to urbanization is still lacking unified theories across spatial scales, with repeatable and robust methods, especially for species-specific measurements of response to urbanization.

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, 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), and broad multi-city analyses are rare in comparison (Clergeau et al. 2006a, 2006b, Morelli 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 are rarely available within a specific city, limiting environmental planners' ability to make informed decisions, highlighting the importance of local-scale data (or proxies) for urban planning and management. 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, Jokimäki et al. 2017, Horton et al. 2018), including bird responses to urbanization (Bino et al. 2008). 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 derived from citizen science data. Importantly, however, the reliance on continental citizen science data needs to be robust, and the minimum number of citizen science observations to make robust generalizations needs to be quantified.

We assessed how bird species respond to urbanization across spatial scales (i.e., based on a measure of urban-tolerance), testing whether species-specific responses (i.e., changes in relative abundance across 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 responses to urbanization, derived from systematic sampling. The former relies on novel methods to assign species-specific continental urbanization responses in Australia, integrating broad-scale biodiversity data — collected through eBird (Sullivan et al. 2009, 2014, Wood et al. 2011) — with remotely-sensed landcover maps of continuous measures of urbanization. The latter relies on modelled responses to urbanization derived from local-level bird surveys within four small cities in Australia. We then tested the relationship between these two differential measures of bird responses to urbanization.

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 (Blair 1996, McDonnell and Hahs 2015, 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 where very few observations would be in or near high levels of urbanization, contrasting with an urban exploiter which would have a predicted distribution of observations largely skewed to higher levels of urbanization (Fig. 1).

We first filtered all eBird data (version ebd_relFeb-2018) to include data between January 1st, 2010 and February 28th, 2018. This corresponded to the richest period of eBird data and minimizes undue leverage of mismatch between changes in eBird observations and urbanization values. The majority of these data corresponds to the period of local-level sampling (see below), as most eBird data are contributed from the recent past. We further filtered the entire suite of eBird data to the best quality lists (e.g., La Sorte et al. 2014, Callaghan et al. 2017), removing potential outliers such as extraordinary long eBird checklists or eBird checklists which travelled long distances, as these checklists are most likely to introduce undue leverage on the results (e.g., include species in an area that was recorded from a great distance away). 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 also filtered these checklists to those 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 (i.e., one checklist was randomly selected), and all seabirds were omitted from the potential suite of species. Only species with a minimum of 100 observations were considered for assignment of continental-scale urban scores. Based on visual interpretation and our understanding of Australian birds, the data showed that species with < 100 observations had large variability in response to urban environments. However, when considering the species recorded at the local-scale (N=94; see below), the mean number of observations for continental-scale assignment was 32,642 ± 32,846 (sd). All but three species (Spotted Quail-Thrush, Pilotbird, Beautiful Firetail) in our analysis had > 1000 continental eBird observations (Table S1), and these were removed from analyses because they did not meet the minimum local-scale observation threshold (see below). 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 to account for travelling checklists throughout an area) and the size of the buffer has no discernible influence on the relative 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 because it is correlated positively with impervious surface cover and human population density (Pandey et al. 2013, Zhang and Seto 2013, Stathakis et al. 2015) and because of its global availability and ease of use with Google Earth Engine (Gorelick et al. 2017). For each buffer, raw radiance values were used — after filtering of the data to minimize the influence of fires, degraded data and other light source contamination (Elvidge et al. 2017) — between 2013-2017 and the average raw radiance value was taken as an annual composite. This approach of assigning urban scores shows strong agreements with other measures of urbanization such as human population density (Callaghan et al. 2019a, 2019b). Each species' observations then corresponded to a different distribution of VIIRS night-time lights (Fig. 1), and we defined the median of this distribution as a species-specific urban-tolerance score. For more methodological details, and a published list of species-specific urban scores, see Callaghan et al. (2019a, 2019b).

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 (N=24) were spaced ~ 500 m apart on each transect to ensure independence of sampling points. Woodford (population ~ 2,500), Lawson (population ~ 2,600), and Hazelbrook (population ~ 5,000) had 5 points each, while Katoomba (population ~ 8,000) 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 within a 250-m radius. Surveys were 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 (i.e., order of points visited) 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) — a commonly employed approach within small-scale urbanization studies. 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, our approach compared different spatial grains, albeit measuring the same environmental response in urbanization.

We extracted species-specific responses to urbanization at a local scale, using a modelling approach and generated parameter estimates for each species, that were treated as the 'local-scale urbanness'. The response variable in our models was the total number of presences (i.e., if a species occurred in a 5 min sampling event) for each point (N=24) — i.e., the number of presences for a species at a given sampling point. The total number of presences possible was 24, given each survey point was sampled 24 times. The response variable was 'zero-filled', accounting for complete absences of a given species at a given point, and each species thus had a total sample size of 24 observations which were modelled. This response variable was modelled against the percent impervious area at each survey point (N=24). 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 presences across all surveys (out of a possible 576) 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 (N=24). Additionally, many of the seasonal species were excluded from analyses based on our cut-off for minimum of nonzero observations (i.e., many of the possible migrants were only recorded <10 times). Our initial exploration considered negative binomial model distributions, but AIC was consistently lower for Poisson than negative binomial, and more species failed to converge regardless of differing theta parameter estimations in the glmer fitting procedure (i.e., only 44 species would have been included in final comparisons). Thus, we specified our models with Poisson distributions to maximize the number of species which could be compared with continental-scale species-specific urban scores. But the results using negative binomial and Poisson distributions were similar when comparing the modelling approaches. We also explored the modelling results when only including species which were detected within 100-m of the survey point, and the results were similar when including all species detected within 250-m radius of the survey point. 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 (Table S1). Fifty-one species had > 10 presences across all surveys (Table 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 S1), likely resulting from a small sample size. Thus, 49 species were used in our regression of continental and local-scale urban tolerance measures, with their continental-scale species-specific urban scores being log-transformed. Models were fitted using the 'lm' function in R. We fitted this model first without any weighting, and then re-fitted the model by weighting the model by the standard error of the local-scale urban scores' parameter estimates. This gave more weigh to the model based on the confidence (i.e., standard error of model fits) of the GLMMs, and provided us with a more robust approach to test the relationship between continental and local-scale urban tolerance measures.

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 (Table 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: -0.08; Fig. S3; full model results, including significance of GLMMs can be found in Table S2). Of the 94 potential species, 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 ± 2.81 (Fig. S4). Thus, Rock Pigeon had both the highest local-urban score and continental-urban species-specific score showing some qualitative agreement between the two approaches. Similarly, Superb Lyrebird had the second lowest local-urban score and the lowest continental-urban species-specific score (cf. Fig. S5 and Fig. S6). Some species (e.g., Crested Pigeon, Spotted Pardalote, New Holland Honeyeater) had relatively high continental-scale urban scores (i.e., ranked in the top 50%) but were still negatively associated with urbanization at the local-scale. Conversely, some species (e.g., Gray Butcherbird, Satin Bowerbird) had relatively low continental-scale urban scores (i.e., ranked in the bottom 50%) but were positively associated with urbanization at the local scale (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 for continental-scale urban scores from 10 to 1000 there was little differentiation in the underlying relationship (Fig. 2a), and the R^2 for these models leveled off after ~ 250 observations (Fig. 2b).

