Validation of a globally-applicable method to measure urban tolerance of birds using citizen science data

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ABSTRACT

Understanding species-specific responses to urbanization is essential to mitigate and preserve biodiversity in the face of increasing urbanization, but a major challenge is how to estimate urban tolerances for a wide array of species applicable over disparate regions. A promising approach is to assess urban tolerance by integrating geo-referenced information on species detections from citizen science data with estimations of urbanization intensity based on remotely-sensed night-time lights. While such citizen science urbanness scores (CSUS) are cost-effective, intuitive, and easily-repeatable anywhere in the world, whether the scores accurately describe urban tolerance still awaits empirical verification. By analyzing >900 bird species worldwide, we find that CSUS correlates well with a standard measure of urban tolerance based on changes in abundance between urbanized and non-urbanized nearby habitats. Our analyses show that there is substantial variability in the relationship between these two metrics, but nevertheless highlights the potential for the CSUS approach in the future. Future improvements to the index, including incorporating rare species, and understanding the influence of intra-specific variability in response to urbanization, will be necessary to maximize the broad utility of the approach.

Keywords: big data; biodiversity; birds; citizen science; urban tolerance; urban ecology

INTRODUCTION

Cities are novel environments relative to the evolutionary history of nearly all terrestrial organisms. In such artificial environments, natural vegetation is replaced by artificial structures (Kenneth et al. 2005), perturbations associated with human activities become pervasive, the levels of chemical, noise, and light pollution dramatically increase (Swaileh and Sansur 2006, Francis et al. 2011, La Sorte et al. 2017), and primary productivity substantially decreases (Milesi et al. 2003). These novel challenges may generate maladaptations, causing many species to avoid cities or lead to their failure to persist there (Sol et al. 2014). However, not all species are negatively affected by urbanization. In fact, in urban environments some species are even doing better than ever, to the point they become pests. With a projected increase in urban land cover of around 2-3 billion km^2 by 2050 (Huang et al. 2019), identifying which species will be 'losers' or 'winners' when facing urbanization has become essential to assess the impact of urbanization on biodiversity and to help prioritize conservation plans within cities.

There has historically been a suite of vastly different approaches to quantify urban tolerance — defined as the ability of a species to persist in urban environments (reviewed in Sol et al. 2013). Ranked from simple to complex, these include: (1) assigning species as being either 'urban' or 'non-urban' based on their presence in the respective habitats at any given time (Møller et al. 2009); (2) classifying species based on the mention of human-built structures in published habitat descriptions (Cardoso 2014); (3) classifying species based on breeding evidence in a city (e.g., Croci et al. 2008); (4) circulating surveys to birdwatchers and ornithologists to compile lists of common native breeding birds in their respective cities (Bonier et al. 2007); and (5) estimating species sensitivity to urbanization by quantifying changes in their relative abundances or densities along urbanization gradients (Evans et al.

2011, Sol et al. 2014, Sol et al. 2017, Sayol et al. 2020). Although the application of these metrics has largely improved our understanding of organismal responses to urbanization, they have limitations when it comes to uncovering patterns at large spatial scales. For example, categorizing species based on their presence/absence in cities fails to account for the continuous nature of species-specific responses to urbanization (Evans et al. 2011, Sol et al. 2013, Callaghan et al. 2020), and is likely to inadequately identify species which do not tolerate cities well, but are present there through source-sink dynamics. It also ignores that a species can be absent in the city not because it cannot tolerate it, but because it is too scarce in the surrounding habitats to generate propagules (Sol et al. 2013, 2014). Moreover, a species categorized as an urban adapter in one city may be an urban avoider in another city. Measuring tolerance to urbanization using indices derived from surveys along urbanization gradients provides higher resolution, yet sampling assemblages over large regions is costly and time-consuming. This means that information is only available for some regions, mostly from highly-developed countries (Sol et al. 2020). Moreover, combining information from different regions is challenging because different studies often use different survey protocols and different definitions of urbanization gradients (but see Sol et al. 2014, 2020). A more general measure of urban tolerance — applicable from local to global scales — is clearly needed to enhance our understanding of organismal responses to urbanization.

Recently, Callaghan et al. (2019a, 2020a) proposed an alternative measure of urban tolerance that capitalizes on citizen science data, providing species-specific urbanness scores (CSUS, hereafter). The CSUS approach intersects broad-scale citizen science observations of species with estimates of human settlements based on globally available, remotely-sensed, VIIRS (Visible Infrared Imaging Radiometer Suite) night-time lights. Species' urban tolerances are defined as the median VIIRS night-time lights across their range of observations (urbanness scores, hereafter). Assuming that species' observations are equally sampled in urban and non-urban areas, species with high urbanness scores are interpreted to be more urban-tolerant than species with low urbanness scores (Callaghan et al. 2020a).

