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Urbanization negatively impacts frog diversity at continental, regional, and local scales

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Abstract

Urban environments are novel ecosystems, with increased chemical, sound, and light pollution differentially impacting many animals. Understanding the impacts of urban environments on biodiversity is the first step to understanding how to best mitigate biodiversity losses in an increasingly urbanizing world. Analyses with broad geographic and taxonomic coverage can offer critical context for informing urban biodiversity conservation. But such studies are currently lacking, especially for under-studied, but likely highly impacted, taxa such as frogs. Our objective was to document frog diversity in relation to urban environments at continental, regional, and local scales. We used FrogID data, an opportunistic citizen science dataset generated by volunteers recording calling frogs using a smartphone and validated by experts throughout continental Australia, to calculate species richness, Shannon diversity, and phylogenetic diversity of frogs in urban and non-urban areas, as well as along a continuous urbanization gradient. The overall species richness of frogs was, on average, 57% less in urban than non-urban areas across six ecoregions. Further, we found significantly lower frog diversity in urban environments compared with non-urban environments across the country, with an average reduction of 59% species richness, 86% Shannon diversity, and 72% phylogenetic diversity. We also found evidence for a steady decrease in frog diversity along an urbanization gradient, with no obvious thresholds. Our results highlight the negative impacts of urbanization, at a continental scale, on frog diversity, and clearly highlight the necessity to consider frog diversity in future urban land development decisions.

Keywords: Anurans; Biodiversity; Urban ecology; Species richness; Phylogenetic diversity; Shannon diversity; Urban gradients; Cities

Introduction

The conversion of natural habitat into urbanized land (Vliet, 2019), combined with anthropogenically-driven increases in light-pollution, noise pollution, and habitat fragmentation within urban environments (Swaileh &

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Sansur, 2006; Francis Ortega, & Cruz, 2011; Liu, He, & Wu, 2016), generally leads to negative impacts on local biodiversity (McKinney, 2006). Species richness (Concepción, Obrist, & Moretti, 2015), species diversity (Wang, Lyons, Kanehl, & Bannerman, 2001), functional diversity (Nock, Paquette, & Follett, 2013), and phylogenetic diversity (Knapp et al. 2017) for example, have all been shown to be negatively impacted by urbanization. In contrast, urban areas may also serve as refugia for different ecosystem functions such as pollination (e.g., Staab, Pereira-Peixoto, & Klein, 2020) or threatened species (Ives et al. 2016). And diversity can even be increased within urban areas compared with non-urban areas (Callaghan, Bino, & Major, 2019). Regardless of a species or community response to urbanization, urban environments are expanding at a rate of almost 10,000 km^2 per year (Liu, Huang, & Xu, 2020), making it essential to better understand and quantify the impacts of urban environments on biodiversity.

Our knowledge of how biodiversity responds to urbanization is largely dominated by taxa such as birds and mammals, with comparatively little understanding of the impacts of urbanization on fish, plants, and amphibians (Magle, Hunt, Vernon, & Crooks, 2012). Amphibians have characteristics that are likely to make them more susceptible to urban environments compared with other taxa (Hamer & McDonnell 2008; Hopkins, 2007). Their bi-phasic lifestyle with reliance on both freshwater and terrestrial habitats, often specific habitat requirements (Semlitsch, 2000), and low vagility compared to most birds or mammals renders most amphibian species highly sensitive to environmental perturbations. Unsurprisingly then, more than 40% of all amphibian species are threatened by residential and commercial development alone (IUCN 2020). Habitat modification (e.g., roads, residential developments) within 1 km of breeding sites can reduce species occurrence and abundance (Gagné & Fahrig 2010; Villaseñor et al. 2017; Anderson, 2019). Urban environments reduce available breeding habitat (Westgate et al. 2015) and can inadvertently create ecological traps (Sievers, Parris, Swearer, & Hale, 2018), reducing both juvenile and adult survival due to poor water quality (Hamer & McDonnell 2008; Snodgrass, Casey, Joseph, & Simon, 2008). Moreover, urban environments can modulate or impede the transmission of mating calls due to increased sensory pollutants (Simmons & Narins 2018), and there can be increased road mortality in urban environments (Fahrig et al. 1995). Overall, such anthropogenic pressures can both singularly and cohesively negatively influence the mating success and survival of amphibians in urban areas.