Discussion

We demonstrated a novel empirical relationship between continental-scale urbanness of birds in Australia and local-scale urbanness among four small cities, relying on > 3 million citizen science bird observations combined with intensive local-scale bird surveys, highlighting the potential applications of broad-scale citizen science data. We found that a relatively small number of citizen science observations (~250) are needed to provide reasonable estimates of local-scale responses to urbanization. This approach highlights that continental-scale data may be a sufficient proxy throughout regional cities to help guide urban planning and development – even when these cities lack the appropriate citizen science data. For example, urban planners in developing cities can look at the continental ranking of species' urban tolerance and sufficiently design cities that provide habitat and resources for those species most at risk (i.e., providing artificial hollows for hollow-nesting birds or ensuring urban grasslands for at-risk granivorous species). Concomitantly, urban planners can mitigate risks from the most harmful species (i.e., despotic species which likely have the highest urban-tolerance scores).

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 most at-risk of urbanization (Møller 2010). 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 across spatial scales (Hostetler and Holling 2000, Clergeau et al. 2006b). This method moves past the traditional notion of characterizing species based on known responses to urbanization (Kark et al. 2007, Geschke et al. 2018), and instead relies 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 inter-specific variation.

There is currently 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 (e.g., urban development and planning) 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 generalizable among spatial scales are unavailable for environmental planners. Our results provide empirical evidence that continental-scale data reflects local-scale relevance, albeit within one localized study site. These species-specific urban scores have the ability to move beyond species-specific measures to community-level measures of response to urbanization (Callaghan et al. 2019a). And this community-level index can be tracked through time (among years) in response to restoration and/or degradation of urban greenspaces, highlighting the success or failures of restoration projects, for instance. Our results provide a ‘ranking’ of urban-tolerance that urban planners can use — in combination with local natural history — to successfully plan urban development that benefits species which are particularly susceptible to urbanization (i.e., that have low continental-scale urban-tolerance scores). An example would be actively incorporating grasslands in urban planning at a local-scale, providing habitat specifically for granivores (Callaghan et al. 2019a, 2019b). Importantly, such community-level indices can be calculated using citizen science data, potentially allowing for long-term monitoring of urban greenspaces in urban areas. Although we investigated local-scale impacts within small cities, we predict that similar empirical patterns would likely emerge for local-scale impacts within medium and large-sized cities. This is because we would expect continental-scale patterns to be most different from local-scale patterns in smaller cities because the likelihood of urbanization impacting species-specific responses along an urbanization gradient is likely to be more easily detected in medium and small-size cities.

This methodological approach of assessing species-specific urbanness of birds based on continental citizen science data is in its infancy, and we highlight here some potential opportunities for future research. First, and foremost, this approach may be applicable across other taxa (e.g., butterflies, dragonflies, mammals), reliant mainly on spatial coordinates of a large number of sightings – increasingly available via broad scale citizen science data (Chandler et al. 2017). Second, although our analysis is focused on species-specific responses to urbanization, we highlight that the broad-scale assignment of a species-specific response to its environment may be repeated with other environmental factors (e.g., tree-cover, water-cover), albeit these responses will be inter-correlated. This approach could use remotely-sensed landcover products — other than urbanization — to assign species-specific responses. But species' responses to other environmental factors should also be tested across spatial scales. Third, 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). For example, some species did not conform to the general results (e.g., New Holland Honeyeater, Spotted Pardalote, Galah) which is likely explained by intra-specific variation in their continental population with some populations being more 'urban' than other populations, which may not necessarily manifest in a specific location (i.e., our local-scale study site). Fourth, 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 (i.e., among years and seasons), showing localized adaptations (Evans et al. 2009, Martin et al. 2010, Yackulic and Ginsberg 2016). This approach should be able to measure species-specific responses to urbanization through decadal responses. This approach should also be adopted to regions where the fauna has differing migration strategies, thereby assessing species-specific responses to urbanization intra-annually.

Citizen science data are 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). However, there are a number of biases associated with citizen science data, including spatial and temporal sampling biases (Uychiaoco et al. 2005, Belt and Krausman 2012, Boakes et al. 2010) with data disproportionately skewed towards urban areas (Kelling et al. 2015). Detection probability also varies among species and between habitats (e.g., urban versus rural habitats), potentially limiting the ability to draw inferences to poorly sampled species and habitats. For example, in our study, we predominantly looked at common species, and our results may be only applicable to common species, with more research necessary to understand how our results translate to uncommon and rare species. This study was conducted in Australia — an area with relatively large amounts of citizen science data — and our results may not be generalizable or applicable to other parts of the world with less data (La Sorte and Somveille 2019) — and this should be tested in the future. But with the global increase in such data (Chandler et al. 2017), we are hopeful that our approach will be applicable to historically poorly sampled parts of the world (e.g., tropics, developing countries). Given these biases, we do not suggest that systematic sampling should be replaced with citizen science data, but rather, that they can complement one another to provide a more generalized understanding in biodiversity research (Bayraktarov et al. 2019). Nevertheless, methods such as the one we introduce here will likely be essential to track biodiversity responses to urbanization into the Anthropocene.

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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 continental 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) Continental-scale urbanness (x-axis) is the median of a species' distribution of all continental eBird observations in response to VIIRS night-time lights, presented on a log-scale: greater values equate to greater urban-tolerance (see Figure S6). Local-scale urbanness (y-axis) is the parameter estimate from a modelled relationship between number of presences at a survey point and the estimated percent impervious surface area at that survey point: positive values represent a positive response to urbanization and negative values represent a negative response to urbanization (see Figure S5). This regression of log-transformed continental-scale urbanness versus local-scale urbanness is shown for 49 species. Standard error is shown for local-scale urbanness as the standard error retrieved 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. An interactive version of this figure is available here. b) R^2 for each of the 100 different linear models fitted, using 10-1000 data points to calculate the continental-scale urban scores. The red line shows the overall R^2 (0.51) while the blue line represents a smoothed response fitted through the different linear models fitted with the shaded gray area representing the standard error of this model fit.

Table 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	Scientific Name	Number of local observations	Number of continental observations	Included in regression
Eastern Spinebill	*Acanthorhynchus tenuirostris*	412	27990	Yes
Red Wattlebird	*Anthochaera carunculata*	390	84046	Yes
Sulphur-crested Cockatoo	*Cacatua galerita*	383	80030	Yes
Pied Currawong	*Strepera graculina*	291	65858	Yes
Crimson Rosella	*Platycercus elegans*	269	45991	Yes
Australian Magpie	*Gymnorhina tibicen*	229	158615	Yes
Yellow-faced Honeyeater	*Caligavis chrysops*	210	35557	Yes
White-throated Treecreeper	*Cormobates leucophaea*	179	28238	Yes
Spotted Pardalote	*Pardalotus punctatus*	117	36944	Yes
Rainbow Lorikeet	*Trichoglossus haematodus*	111	117290	Yes
Brown Thornbill	*Acanthiza pusilla*	108	48114	Yes
Satin Bowerbird	*Ptilonorhynchus violaceus*	108	12580	Yes
Gray Butcherbird	*Cracticus torquatus*	104	59384	Yes
Australian King-Parrot	*Alisterus scapularis*	103	22845	Yes
New Holland Honeyeater	*Phylidonyris novaehollandiae*	96	39402	Yes
Gray Fantail	*Rhipidura albiscapa*	93	77707	Yes
Common Myna	*Acridotheres tristis*	74	62497	Yes
Silver-eye	*Zosterops lateralis*	70	58159	Yes
Rock Pigeon	*Columba livia*	66	29618	Yes
Australian Raven	*Corvus coronoides*	65	53001	Yes
Rufous Whistler	*Pachycephala rufiventris*	59	38256	Yes
Eastern Yellow Robin	*Eopsaltria australis*	52	35185	Yes
Gray Shrikethrush	*Colluricincla harmonica*	49	50951	Yes

