

ECOGRAPHY

Research

A continental measure of urbanness predicts avian response to local urbanization

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Ecography

43: 528–538, 2020

doi: 10.1111/ecog.04863

Subject Editor: Tim Bonebrake

Editor-in-Chief:

Jens-Christian Svenning

Accepted 29 November 2019



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: citizen science, eBird, spatial scales, species–environment relationships, urban ecology, urbanization

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,



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Dufflot 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 Chelvig 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, b, 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 (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,

b, 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 (ver. ebd_relFeb-2018) to include data between 1 January 2010 and 28 February 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 (La Sorte et al. 2014, Callaghan et al. 2017), removing potential outliers such as extraordinarily 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 and 240 min 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 $32\,642 \pm 32\,846$ (SD). All but three species (spotted quail-thrush, pilotbird, beautiful firetail) in our analysis had > 1000 continental eBird observations (Supplementary material Appendix 1 Table A1), 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 nighttime 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.

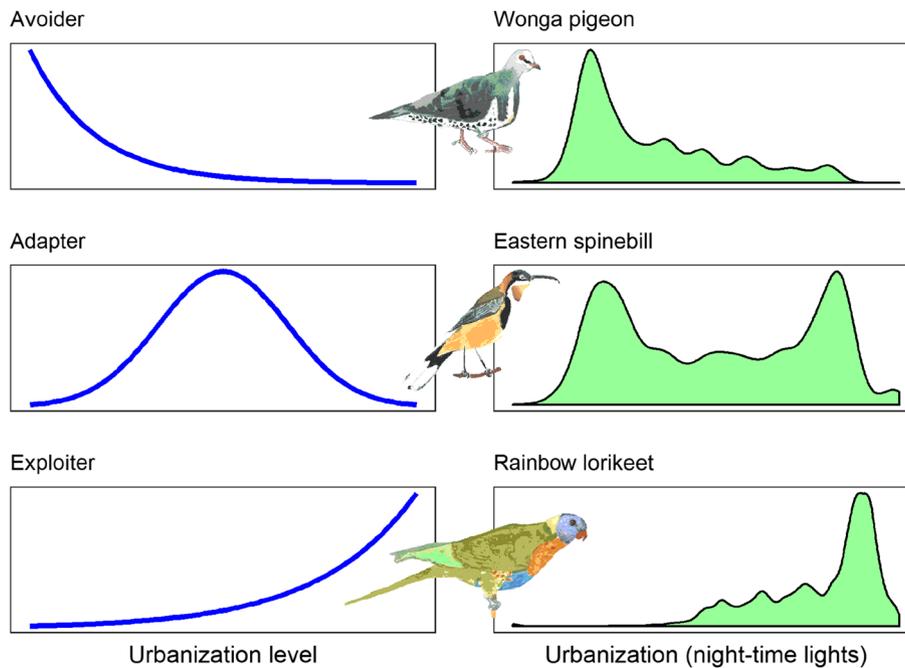


Figure 1. The theoretical expected distributions for the three types of commonly assigned responses to urbanization: urban avoider, urban adapter and urban exploiter. Also, showing three species' distributions in response to night-time lights based on their continental eBird data observations, demonstrating 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.

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 and 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, b). 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, b).

Local-scale species-specific responses to urbanization

We conducted bird-surveys within the Greater Blue Mountains World Heritage Area (GBWHA), which is ~10 000 km² 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 (Supplementary material Appendix 2 Fig. A1).

Points (n = 24) were spaced ~500 m apart on each transect to ensure independence of sampling points. Woodford (population ~2500), Lawson (population ~2600) and Hazelbrook (population ~5000) had five points each, while Katoomba (population ~8000) had nine points (Supplementary material Appendix 2 Fig. A1). 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 h 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; Supplementary material Appendix 2 Fig. A2) – 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 (Supplementary material Appendix 1 Table A1). Fifty-one species had > 10 presences across all surveys (Supplementary material Appendix 1 Table A1) 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; Supplementary material Appendix 2 Derivation A1), 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 weight 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 10–1000 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 (Supplementary material Appendix 1 Table A1). 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 ; Supplementary material Appendix 2 Fig. A3; full model results, including significance of GLMMs can be found in Supplementary material Appendix 2 Table A2). 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 (Supplementary material Appendix 2 Fig. A4). 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. Supplementary material Appendix 2 Fig. A5, A6). 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. Supplementary material Appendix 2 Fig. A5, A6).