Despite the general recognition of the threats that urban environments pose, there remains little broad-scale evidence of the extent to which urbanization impacts amphibians. Our current understanding of the impacts of urbanization on amphibian diversity is currently geographically and taxonomically restricted. The majority of studies which have quantified the impact of urbanization on amphibians have been across relatively small scales, often incorporating single cities or local regions (Houlahan & Findlay 2003; Pillsbury & Miller 2008; Westgate et al. 2015). Consequently, the taxonomic coverage of these studies is often limited (Scheffers & Paszkowski, 2012), failing to incorporate a full suite of species and often disproportionately focused on pond-breeding species (Gagné & Fahrig, 2010; Kaczmarski, Benedetti, & Morelli, 2020). Thus, increased taxonomic coverage in analyses will provide a greater understanding of how specific lineages of frogs are differentially impacted by urbanization.

While analyses at broad spatial-scales are necessary to fully quantify the extent of urbanization on amphibian diversity, quantifying the local-scale impacts of urbanization will ultimately help inform conservation planning. For example, birds often respond non-linearly to increasing levels of urbanization (e.g., Batáry, Kurucz, Suarez-Rubio, & Chamberlain, 2017; Callaghan et al., 2019), meaning that there may be ‘sweet spots’ across an urbanization gradient where bird diversity peaks or is most significantly negatively impacted. Yet this pattern remains largely untested for amphibian diversity. It is therefore important to understand how amphibian diversity responds across an urbanization gradient, and whether there are certain levels of urbanization where amphibian diversity is most negatively impacted (i.e., thresholds). If specific thresholds exist, for example, then these levels of urbanization could be prioritized for mitigation of amphibian diversity in future urban planning processes.

To provide generalizable patterns — both geographically and taxonomically — of frog diversity to urbanization, broad-scale empirical datasets are necessary. We use a continental-scale citizen science dataset to understand the influence of urban environments on amphibians (241 species of frogs, as of April 2020) in Australia. First, for a total of 196 species of Australian frogs we summarize the number of species found in urban and non-urban areas. Second, we compare frog species richness, Shannon diversity, and phylogenetic diversity in urban areas with non-urban areas using a resampling approach, also treating each urban area as a discrete unit of replication. Third, we move past a categorical representation of urbanization and assess how frog diversity responds to a continuous urbanization gradient, predicting that there would be a threshold where diversity significantly drops. Overall, our analyses provide a continental assessment of the impacts of urban environments on frog diversity.

Materials and methods

Frog observation data using citizen science

FrogID is a national citizen science project in Australia, led by the Australian Museum (Rowley et al. 2019; Rowley & Callaghan 2020). Volunteers use a smartphone app to submit 20−60 second audio recordings of calling frogs with associated spatiotemporal metadata provided from the smartphone app. Each submitted recording is identified by a team of experts. We used FrogID data validated from 10th November 2017 to 13th April 2020, contributed by 12,377 volunteers from 65,499 unique locations (i.e., latitude/longitude combinations). We excluded any submissions that had a geolocation accuracy > 3 km, because these represent submissions which indicated the app was unsure of the location (i.e., potentially > 100 km away; Rowley et al. 2019).

Quantifying frog diversity in urban and non-urban areas

We assigned all FrogID records to a Significant Urban Area throughout Australia (*sensu* Ives et al. 2016). A Significant Urban Area (hereafter SUA) is a predefined measure used by the Australian Statistical Geography Standard, defined by combining one or more adjacent Statistical Areas Level 2 that include one or more Urban Centres. Each SUA has at least one urban center with an urban population of at least 7000 people, an aggregate urban population of at least 10,000 people, and the underlying statistical areas are all in the same labour market. SUAs may cross state or territory boundaries, and there was a total of 101 unique SUAs in our dataset. See ASGS Volume 4 (2016) for more details on the methodology and definition of SUAs.