Although the CSUS metric is based on occurrences rather than abundances, it has the advantage of being cost-effective, intuitive, and easily-repeatable anywhere in the world. The CSUS approach assumes that species' observations across an urbanization gradient represent a species' likelihood of using habitats along this urbanization gradient, and severe violations of this assumption could make the CSUS metric imprecise and thus unreliable in macroecological analyses. Therefore, a limitation of the approach is the need of relatively large numbers of observations to accurately capture the species-specific variation in response to urbanization. However, this limitation is currently less important in the "big data" era, particularly for taxonomic groups like plants and birds which are easy to observe and for which observations are rapidly accumulating worldwide. In birds, for example, the eBird project (Sullivan et al. 2009) currently has more than 800 million observations all over the worlds. In birds, the CSUS approach has been used to assess ecological and life-history traits associated with urban tolerance (Callaghan et al. 2019a) and assign community-measures of urbanness (Callaghan et al. 2019b), albeit this approach is currently restricted to the common species.

While the CSUS approach provides promise for advancing our understanding of species' tolerance to urbanization (see Callaghan et al. 2020a), its robustness remains to be demonstrated. Testing the general validity of the approach is the goal of the present study. Specifically, we estimate the urbanness scores for >900 species from 26 cities worldwide, and compare the scores with previously published information on species tolerance to urbanization from the same regions estimated as changes in abundance between urban and non-urban surrounding environments. Our analyses show that there is substantial variability in the relationship between these two metrics, but nevertheless highlights the potential for the CSUS approach in the future.

METHODS

Urbanness scores

We followed Callaghan et al. (2019a, 2020a) to assign species-specific urbanness scores. We first gathered all available observations in the eBird citizen science dataset (version ebd_relMay-2019; Sullivan et al. 2009) for the species from the 26 cities studied, excluding species that primarily rely on coast-lines and/or large water bodies (habitats that are little represented in the studied cities). After filtering the eBird data by removing potential outliers (see Callaghan et al. 2019b), we assigned a measure of VIIRS night-time lights to each observation. Monthly scenes of average radiance (nW cm^{-2} sr^{-1}) between January 1st, 2014 and January 1st, 2019 were used, and the temporal median radiance was calculated per pixel at the native 500 m resolution, which was reprojected into a pixel size of 5 km using a composite stack of the 2014-2019 VIIRS night-time light layers. Finally, we estimated the urbanness score for each species at two spatial scales: as the median value across all observations within a 250 km buffer around the city (regional scale) or the entire continent where a city was located (Table S1). A 250 km buffer was chosen to incorporate landscape-scale observations, and assumes that the common species sampled within this buffer have an equal opportunity to occupy the area throughout the buffer (i.e., their range encompasses the entire buffer), depending on habitat preferences (i.e., level of urban tolerance). A test with 100 km buffer showed qualitatively similar results to that of a 250 km buffer. We used a random sampling analysis to test the influence of sample size in the estimation of urbanness scores and found that at ~100 observations the variation in the urbanness score was significantly lower for most species (see Figure S1). Thus, we only estimated urbanness scores for species with a minimum of 100 eBird observations (Callaghan et al. 2019a). However, we note that a cutoff of 250 observations yielded qualitatively similar results. We also restricted the analyses to cities with a minimum of 10 species. After filtering, we were left with a total of 771 species from 25 cities for the regional-scale comparison (Figure S2), incorporating 22,839,841 species' observations. For the continental-scale comparison, after filtering, we were left with a total of 934 species from 26 cities (Figure 1; Figure S3), incorporating 226,388,416 species' observations.