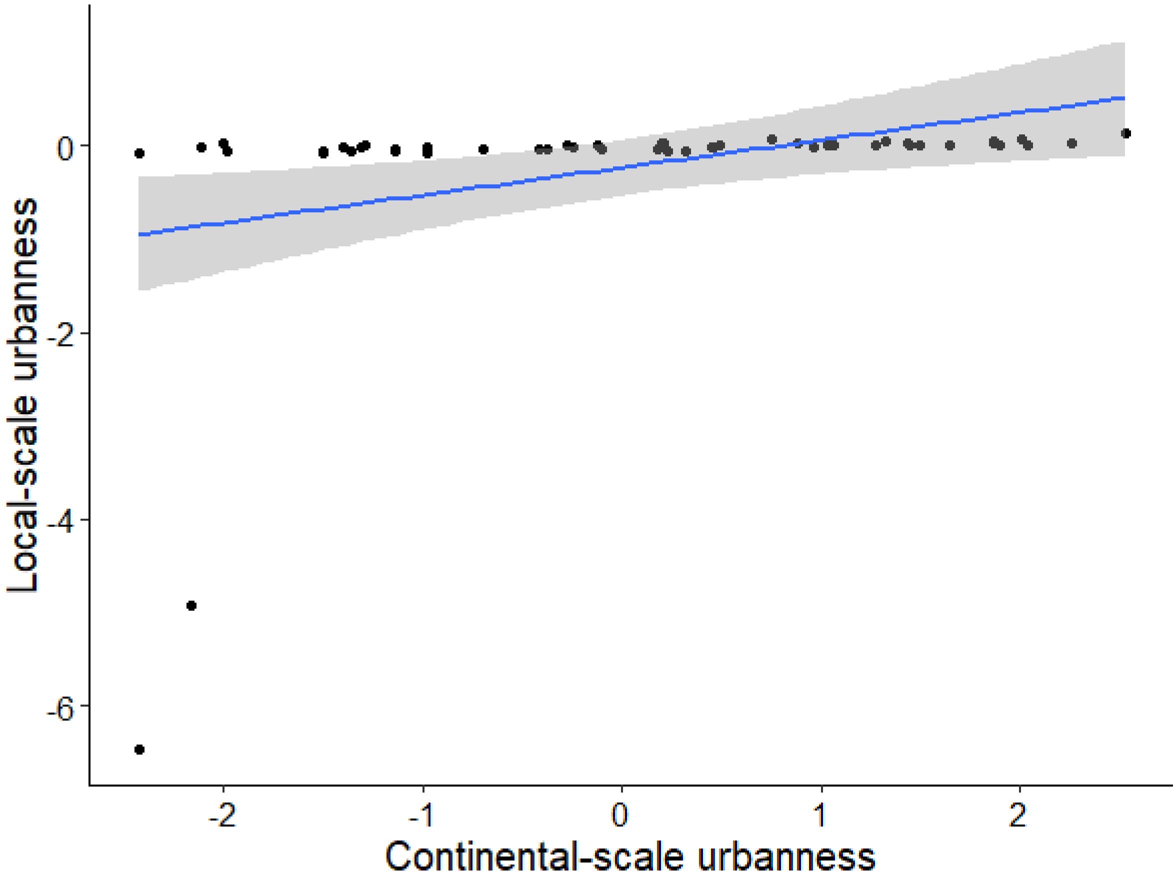
Eurasian Blackbird	*Turdus merula*	48	43878	Yes
White-naped Honeyeater	*Melithreptus lunatus*	48	9612	Yes
Striated Thornbill	*Acanthiza lineata*	44	11878	Yes
Eastern Whipbird	*Psophodes olivaceus*	42	29452	Yes
Laughing Kookaburra	*Dacelo novaeguineae*	41	70107	Yes
White-browed Scrubwren	*Sericornis frontalis*	40	43541	Yes
Fan-tailed Cuckoo	*Cacomantis flabelliformis*	38	15908	Yes
Pacific Koel	*Eudynamys orientalis*	36	15357	Yes
House Sparrow	*Passer domesticus*	35	36193	Yes
Superb Lyrebird	*Menura novaehollandiae*	34	4247	Yes
Lewin's Honeyeater	*Meliphaga lewinii*	33	35617	Yes
Yellow-tailed Black-Cockatoo	*Calyptorhynchus funereus*	33	13862	Yes
Golden Whistler	*Pachycephala pectoralis*	29	31744	Yes
Little Wattlebird	*Anthochaera chrysoptera*	23	28734	Yes
Black-faced Cuckooshrike	*Coracina novaehollandiae*	19	55254	Yes
Galah	*Eolophus roseicapilla*	19	80009	Yes
Crested Pigeon	*Ocyphaps lophotes*	18	69964	Yes
Superb Fairywren	*Malurus cyaneus*	17	86836	Yes
Noisy Miner	*Manorina melanocephala*	16	89821	Yes
Welcome Swallow	*Hirundo neoxena*	15	109006	Yes
Magpie-lark	*Grallina cyanoleuca*	14	131621	Yes
White-eared Honeyeater	*Nesoptilotis leucotis*	14	9179	No
Noisy Friarbird	*Philemon corniculatus*	13	25532	Yes
Red-whiskered Bulbul	*Pycnonotus jocosus*	13	4524	Yes
Scarlet Myzomela	*Myzomela sanguinolenta*	13	14387	Yes
Masked Lapwing	*Vanellus miles*	12	80029	Yes
Mistletoebird	*Dicaeum hirundinaceum*	11	25640	Yes
Pilotbird	*Pycnoptilus floccosus*	11	749	No

Channel-billed Cuckoo	*Scythrops novaehollandiae*	10	9686	Yes
Gang-gang Cockatoo	*Callocephalon fimbriatum*	9	5248	No
Leaden Flycatcher	*Myiagra rubecula*	9	13615	No
Tree Martin	*Petrochelidon nigricans*	8	18471	No
Variegated Fairywren	*Malurus lamberti*	8	15152	No
Wonga Pigeon	*Leucosarcia melanoleuca*	8	7094	No
Red-browed Treecreeper	*Climacteris erythrops*	7	1286	No
Sacred Kingfisher	*Todiramphus sanctus*	7	25194	No
Brown-headed Honeyeater	*Melithreptus brevirostris*	6	7435	No
Little Corella	*Cacatua sanguinea*	6	30860	No
Shining Bronze-Cuckoo	*Chrysococcyx lucidus*	6	9331	No
Brown Cuckoo-Dove	*Macropygia phasianella*	5	10589	No
Red-browed Firetail	*Neochmia temporalis*	5	33456	No
Brown Gerygone	*Gerygone mouki*	4	9410	No
Common Cicadabird	*Edolisoma tenuirostre*	4	6728	No
Maned Duck	*Chenonetta jubata*	4	56221	No
Scarlet Robin	*Petroica boodang*	4	7211	No
Crescent Honeyeater	*Phylidonyris pyrrhopterus*	3	3293	No
Crested Shrike-tit	*Falcunculus frontatus*	3	3933	No
Olive-backed Oriole	*Oriolus sagittatus*	3	22539	No
Striated Pardalote	*Pardalotus striatus*	3	44295	No
Wedge-tailed Eagle	*Aquila audax*	3	11006	No
Australian Owlet-nightjar	*Aegotheles cristatus*	2	2836	No
Black-faced Monarch	*Monarcha melanopsis*	2	6181	No
European Starling	*Sturnus vulgaris*	2	53070	No
Long-billed Corella	*Cacatua tenuirostris*	2	10453	No
White-throated Needletail	*Hirundapus caudacutus*	2	3515	No
Beautiful Firetail	*Stagonopleura bella*	1	906	No