We further stratified our analyses by ecoregion to account for the biogeographical boundaries of many frog species throughout Australia (*sensu* Callaghan, Roberts, & Poore, 2020). These terrestrial ecoregions were developed by the World Wildlife Fund to reflect the broad range of fauna and flora across the entire planet (Olson, Dinerstein, & Wikramanayake, 2001). Because the ‘Montane Grassland & Shrublands’ ecoregion had no SUAs within it, we removed this ecoregion — and associated data — from analyses. We used the sf package (Edzer, 2018) in the R statistical environment (R Core Team 2019) to spatially intersect each FrogID record with SUAs and ecoregions. Any records which were not spatially intersected (e.g., records where the geoaccuracy placed it in the ocean) were eliminated from further analyses. By stratifying to biogeographical boundaries, this also helps to minimize the effect of spatial and/or temporal biases on our analyses, for instance by keeping effect sizes from well-sampled regions (e.g., Temperate Broadleaf & Mixed Forests) different from poorly-sampled regions (e.g., Deserts & Xeric Shrublands). One source of such bias is the temporal bias in FrogID submissions with unequal sampling across the year. But survey effort is proportional to known calling activity of frogs within a given region (cf. Perth and Darwin SUAs; see Appendix A: Fig. 1). Within an ecoregion, the number of observations per month is largely similar among SUAs (Appendix A: Fig. 2). This systematic bias is therefore unlikely to bias our results surrounding frog diversity in urbanization.

We first summarized the total species richness for urban and non-urban areas, regardless of their ecoregion classification. We then stratified this summary to each respective ecoregion. We used the IUCN Red List of Threatened Species (IUCN 2020) to assign the threatened status of each species in our analysis.

Second, we calculated a mean resampled measure of biodiversity, both within and outside urban areas, stratified by ecoregion. To do so, we performed a resampling technique where we randomly sampled 100 FrogID observations that were classified as urban and 100 FrogID observations that were classified as non-urban, per ecoregion, and for each sample we calculated the species richness, Shannon diversity, and phylogenetic diversity. We used these three measures of biodiversity due to their longstanding use in the literature and consequently their ease of interpretation, and because they do not rely explicitly on abundance data, which our data do not encompass. Multiple measures were used to account for the nuanced differences that can occur between species richness and species diversity (Spellerberg & Fedor 2003). Species richness was calculated as the total number of species found in the random sample. Shannon diversity was the Shannon diversity index performed on the number of observations per species found in each random sample, calculated using the vegan package version 2.5−7 (Dixon, 2003; Oksanen, Blanchet, & Friendly, 2020). Phylogenetic diversity, a measure incorporating the phylogenetic difference among species (Faith 1992), was calculated using the picante package version 1.8.2 (Kembel, Cowan, & Helmus, 2010) and performed on the number of observations per species found in each random sample. For phylogenetic analyses we used the consensus tree for amphibian phylogeny from Jetz and Pyron (2018). While we recognize that these measures of diversity are not traditional and subject to biases, we assume that the number of observations is representative of the total abundance in a region (e.g., Enquist, Feng, & Boyle, 2019).

This random sampling approach was repeated 1000 times to generate a distribution of biodiversity variables for urban and non-urban areas, for each ecoregion. This random sampling approach is designed to account for the spatial and temporal autocorrelation and biases because any observation can be drawn at random, and the extent of autocorrelation will vary within each random draw, thereby influencing the estimate of the respective biodiversity variable. Qualitative exploration indicated that 1000 random samples was enough to capture the different autocorrelation within and among random samples. For each measure of biodiversity, we tested for overall statistical significance between urban and non-urban areas (i.e., across all ecoregions) using a linear mixed model where the biodiversity variable was the response variable, ecoregion was a random effect, and the urban or non-urban classification was a fixed effect. We additionally tested this relationship separately for each ecoregion using a linear model where the biodiversity variable was the response variable, and the urban or non-urban