Urban tolerance based on abundance data

We used a dataset of bird assemblages across 26 cities worldwide (Sol et al. 2014, 2017, Sayol et al. 2020) to derive an abundance-based measure of urban tolerance (Figure 1). These data are a comprehensive compilation of published datasets incorporating characterized assemblages with local survey data available in both urban and nearby rural/natural habitats. The 26 cities were spread among 7 regions: Africa (N=1); Asia (N=4); Australia (N=3); Europe (N=5); New Zealand (N=1); North America (N=8); and South America (N=4). To the best of our knowledge, this is the most robust dataset available for comparison with the CSUS approach. Importantly, although we use these data to show the correlation with the CSUS approach, the data for the CSUS approach (i.e., eBird data) are generally globally-available (although heterogeneous across the world) as are the VIIRS night-time lights data. For each city in the dataset, bird abundances were available within built-up urban environments and in the surrounding non-urbanized habitats. The dataset comprises assemblages sampled in four types of habitats, ranging from natural vegetation, little urbanized environments, moderately urbanized environments, and highly urbanized environments (Sol et al. 2020). The urban tolerance index of a species was estimated as the log-log difference between its abundance within (i.e., from the highest possible urbanization category a species was observed) and outside (i.e., natural vegetation) the city (see Sol et al. 2014, Sayol et al. 2020). A positive value indicates that the species was more common in the city than in the surrounding natural habitats whereas a negative value indicates that the species was less common in the city than in the surrounding natural habitats. Because values close to zero are difficult to interpret (Sol et al. 2013), we further categorized the urban tolerance abundance index into four categories (*sensu* Sol et al. 2014; 2017): (1) Urban Absent (i.e., a species was observed only in wild areas); (2) Urban Increase (i.e., a species' abundance was greater in urban than in wild habitats); (3) Wild Increase (i.e., a species' abundance was greater in wild than in urban habitats); and (4) Wild Absent (i.e., a species was observed only in urban areas).

Statistical analysis

All analyses were conducted in R statistical software (R Core Team 2020). We tested the extent to which our CSUS approach is predicted by the local-scale abundance-based urban tolerance by means of a phylogenetic mixed-effects model. The response variable was log-transformed urbanness scores and the predictor variable was the local-scale abundance-based urban tolerance index. We used the MCMCglmm R-package (Hadfield 2010) to fit a mixed model that included both city and phylogeny as random effects. Cities were included as a random effect to account for possible significant differences among cities (e.g., level of urbanization, size, differing population density dynamics). For these models, we used an inverse-wishart priors for the random effects (V = 1, nu = 0.002), and ran the models for 1010000 iterations, with a burn-in of 10000 and a thinning interval of 1000, resulting in a posterior distribution of 1000 samples. We ensured that the autocorrelation of samples was below 0.1 and that the model converged properly. We also fit these models with only the intercept to assess the variability in the response determined by phylogeny and city. The phylogenetic tree included in the models was a MCC tree from the posterior distribution of all trees with Ericsson backbone, extracted from the BirdTree.org project (Jetz et al. 2012). All models were run at the regional and continental scales separately. Lastly, we used a linear model to test how our urbanness measures categorically separated species, based on categorical classifications of the local-scale abundance-based urban tolerance index. Effect sizes of pairwise differences among categories were extracted using the emmeans R-package (Lenth 2020).

RESULTS

Our analyses revealed a good correspondence between the urbanness scores and the local-scale abundance-based urban tolerance indices. At the regional-scale, the urbanness scores showed a clear positive relationship, albeit with a small effect size, with the continuous version of the local-scale abundance-based urban tolerance index after controlling for city and phylogenetic effects (posterior mean and 95% C.I. ß=0.035 [0.028-0.043], pMCMC<0.001; Figure 2a; Figure S4a). We also found evidence for phylogenetic signal in the urbanness scores (Intra-class coefficient = 0.529, 95% C.I. = 0.525 to 0.533), and some heterogeneity among cities (Intra-class coefficient = 0.234, 95% C.I. = 0.230 to 0.238). The urbanness scores were also well-predicted by the categorical representation of the local-scale abundance-based urban tolerance (Figure 2a), with the lowest mean being derived from the urban absence category (1.49 ± 2.28), substantially lower than that in the wild absence category (4.31 ± 6.34) and the urban increase category (5.48 ± 8.03) and the pairwise effect sizes supported these comparisons (Table S2). When looking at city-specific correlations

(Figure S5; Table S3), all cities were positively correlated with the exception of Tornio, Santa Fe, La Paz, and Cayenne (average correlation = 0.16, range 0.005-0.44).

As with the regional-level analyses, the continental-scale analysis of urbanness scores also revealed a positive relationship with the local-scale abundance-based urban tolerance once city and phylogenetic effects were accounted for (posterior mean and 95% C.I. ß=0.012 [0.005-0.018], pMCMC<0.001); Figure 2b; Figure S4b). However, this relationship was much weaker than that for the regional-scale analysis (Figure S4). We also found evidence for phylogenetic signal in the urbanness scores calculated at the continental-scale (Intra-class coefficient = 0.910, 95% C.I. = 0.908 to 0.911), and less heterogeneity among cities (Intra-class coefficient = 0.041 95% C.I. = 0.040 to 0.042). The urbanness scores were also well-predicted by the categorical representation of the local-scale abundance-based urban tolerance (Figure 2b) with the lowest mean urbanness score being derived from the wild increase category (1.52 ± 1.6) followed by the urban absence category (1.57 ± 3.43) and the highest mean being derived from the wild absence category (3.58 ± 7.30) followed by urban increase (3.21 ± 4.88) and the effect sizes confirmed these patterns (Table S2). When looking at city-specific correlations (Figure S5; Table S3), nearly all cities had a positive correlation between both metrics (average correlation = 0.15, range 0.0002-0.48).