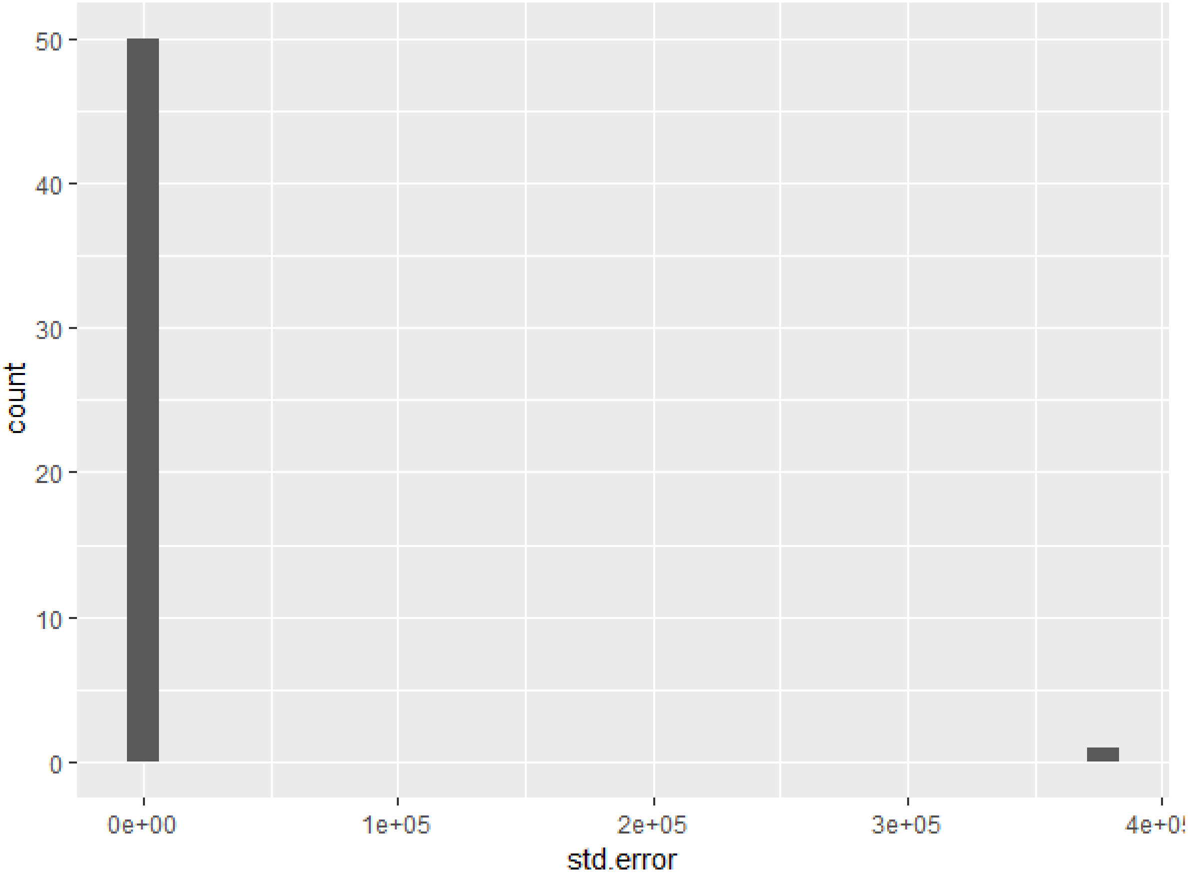
Brown Goshawk	*Accipiter fasciatus*	1	9918	No
Buff-rumped Thornbill	*Acanthiza reguloides*	1	7033	No
Collared Sparrowhawk	*Accipiter cirrocephalus*	1	4270	No
Common Bronzewing	*Phaps chalcoptera*	1	15076	No
Fuscous Honeyeater	*Ptilotula fusca*	1	4085	No
Horsfield's Bronze-Cuckoo	*Chrysococcyx basalis*	1	8035	No
Little Lorikeet	*Glossopsitta pusilla*	1	4865	No
Peregrine Falcon	*Falco peregrinus*	1	2960	No
Red-capped Robin	*Petroica goodenovii*	1	4299	No
Rufous Fantail	*Rhipidura rufifrons*	1	10113	No
Spotted Quail-thrush	*Cinclosoma punctatum*	1	423	No
Varied Sittella	*Daphoenositta chrysoptera*	1	4854	No
White-headed Pigeon	*Columba leucomela*	1	4069	No
Willie-wagtail	*Rhipidura leucophrys*	1	106114	No
Yellow Thornbill	*Acanthiza nana*	1	12237	No

Appendix S1. 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.

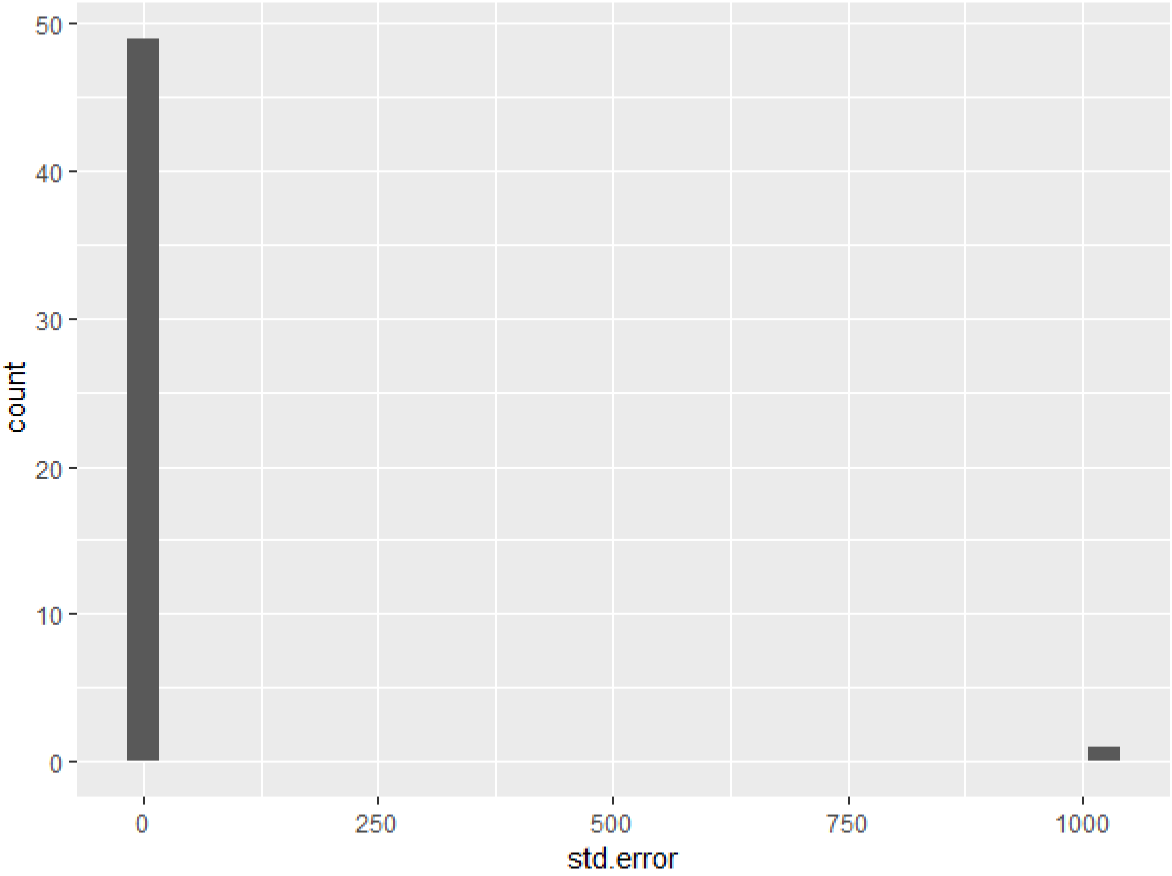
1.) Investigated relationship between all 51 species' parameter estimates and their continental-scores – 51 species had > 10 observations, meeting our a priori cut-off for modelling consideration.