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 interspecific variation, although we note that species can indeed be clustered into those which respond to urbanization positively, negatively and show mixed responses (Fig. 1). The difference,

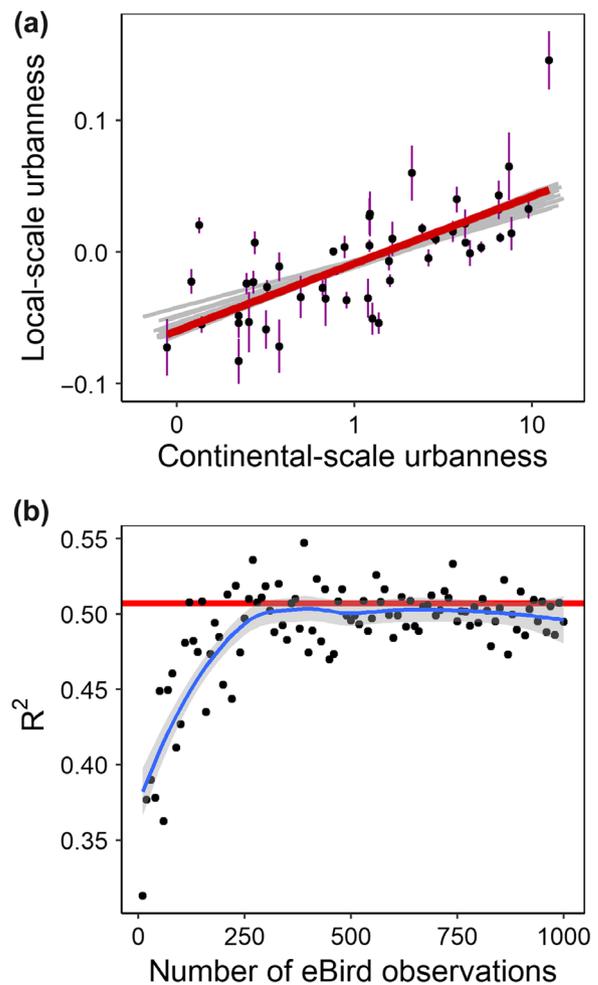


Figure 2. (a) Continental-scale urbanness (x-axis) is the median of a species' distribution of all continental eBird observations in response to VIIRS night-time lights, presented on a log-scale: greater values equate to greater urban-tolerance (Supplementary material Appendix 2 Fig. A6). Local-scale 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 (Supplementary material Appendix 2 Fig. A5). 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 <https://coreytcallaghan.github.io/ECOG-04863/local_cont_urbanness.html>. (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.

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 (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, b). 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 (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, Boakes et al. 2010, Belt and Krausman 2012) 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.

Data availability statement

Code and data necessary to reproduce these analyses have been uploaded as Supplementary material and available archived from the Zenodo Digital Repository: <<http://dx.doi.org/10.5281/zenodo.3559181>> (Callaghan et al. 2019c).

Acknowledgements – Mark Ley, Simon Gorta and Max Breckenridge were instrumental in conducting surveys in the Blue Mountains. We also are grateful to the numerous volunteers who submit their data to eBird, and the dedicated team of reviewers who ensure the quality of the database. We thank the associate editor and two anonymous reviewers for comments that improved this manuscript.

Funding – Funding for this work was provided by the Australian Wildlife Society.

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.

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Supplementary material (available online as Appendix ecog-04863 at <www.ecography.org/appendix/ecog-04863>). Appendix 1–2.