DISCUSSION

We leveraged increasingly available and accessible citizen science data and provided evidence that a simple and intuitive method of deriving species-specific urbanness scores correlates with local-level abundance data from 26 cities across the world (Figure 2), and that the accuracy improves with the number of observations used to assess the species-specific urbanness scores (Figure S1). This study is the broadest validation of the CSUS approach, demonstrating its potential future utility in urban ecology. Importantly, while the CSUS approach showed correlation with local-scale survey data from a subset of worldwide cities (Figure 1), the data used to derive the CSUS approach are globally-applicable (i.e., eBird data are nearly global, albeit heterogeneously distributed; and VIIRS night-time lights are globally available).

The urbanness scores calculated at the regional-scale were more strongly related to the local-scale abundance-based urban tolerance than those derived from continental-scales, and the relationship at the continental scale was overall quite weak. However, both relationships were statistically significant and positive (Figure 2; Figure S4), confirming that continental-scale data correlates, albeit weakly, with regional-scale responses to urbanization (Callaghan et al. 2020a). The main advantage of a continental-scale approach is to broaden species coverage by increasing the number of observations. In our case, this meant an increase from 771 to 934 species by the addition of species which met the threshold for the minimum number of observations. However, the use of a continental-scale approach likely comes at a cost of more variability in species-specific responses, and as the sample sizes continue to increase in global citizen science data, regional-scale urbanness scores will likely be easier to calculate for a broader suite of species (i.e., more species will meet the necessary sample thresholds).

Although we found a consistent correspondence between the urbanness scores and local-scale abundance-based urban tolerance (Figure 2), there still remained variability among cities, especially at the regional scale (i.e., 23% of the variability in the model was explained by city). The cities that showed the weakest correlation (e.g., Valencia) tended to be coastal cities, where the VIIRS night-time lights measures are more likely to be affected by large bodies of water. The differences among cities could also be a result of the differing likelihoods of detection for species in different regions or the differing patterns of use in eBird among the different regions in our analysis. For example, cities in the US were all relatively well-correlated, with Gainesville having the highest correlation among cities (R^2=0.44), and Iowa (R^2=0.26), and Minneapolis/St. Paul (R^2=0.24) were also strongly-correlated, likely reflecting the fact that the United States is where eBird data are currently most numerous. There are many other city-specific differences that likely influences the variability among cities, including the connectivity of green areas, the compactness of a city (i.e., land sharing vs land sparing), the biophysical characteristics of a city, and the human population density throughout a city. Each of these factors should be further explored in the context of how the CSUS performs on a city-by-city basis. Although more research is needed to fully understand the differences among cities, our results suggest that as eBird, and other large-scale citizen science projects, grow in popularity in other parts of the world, the utility of our approach may also increase.

Importantly, we found evidence of phylogenetic effects in the urbanness scores at both the regional and continental scales, confirming previous results (Sol et al. 2014) with a conceptually distinct metric. The existence of phylogenetic effect suggests that closely-related species tend to respond to urbanization in a similar way. This is to be expected considering that some of the adaptations found to affect tolerance to urbanization, like an encephalized brain or a slow life history strategy, are highly conserved phylogenetically. Interestingly, we found a much stronger effect of phylogeny when considering urbanness scores calculated at the continental-scale than the regional-scale, likely a result of macroecological differences in habitat use reflected by phylogeny over the larger macroecological scales. Our CSUS approach provides the necessary data to further disentangle the degree to which urban tolerance is phylogenetically conserved for many species.