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.

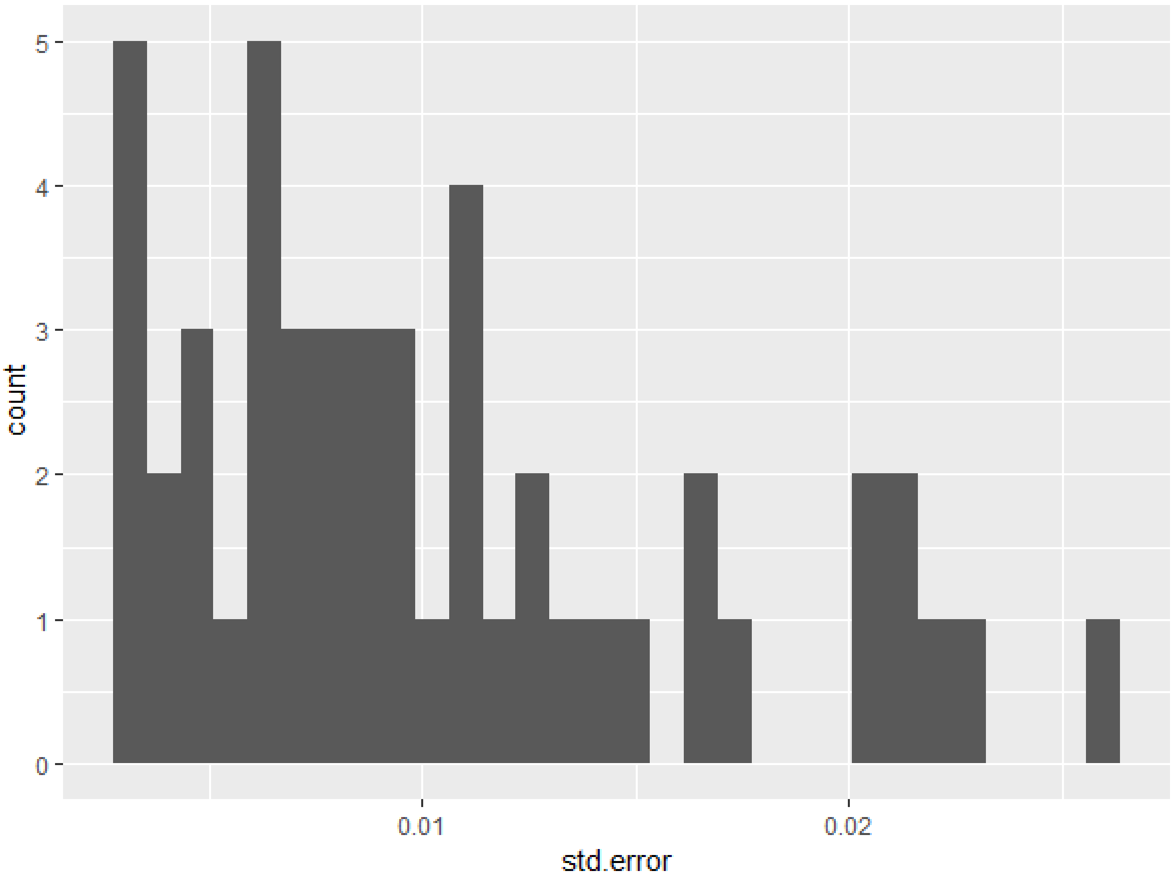


Table S2. The results of the modelled relationships of the local-scale responses to urbanization, for the 49 species included in the final analysis. Bolded p-values represent significance at the α=0.05 level.

Species	Parameter estimate	Standard error	Statistic	p-value	Deviance	Continental urban score
Australian King-Parrot	0.005	0.005	1.039	0.299	49.236	1.217
Australian Magpie	0.011	0.003	3.804	**0.000**	106.265	2.807
Australian Raven	-0.005	0.006	-0.733	0.463	28.513	2.607
Black-faced Cuckooshrike	-0.035	0.015	-2.383	**0.017**	30.899	1.193
Brown Thornbill	-0.037	0.006	-5.902	**0.000**	22.951	0.903
Common Myna	0.033	0.007	4.562	**0.000**	37.714	9.588
Crested Pigeon	-0.001	0.010	-0.100	0.920	35.677	4.471
Crimson Rosella	0.000	0.003	0.069	0.945	42.610	0.761
Eastern Spinebill	-0.015	0.003	-4.603	**0.000**	39.544	0.784
Eastern Whipbird	-0.059	0.014	-4.068	**0.000**	37.225	0.319
Eastern Yellow Robin	-0.049	0.010	-4.902	**0.000**	20.013	0.224
Eurasian Blackbird	0.043	0.011	3.919	**0.000**	35.554	6.489
Fan-tailed Cuckoo	-0.023	0.009	-2.631	**0.009**	34.617	0.269
Galah	0.027	0.014	1.994	**0.046**	24.625	1.217
Golden Whistler	-0.072	0.020	-3.553	**0.000**	19.413	0.377
Gray Butcherbird	0.003	0.004	0.812	0.417	104.344	5.178
Gray Fantail	-0.027	0.006	-4.597	**0.000**	22.647	0.663
Gray Shrikethrush	-0.054	0.011	-4.791	**0.000**	37.411	0.223
House Sparrow	0.040	0.010	4.067	**0.000**	20.147	3.771
Laughing Kookaburra	0.004	0.009	0.431	0.666	38.574	0.879
Lewin's Honeyeater	-0.011	0.011	-1.025	0.305	33.769	0.377
Little Wattlebird	0.010	0.004	2.236	**0.025**	22.663	2.882
Magpie-lark	0.021	0.011	1.965	**0.049**	36.199	4.189
Masked Lapwing	0.010	0.013	0.781	0.435	39.177	1.635
Mistletoebird	-0.053	0.023	-2.318	**0.020**	16.692	0.256