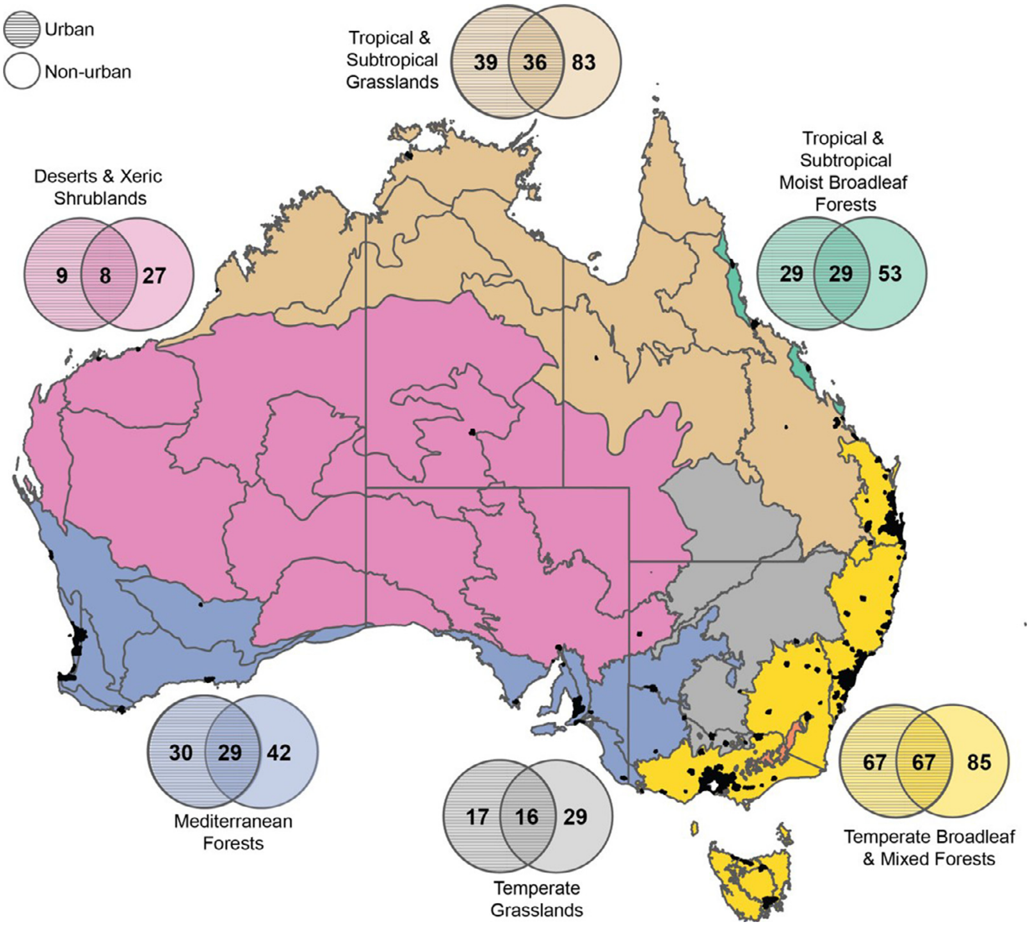

Fig. 1. Our study area of continental Australia, stratified by ecoregion, and the significant urban areas (SUAs) are illustrated in black. For each ecoregion, we summarized the total species richness of frogs in urban and non-urban areas using a Venn diagram. The gray lines represent the bioregions of Australia.

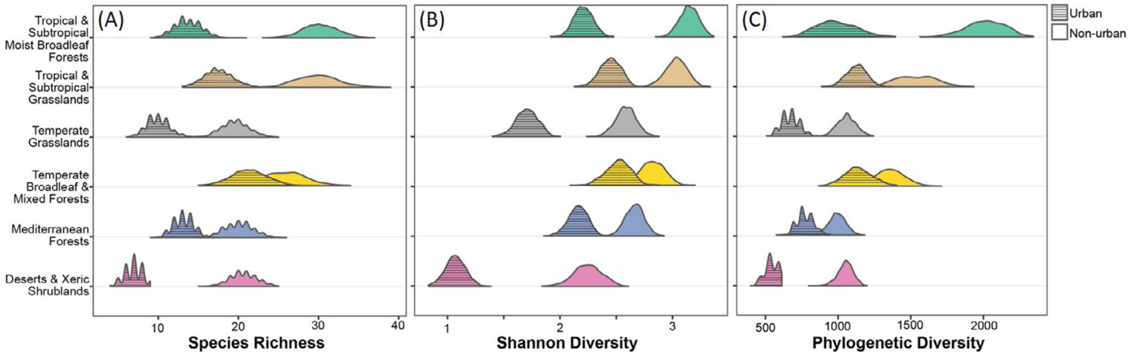

Fig. 2. Resampled measures of (A) species richness, (B) Shannon diversity, and (C) phylogenetic diversity for urban and non-urban areas within each ecoregion. Non-urban areas consistently had greater biodiversity than non-urban areas when using a resampling approach.

classification was the predictor variable. This additional test helps to account for the differential amount of sampling among regions.