Our CSUS approach clearly shows promise, but future work should build upon this foundation and improve this approach to further maximize its utility and validity. First, we currently focus on macro-ecological patterns (i.e., regional to continental scales), but it is possible this approach could be used to further inform more localized patterns. For example, some species change their adaptability to urbanization through time (e.g., Evans et al. 2009), and future research should test the ability of this approach to appropriately track species' changes to urban tolerance through time; both intra-annually and inter-annually. For example, the utility of VIIRS night-time lights for understanding intra-annual patterns of individual gulls at a local-scale using GPS-tracking data has recently highlighted the potential for future work on local-scale urban tolerance (Ramírez et al. 2020). Second, we currently only look at the presence or absence of a species across an urbanization gradient. Yet, eBird data can provide relative abundance estimates across this gradient. Future work should thus test whether there are significant differences between presence/absence and abundance-weighted measures of the CSUS approach because abundance-weighted measures could provide valuable insights and more power to differentiate among species-specific responses to urbanization (e.g., Sol et al. 2020). Third, our approach does not account for the differing levels of available urban habitat among species' geographic ranges, potentially influencing our urbanness scores (Callaghan et al. 2020b). For example, a species may be often observed in urban areas, yet have a low urbanness score because its geographic range is relatively non-urban. Indeed, this is probably why we found a stronger relationship for regional-scale urbanness scores than continental-scale urbanness scores when compared with the local-scale abundance-based urban tolerance index. At a regional-scale (i.e., a 250km buffer) it would be unlikely that species' have significantly differing range sizes and most species found within the city likely have ranges that encompassed the entire regional-buffer, whereas at a continental-scale species' geographic ranges would more likely differ and thus the available urban habitat for that species could also differ; and this probably differentially affects generalists and specialists. However, methods which account for the available urban habitat in a species' range (e.g., by standardizing urbanness scores by a range-wide urbanness measure) may further enhance our CSUS approach and this should be formally tested (Callaghan et al. 2020b). Fourth, the CSUS approach relies on the median of the distribution, potentially missing multimodal responses of a given species. A multimodal distributional response to urbanization is likely a result of sampling biases from citizen science data, where birdwatchers preferentially go to known sites for specific species. However, it is also possible that a given species could show intra-specific variability in their response to urbanization, for example where one population of a species is an urban adapter in one part of its range but an urban avoider in another part of its range. We suggest that at the regional-scale (i.e., 250 km buffer) this is unlikely to be the case because for the common species, they are most likely able to use any part of the habitat within that buffer. But at continental-scales, it is possible for species to have differing levels of urban tolerance. Currently, our approach cannot disentangle multimodal responses to urbanization, but future development should investigate possible statistical approaches to assess multimodal responses and when this represents biological variability versus underlying sampling biases. And lastly, while we demonstrate this approach with data using birds, many other taxa are increasingly studied in urban areas using citizen science projects, such as bees (Mason and Arathi 2019), butterflies (Matteson et al. 2012), and mammals (Williams et al. 2015). Therefore, our approach should be formally implemented using other taxa, potentially relying on broad-scale citizen science projects such as iNaturalist.

Current methods of assigning urban tolerance to species have been fundamental in enhancing our understanding of biodiversity responses to urbanization, but they also have limitations concerning their interpretation and sampling biases (Sol et al. 2013, 2020). Our approach also has limitations, as described above, yet it extends previous methods by providing a continuous measure of tolerance for most species and regions of the planet. Moreover, integrating our approach with previous metrics will likely provide much promise in our ability to better predict the responses of biodiversity to urbanization (e.g., Fithian et al. 2014). The CSUS approach should be used to further our understanding of the effects of urbanization on biodiversity in under-studied regions where professionally-collected data are often lacking (e.g., tropical regions), across broad taxonomic coverage (e.g., including many more species than previously possible), through time (e.g., intra- and inter-annual changes in responses to urbanization), and across spatial scales (e.g., understanding how species respond to urbanization at different scales). In conclusion, we showed that there is strong potential in our CSUS approach, especially at regional scales, and future work should further unlock this potential and utilize this approach to make broad-scale comparisons advancing urban ecological and conservation research.

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REFERENCES

Aceves-Bueno, E., Adeleye, A.S., Bradley, D., Brandt, W.T., Callery, P., Feraud, M., Garner, K.L., Gentry, R., Huang, Y., Mccullough, I., Pearlman, I., Sutherland, S.A., Wilkinson, W., Yang, Y., Zink, T., Anderson, S.E. & Tague, C. (2015) Citizen Science as an Approach for Overcoming Insufficient Monitoring and Inadequate Stakeholder Buy-in in Adaptive Management: Criteria and Evidence. *Ecosystems*, **18**, 493–506.

Bonier, F., Martin, P.R. & Wingfield, J.C. (2007) Urban birds have broader environmental tolerance. *Biology Letters*, **3**, 670–673.