New Holland Honeyeater	-0.054	0.008	-6.587	**0.000**	50.585	1.369
Noisy Friarbird	-0.035	0.021	-1.716	0.086	11.444	0.688
Noisy Miner	0.014	0.013	1.091	0.275	44.768	7.661
Pacific Koel	0.015	0.008	2.017	**0.044**	27.592	3.575
Pied Currawong	0.007	0.003	2.355	**0.019**	55.863	4.232
Rainbow Lorikeet	0.032	0.007	4.429	**0.000**	63.526	6.489
Red Wattlebird	0.011	0.003	3.150	**0.002**	101.945	6.636
Red-whiskered Bulbul	0.065	0.026	2.516	**0.012**	20.904	7.431
Rock Pigeon	0.145	0.022	6.542	**0.000**	8.875	12.490
Rufous Whistler	-0.083	0.017	-4.830	**0.000**	19.095	0.224
Satin Bowerbird	0.020	0.006	3.346	**0.001**	68.313	0.134
Scarlet Myzomela	-0.034	0.016	-2.114	**0.034**	28.946	0.499
Silver-eye	-0.007	0.007	-0.955	0.339	39.141	1.564
Spotted Pardalote	-0.022	0.005	-4.444	**0.000**	25.003	1.585
Striated Thornbill	-0.024	0.008	-3.014	**0.003**	34.102	0.247
Sulphur-crested Cockatoo	0.018	0.004	4.553	**0.000**	71.695	2.401
Superb Fairywren	0.029	0.017	1.706	0.088	21.647	1.227
Superb Lyrebird	-0.072	0.021	-3.382	**0.001**	17.221	0.088
Welcome Swallow	0.060	0.021	2.858	**0.004**	9.857	2.107
White-browed Scrubwren	-0.051	0.012	-4.171	**0.000**	37.141	1.260
White-naped Honeyeater	-0.023	0.009	-2.384	**0.017**	26.121	0.121
White-throated Treecreeper	-0.055	0.006	-8.702	**0.000**	47.739	0.138
Yellow-faced Honeyeater	-0.027	0.005	-5.176	**0.000**	28.974	0.321
Yellow-tailed Black-Cockatoo	0.007	0.009	0.789	0.430	30.263	0.275

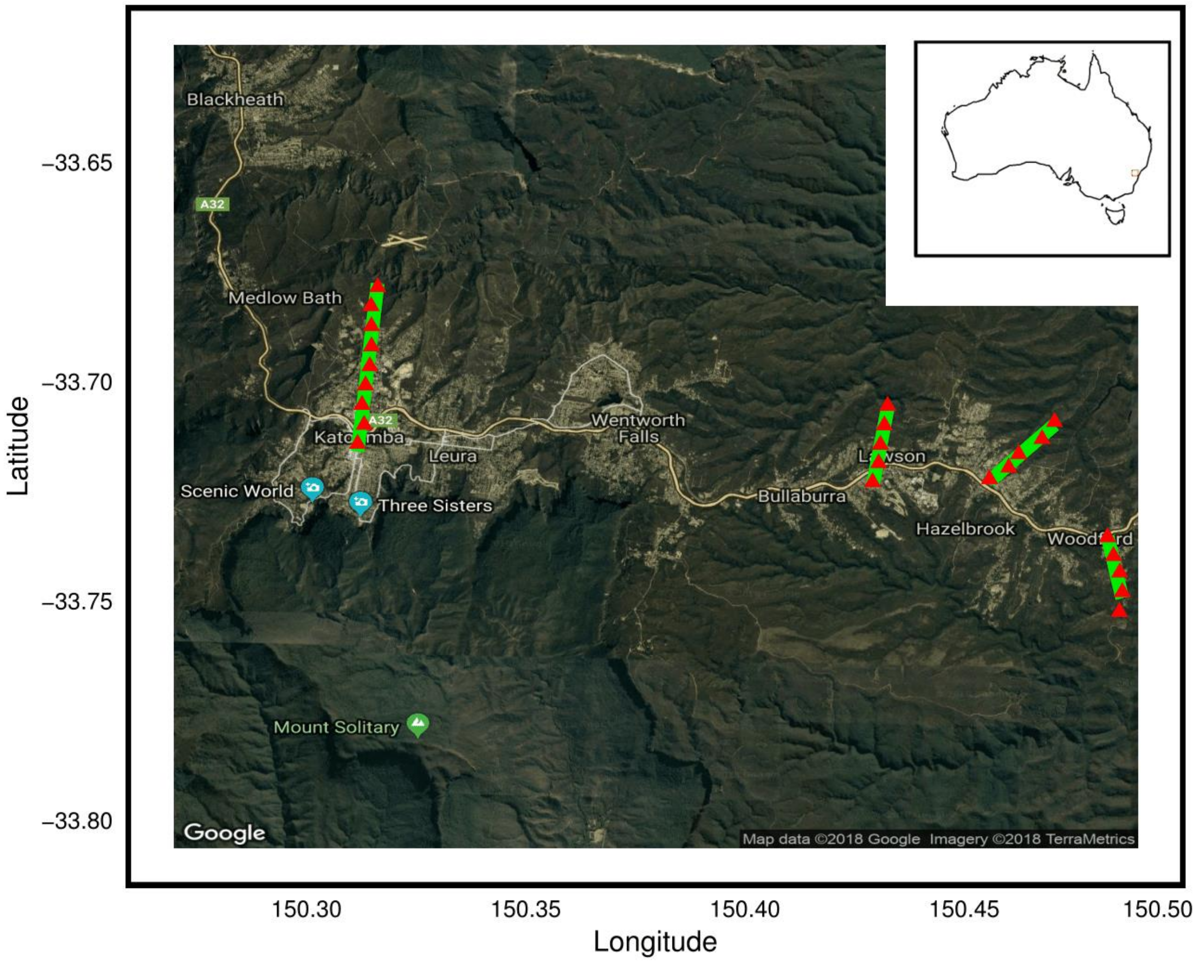


Figure S1. A map of the study area, located in the Blue Mountain World Heritage area, ~ 180 km west of Sydney, New South Wales, Australia.

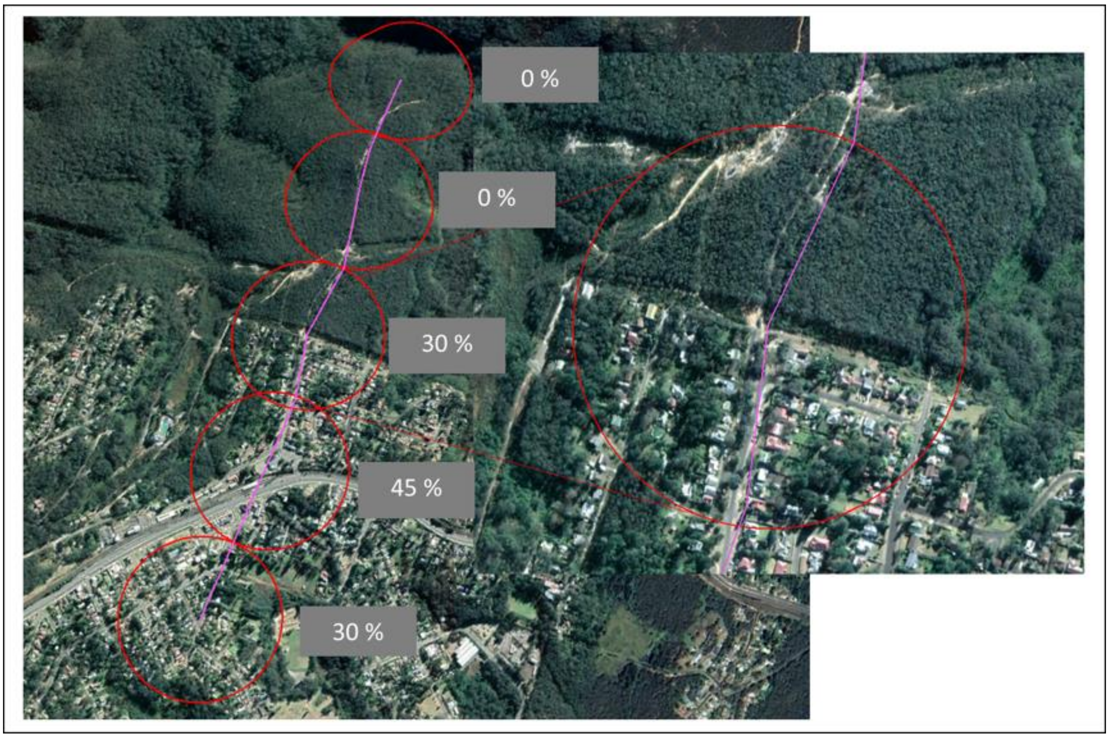


Figure S2. An example of how urbanization was calculated at a given point, showing the Lawson transect. The percent impervious surface was estimated within a 250 m buffer, and is shown in the gray boxes for each of the transect points. The circle on the right is an enlarged version of point C from the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