While the former approach aggregated all SUAs within an ecoregion and treated them as a single urban versus non-urban comparison, we also explored each SUA individually, for any SUA with a minimum of 150 FrogID observations (N=43; Appendix A: Fig. 3). We first investigated the relationship between species richness and area of the SUA by calculating the cumulative species richness within each SUA. We then created a buffer around each SUA using a 100 km buffer, to capture the regional species pool, specific to each SUA. A given buffer, however, could encapsulate other SUAs within the specified buffer distance. We then

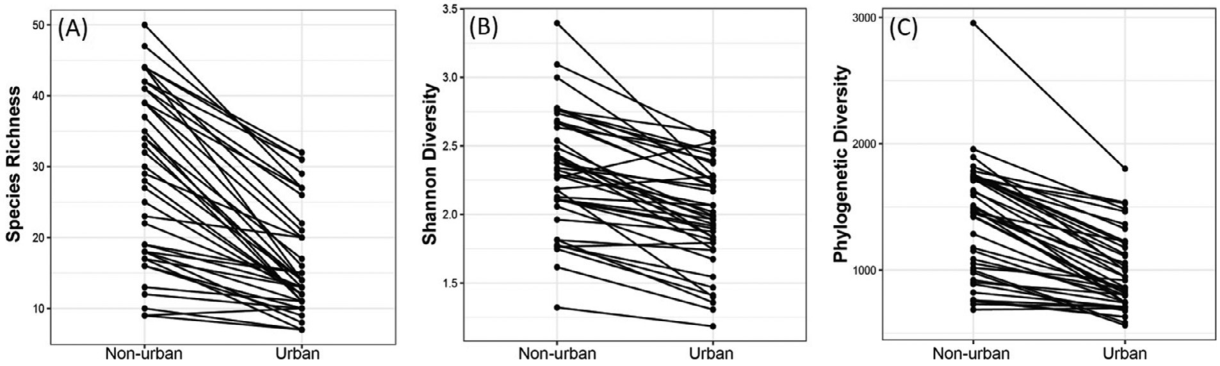

Fig. 3. The total (i.e., among all samples) species richness (A), Shannon diversity (B), and phylogenetic diversity (C) stratified by each significant urban areas (SUA). Each line in the plot above corresponds to a single SUA, connecting a SUA's measure with its corresponding buffer measure of biodiversity. There was consistently greater biodiversity in the corresponding buffer than the SUA.

Table 1. Summary of species richness stratified by ecoregion and the total sum of significant urban areas (SUAs) throughout each ecoregion, as well as the associated number of records from each area.

Ecoregion	Urban classification	Species Richness	Number of records
Deserts & Xeric Shrublands	Non-urban	27	233
Deserts & Xeric Shrublands	Urban	9	208
Mediterranean Forests	Non-urban	42	3232
Mediterranean Forests	Urban	30	10,875
Temperate Broadleaf & Mixed Forests	Non-urban	85	23,843
Temperate Broadleaf & Mixed Forests	Urban	67	38,856
Temperate Grasslands	Non-urban	29	2238
Temperate Grasslands	Urban	17	419
Tropical & Subtropical Grasslands	Non-urban	83	5426
Tropical & Subtropical Grasslands	Urban	39	3720
Tropical & Subtropical Moist Broadleaf Forests	Non-urban	53	2608
Tropical & Subtropical Moist Broadleaf Forests	Urban	29	1510