Callaghan, C.T., Major, R.E., Wilshire, J.H., Martin, J.M., Kingsford, R.T. & Cornwell, W.K. (2019a) Generalists are the most urban-tolerant of birds: a phylogenetically controlled analysis of ecological and life history traits using a novel continuous measure of bird responses to urbanization. *Oikos*, **128**, 845–858.

Callaghan, C.T., Major, R.E., Lyons, M.B., Martin, J.M., Wilshire, J.H., Kingsford, R.T. & Cornwell, W.K. (2019b) Using citizen science data to define and track restoration targets in urban areas. *Journal of Applied Ecology*, **56**, 1998–2006.

Callaghan, C.T., Major, R.E., Cornwell, W.K., Poore, A.G.B., Wilshire, J.H. & Lyons, M.B. (2020a) A continental measure of urbanness predicts avian response to local urbanization. *Ecography*, **43**, 528–538.

Callaghan, C.T., Benedetti, Y., Wilshire, J.H., and Morelli, F. 2020b. Avian trait specialization is negatively associated with urban tolerance. Oikos early view: https://doi.org/10.1111/oik.07356

Cardoso, G.C. (2014) Nesting and acoustic ecology, but not phylogeny, influence passerine urban tolerance. *Global Change Biology*, **20**, 803–810.

Croci, S., Butet, A. & Clergeau, P. (2008) Does Urbanization Filter Birds On The Basis Of Their Biological Traits? *The Condor*, **110**, 223–240.

Er, K.B., Innes, J.L., Martin, K. & Klinkenberg, B. (2005) Forest loss with urbanization predicts bird extirpations in Vancouver. *Biological Conservation*, **126**, 410–419.

Evans, K.L., Gaston, K.J., Frantz, A.C., Simeoni, M., Sharp, S.P., Mcgowan, A., Dawson, D.A., Walasz, K., Partecke, J., Burke, T. & Hatchwell, B.J. (2009) Independent colonization of multiple urban centres by a formerly forest specialist bird species. *Proceedings of the Royal Society B: Biological Sciences*, **276**, 2403–2410.

Evans, K.L., Chamberlain, D.E., Hatchwell, B.J., Gregory, R.D. & Gaston, K.J. (2011) What makes an urban bird? *Global Change Biology*, **17**, 32–44.

Fithian, W., Elith, J., Hastie, T. & Keith, D.A. (2014) Bias correction in species distribution models: pooling survey and collection data for multiple species. *Methods in Ecology and Evolution*, **6**, 424–438.

Francis, C.D., Ortega, C.P. & Cruz, A. (2011) Noise Pollution Filters Bird Communities Based on Vocal Frequency. *PLoS One*, 6.

Hadfield, J.D. (2010) MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *Journal of Statistical Software*, **33**, 1–22.

Huang, K., Li, X., Liu, X. & Seto, K.C. (2019) Projecting global urban land expansion and heat island intensification through 2050. *Environmental Research Letters*, **14**, 114037.

Jetz, W., Thomas, G.H., Joy, J.B., Hartmann, K., & Mooers, A.O. (2012) The global diversity of birds in space and time. *Nature*, **491**, 444–448.

Kenneth, B.H., Innes, J.L., Martin, K., & Klinkenberg, B. (2005) Forest loss with urbanization predicts bird extirpations in Vancouver. *Biological Conservation*, **126**, 410–419.

Mason, L., & Arathi, H. S. (2019). Assessing the efficacy of citizen scientists monitoring native bees in urban areas. *Global Ecology and Conservation*, **17**, e00561.

Matteson, K. C., Taron, D. J., & Minor, E. S. (2012). Assessing citizen contributions to butterfly monitoring in two large cities. *Conservation Biology*, **26**, 557–564.

McKinley, D.C., Miller-Rushing, A.J., Ballard, H.L., Bonney, R., Brown, H., Cook-Patton, S.C., Evans, D.M., French, R.A., Parrish, J.K., Phillips, T.B., Ryan, S.F., Shanley, L.A., Shirk, J.L., Stepenuck, K.F., Weltzin, J.F., Wiggins, A., Boyle, O.D., Briggs, R.D., Chapin, S.F., Hewitt, D.A., Preuss, P.W., * Soukup, M.A. (2017) Citizen science can improve conservation science, natural resource management, and environmental protection. *Biological Conservation*, **208**, 15–28.

McKinney, M.L. (2006) Urbanization as a major cause of biotic homogenization. *Biological Conservation*, **127**, 247–260.

Milesi, C., Elvidge, C.D., Nemani, R.R. & Running, S.W. (2003) Assessing the impact of urban land development on net primary productivity in the southeastern United States. *Remote Sensing of Environment*, **86**, 401–410.