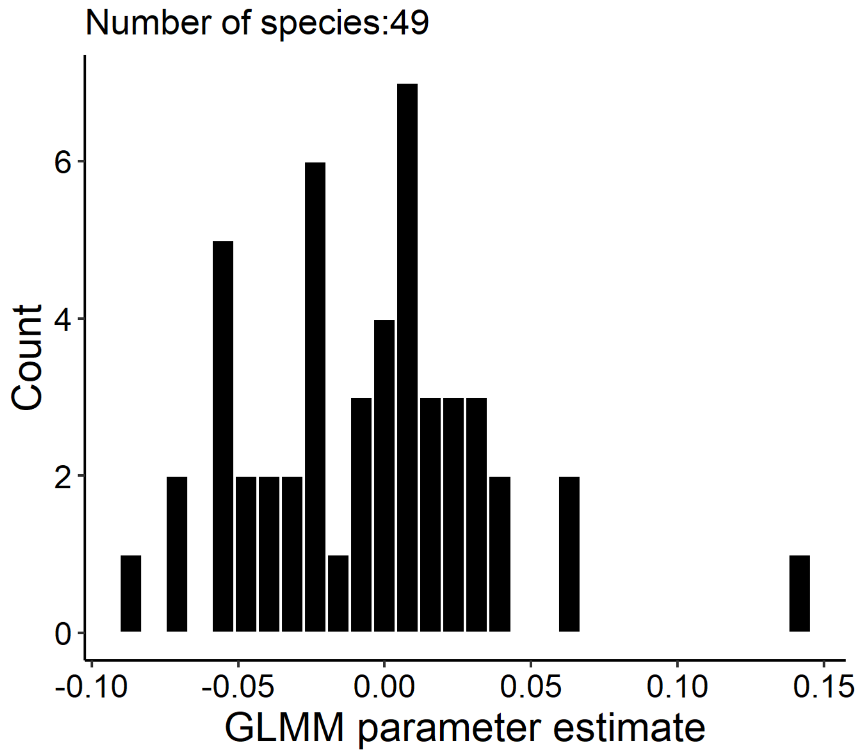


Figure S3. Histogram of the parameter estimates from Generalized Linear Models fitted for each species, representing the local-scale response to urbanization. Species with a parameter estimate > 0 are responding positively to urbanization, while species with a parameter estimate < 0 are responding negatively to urbanization. Model results, including p-values, can be found in Table S2.

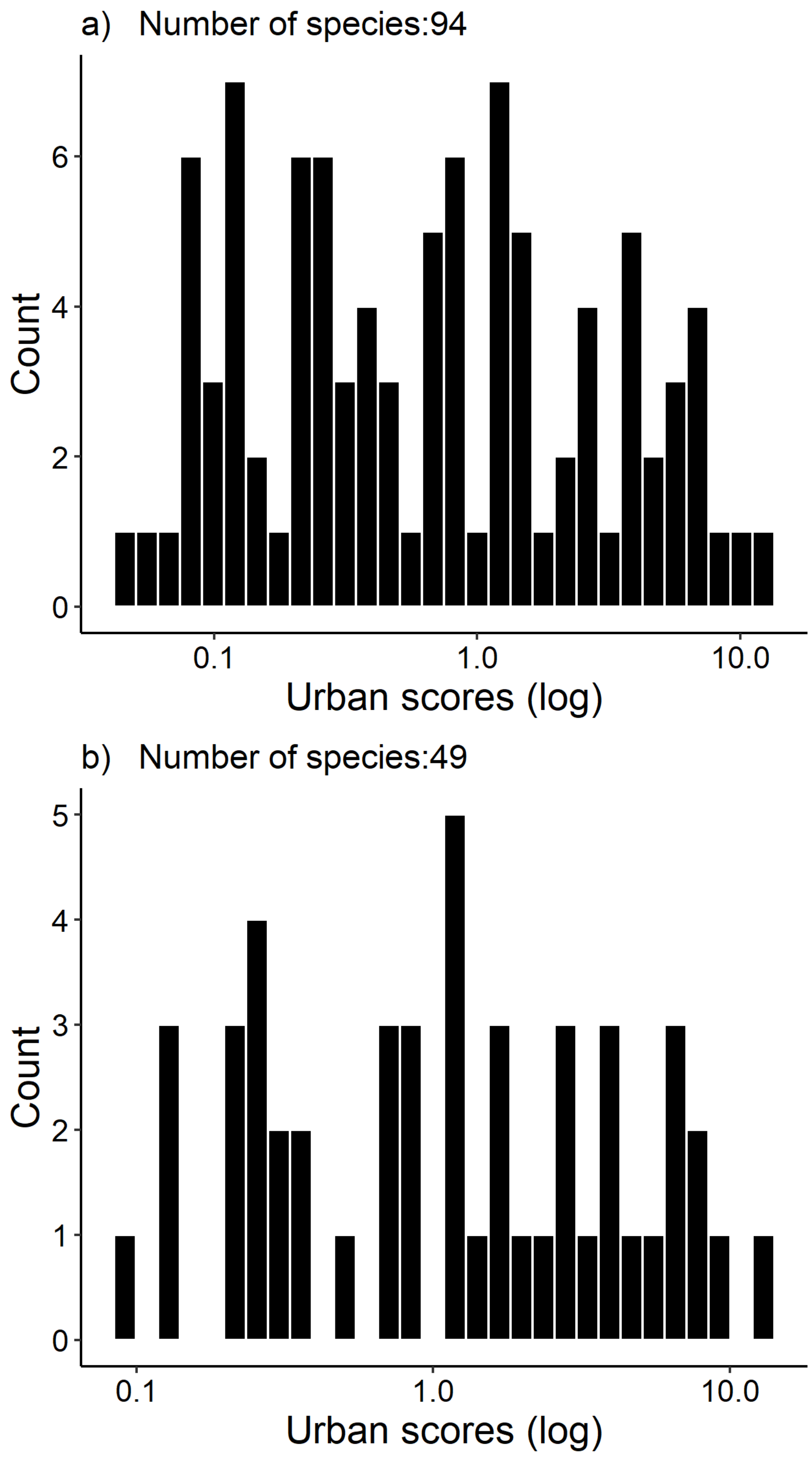


Figure S4. Histogram of the continental-urban scores for the 94 species (a) and for the 49 species included in the analysis (b). The urban-scores are measures of a species-specific distributional response to VIIRS night-time lights, gleaned from eBird data (Callaghan et al. 2019).