compared the total species richness, Shannon diversity, and phylogenetic diversity within each SUA to the total species richness, Shannon diversity, and phylogenetic diversity in the SUA's corresponding buffer. Two SUAs' associated buffers had less than 150 FrogID submissions and these SUAs were removed from analysis as it was deemed to not approximate the true biodiversity value in that area, leaving us with a total of 41 SUAs for analyses (Appendix A: Table 1). We statistically tested whether urban areas had less biodiversity than the surrounding regional buffer by using a linear model where the response variable was the biodiversity variable and the predictor variables were a categorical classification of urban or the non-urban buffer and the number of observations within each region to account for the positive relationship between the number of observations and the biodiversity variables. Because there is spatial autocorrelation in the data (e.g., more FrogID observations in urban areas than non-urban areas), our results would likely be influenced by sampling artefacts, whereby there would be increased diversity in urban environments than non-urban environments largely as a result of sampling bias. However, such biases are largely systematic (i.e., more samples in urban areas than non-urban areas regardless of which SUA and corresponding buffer), and therefore our results comparing the differences between SUA and the buffer among SUAs would not be influenced by such systematic bias. Moreover, because of such known sampling biases, any effect of urbanization negatively impacting biodiversity would be robust and potentially conservative. The area of the SUA and the area of the corresponding buffer were strongly correlated (Appendix A: Fig. 4), and thus we assumed that the influence of area on biodiversity is equally likely for each SUA and buffer comparison, making the statistical assessment of paired values comparable.

Quantifying frog diversity along an urbanization gradient

Because FrogID is an opportunistic citizen science project, and observations are submitted without information on absences (cf. eBird), we employed a resampling approach to assess how biodiversity responds to an urbanization gradient. We artificially created a 'grouping' of FrogID observations along an urbanization gradient to assess how frog