Møller, A.P. (2009) Successful city dwellers: a comparative study of the ecological characteristics of urban birds in the Western Palearctic. *Oecologia*, **159**, 849–858.

Pocock, M.J.O., Tweddle, J.C., Savage, J., Robinson, L.D. & Roy, H.E. (2017) The diversity and evolution of ecological and environmental citizen science. *PloS One*, 12.

Ramírez, F., Afán, I., Bouten, W., Carrasco, J.L., Forero, M.G. & Navarro, J. (2020) Humans shape the year-round distribution and habitat use of an opportunistic scavenger. *Ecology and Evolution*.

Sayol, F., Sol, D. & Pigot, A.L. (2020) Brain Size and Life History Interact to Predict Urban Tolerance in Birds. *Frontiers in Ecology and Evolution*, 8.

Sol, D., Lapiedra, O. & González-Lagos, C. (2013) Behavioural adjustments for a life in the city. *Animal Behaviour*, **85**, 1101–1112.

Sol, D., Bartomeus, I., González-Lagos, C. & Pavoine, S. (2017) Urbanisation and the loss of phylogenetic diversity in birds. *Ecology Letters*, **20**, 721–729.

Sol, D., González-Lagos, C., Moreira, D., Maspons, J. & Lapiedra, O. (2014) Urbanisation tolerance and the loss of avian diversity. *Ecology Letters*, **17**, 942–950.

Sol, D., Trisos, C., Múrria, C., Jeliazkov, A., González-Lagos, C., Pigot, A.L., Ricotta, C., Swan, C.M., Tobias, J.A. & Pavoine, S. (2020) The worldwide impact of urbanisation on avian functional diversity. *Ecology Letters*.

Sorte, F.A.L., Fink, D., Buler, J.J., Farnsworth, A. & Cabrera-Cruz, S.A. (2017) Seasonal associations with urban light pollution for nocturnally migrating bird populations. *Global Change Biology*, **23**, 4609–4619.

Sullivan, B.L., Wood, C.L., Iliff, M.J., Bonney, R.E., Fink, D. & Kelling, S. (2009) eBird: A citizen-based bird observation network in the biological sciences. *Biological Conservation*, **142**, 2282–2292.

Swaileh, K.M. & Sansur, R. (2006) Monitoring urban heavy metal pollution using the House Sparrow (*Passer domesticus*). *Journal of Environmental Monitoring*, **8**, 209–213.

Williams, R.L., Stafford, R., & Goodenough, A.E. (2015) Biodiversity in urban gardens: Assessing the accuracy of citizen science data on garden hedgehogs. *Urban Ecosystems*, **18**, 819–833.