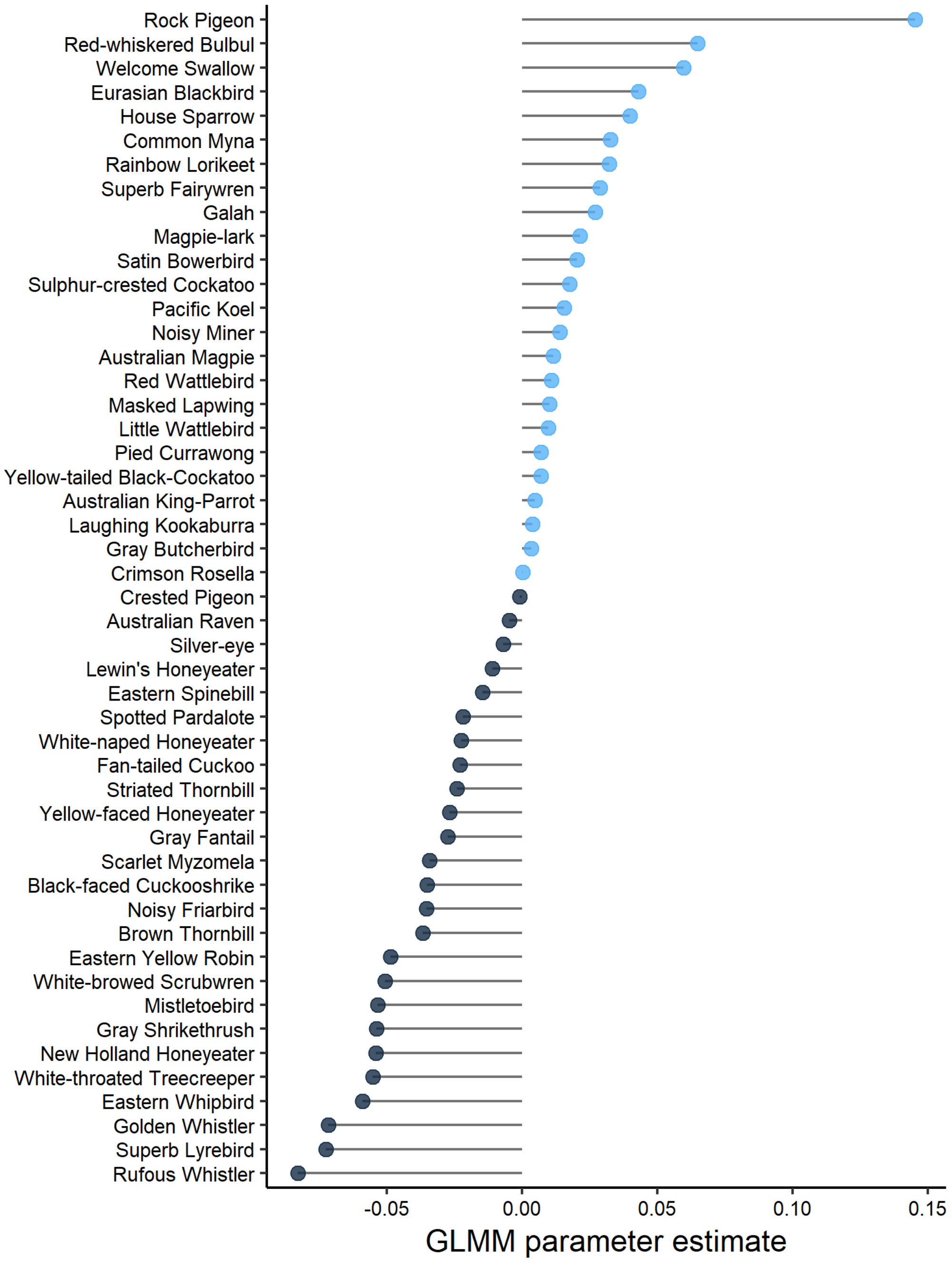


Figure S5. The 49 species included in the study, ranked by their local-scale urban score (i.e., GLMM parameter estimate). Values on the right (light blue) are positively associated with urbanization while values on the left (dark blue) are negatively associated with urbanization.

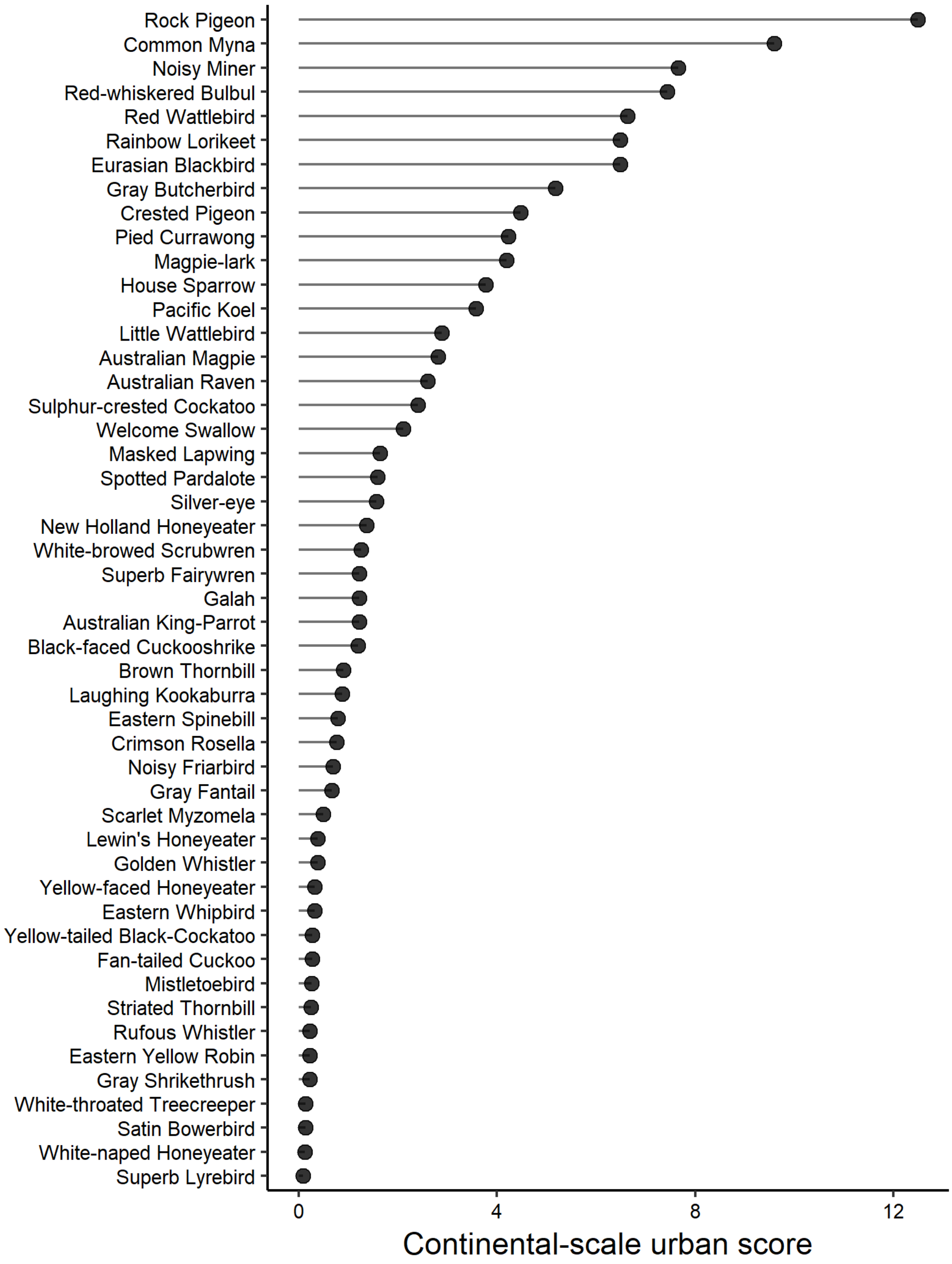


Figure S6. The 49 species included in the study, ranked by their continental-scale urban scores, showing the species most associated with urbanization (Rock Pigeon) to the least (Superb Lyrebird). Compare with Figure S5.