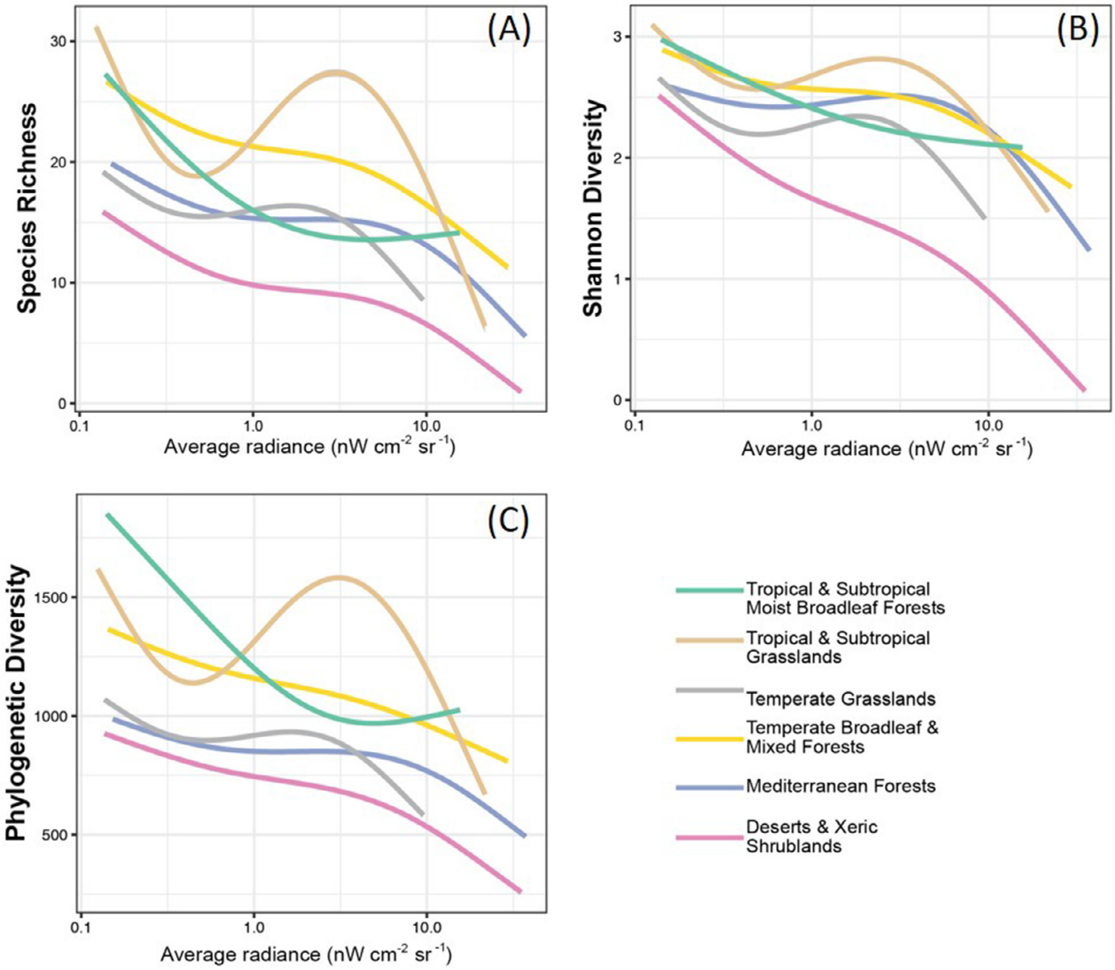

Fig. 4. The relationship between frog diversity and a continuous urbanization gradient, showing the general decreasing trends along an urbanization gradient within each ecoregion. Lines represent a generalized additive model fit where the response variable is (A) species richness, (B) Shannon diversity, and (C) phylogenetic diversity, respectively, and the predictor variable is log-transformed VIIRS night time lights.

biodiversity responds to a continuous gradient of urbanization. We first assigned every FrogID observation a continuous measure of urbanization (*sensu* Callaghan et al., 2020) — VIIRS nighttime lights (Elvidge, Baugh, & Zhizhin, 2017) — using Google Earth Engine (Gorelick et al. 2017). This was done by taking the median value of the average DNB radiance values averaged across a 1 km buffer at each observation's coordinates, from monthly composites of night time light data from 2017 onwards. Accordingly, we were left with a distribution of observations across an urbanization gradient, stratified to ecoregion (Appendix A: Fig. 5).

We then randomly sampled across this distribution using a randomly sampled quantile from 0 to 1. For each random quantile, we sampled the corresponding urbanization value and collated all FrogID records within the corresponding quantile (i.e., the randomly sampled quantile ± 0.05). For each of these random groupings, we randomly sampled 100 FrogID observations and calculated the species richness, Shannon diversity, and phylogenetic diversity as described above. This was repeated 10,000 times to sample over the likelihood of different spatial and temporal biases occurring in the random samples. Because there were comparatively fewer observations within the Deserts & Xeric Shrublands ecoregion (Table 1), all observations were used and not trimmed to 100 FrogID observations. We then had a distribution of randomly sampled urbanization levels and corresponding estimates of biodiversity. We investigated the relationship between frog diversity and urbanization level using a Generalized Additive Model (GAM) in the R package mgcv version 1.8−33 (Wood, 2003), where the urbanization level was a smooth term in the model fitting, allowing for a nonlinear response of diversity to urbanization, with four knots.

Results

We used a total of 167,220 records of 196 species — of a total of 241 species in Australia — in our analyses throughout continental Australia, of which 55% of records were from urban areas and 45% of records were from non-urban areas. Throughout Australia, regardless of ecoregion, a total of 119 species were found at least once in urban areas and a total of 195 species were found at least once in non-urban areas. Of all 196 species, 118 species were found in both urban and non-urban areas (e.g., *Adelotus brevis, Crinia signifera*), 77 species were found only in non-urban areas (e.g., *Litoria pallida, Cophixalus ornatus*, and *Uperoleia altissima*), and one species was found only in urban areas (*Neobatrachus aquilonius*). In our dataset, there were 4 Critically Endangered (i.e., *Litoria myola, Cophixalus concinnus, Litoria booroolongensis*, and *Geocrinia alba*), 15 Endangered (e.g., *Lioria cooloolensis, Cophixalus monitcola*, and *Philora pughi*), and 12 Vulnerable species (e.g., *Cophixalus aenigma, Litoria daviesae*, and *Geocrinia vitellina*) found in non-urban areas, compared with zero Critically Endangered, seven Endangered (e.g., *Litoria raniformis, Litora brevipalmata*, and *Mixophyes iteratus*), and seven Vulnerable species (e.g., *Heleioporus australiacus, Litoria freycineti*, and *Mixophyes balbus*) recorded in urban areas.