FIGURES

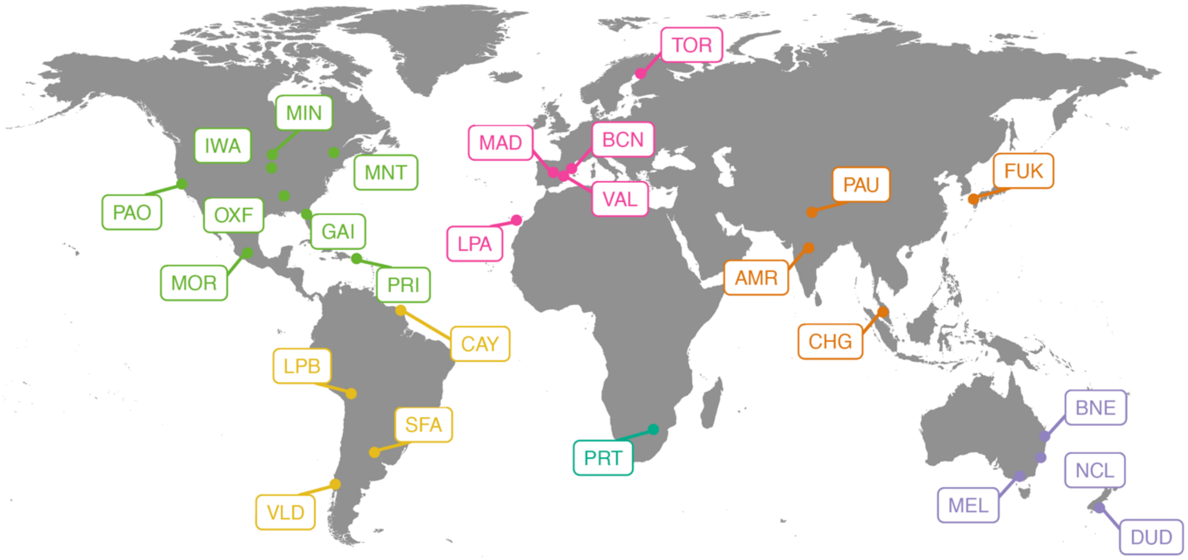
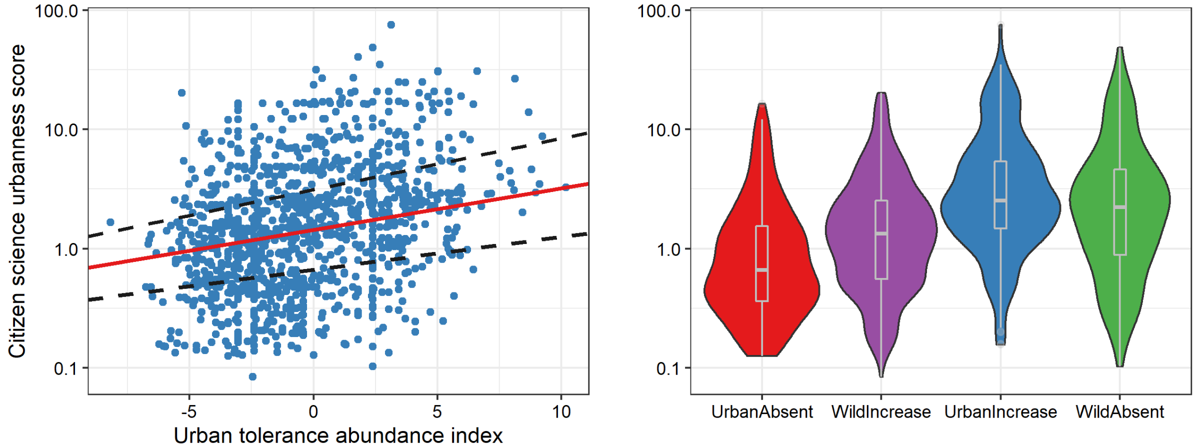


Figure 1. A map showing the 26 cities used in our analysis, colored by general region.


a) Regional-level urban scores (N=771 species)

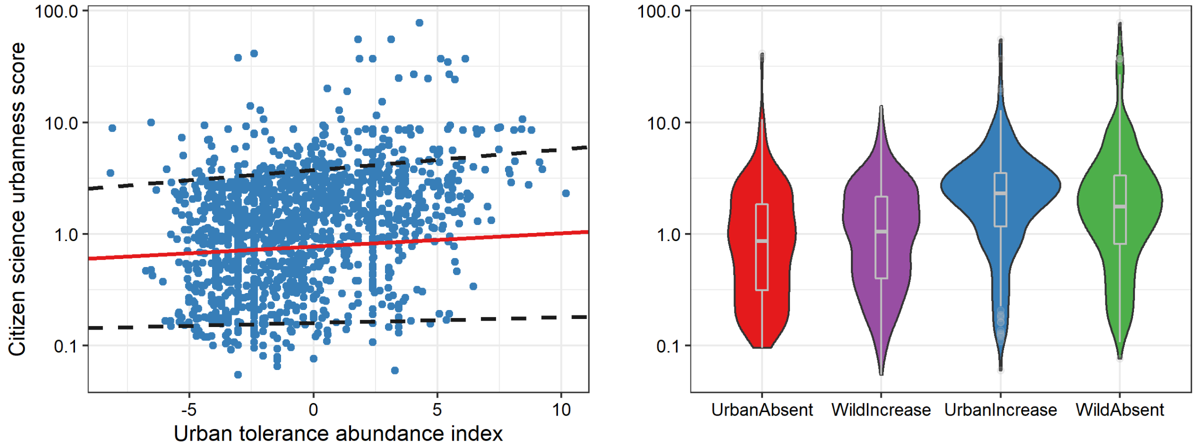

b) Continental-level urban scores (N=934 species)

Figure 2. a) The relationship between our citizen science urbanness measure calculated at the regional-scale (i.e., within a 250 km buffer) and the urban tolerance abundance index for each city shown on a continuous scale and on a categorical scale. b) The same relationship, but shown with urban scores calculated using the continental-level spatial scale (see Table S1). The red line represents the slope and intercept extracted from our MCMCglmm and accounts for the random effect of city and phylogenetic effects, and the black dashed lines represent the 95% CI surrounding the slope. A species may be included more than once, if it is detected in different cities.