Quantifying frog diversity in urban and non-urban areas

When investigating species richness stratified by ecoregion and urban area (Table 1), the highest species richness was found in the Temperate Broadleaf & Mixed Forests non-urban areas (SR=85) followed by Tropical & Subtropical Grasslands non-urban areas (SR=83), whereas the lowest species richness was found in urban areas of Desert & Xeric Shrublands (SR = 9) and urban areas of Temperate Grasslands (N = 17). By ecoregion, the total species richness was always greater in non-urban areas than urban areas (Table 1; Fig. 1): on average, species richness was 57% less in urban than non-urban areas. The greatest difference between urban and non-urban areas was found in the Deserts & Xeric Shrublands ecoregion where urban species richness was 33% of non-urban species richness, followed by Tropical & Subtropical Grasslands where urban species richness was 47% of non-urban species richness. Conversely, the urban species richness comprised 79% of the non-urban species richness for Temperate Broadleaf & Mixed Forests.

The results of our resampling approach were largely similar to that of total species richness: urban areas consistently had less species richness (Fig. 2A), Shannon diversity (Fig. 2B), and phylogenetic diversity (Fig. 2C) than non-urban areas. Across all ecoregions, there was significantly less species richness in urban than non-urban areas ($t=-211.03$, $p<0.001$), and this pattern held true for each respective ecoregion, but the difference was greatest for Tropical & Subtropical Moist Broadleaf Forests (estimate=-16.465) followed by Deserts & Xeric Shrublands (estimate = -13.715), and least different for Temperate Broadleaf & Mixed Forests (estimate = -4.651). Shannon diversity was also significantly less in urban compared with non-urban areas, across all ecoregions ($t = -226.30$, $p < 0.001$) and similarly to species richness, this difference was greatest for Deserts & Xeric Shrublands (estimate=-1.176), followed by Tropical & Subtropical Moist Broadleaf Forests (estimate=-0.940), and least different for Temperate Broadleaf & Mixed Forests (estimate=-0.298). And lastly, we found significantly less phylogenetic diversity in urban areas than non-urban areas, across all ecoregions ($t = -153.68$, $p < 0.001$). This was also true for each ecoregion, but the difference was greatest for Tropical & Subtropical Moist Broadleaf Forests (estimate=-1027.619) followed by Deserts & Xeric Shrublands (estimate=-508.838), and least different for Temperate Broadleaf & Mixed Forests (estimate=-210.162).

All but one SUA had less species richness in the SUA than the surrounding buffer, and on average, species richness was 59% less in urban than non-urban areas. Similarly, all but three SUAs had less total Shannon diversity in urban than non-urban areas, and on average, Shannon diversity was 86% less in urban than non-urban areas. Lastly, phylogenetic diversity was greater in non-urban than urban areas for all but one SUA, and on average, phylogenetic diversity was 72% less in urban than non-urban areas. We also found that there was statistically significant less species richness ($t = -3.234$, $p = 0.002$; Fig. 3A), Shannon diversity ($t = -3.192$, $p = 0.002$; Fig. 3B), and phylogenetic diversity ($t = -2.771$, $p = 0.007$; Fig. 3C) in urban compared with the surrounding non-urban buffer areas, after accounting for the number of observations within each region. Across 41 SUAs throughout Australia (Appendix A: Table 1), there was a slightly positive, but not statistically-significant, relationship between the species richness and the area of a SUA ($t = 1.604$, p-value = 0.116; Appendix A: Fig. 6).

Quantifying frog diversity along an urbanization gradient

We found that within each ecoregion there was a steady decrease in species richness (Fig. 4A), Shannon diversity (Fig. 4B), and phylogenetic diversity (Fig. 4C) along an urbanization gradient. This pattern was relatively consistent among ecoregions, with the exception of Tropical & Subtropical Grasslands where there was a peak at intermediate levels of urbanization. The statistical relationship was significant for each ecoregion. We found no visual evidence of any significant thresholds where frog diversity was negatively impacted.

Discussion

With increasing urbanization at a global scale (Liu, Huang, & Xu, 2020), it is critical to document the impact of urbanization on flora and fauna. It is also critical to understand these impacts across broad spatial scales, allowing for the generalizability of results. Using a continental-scale citizen science dataset (Rowley et al. 2019), we show that urban areas throughout continental Australia have significantly less frog diversity than surrounding non-urban areas, consistent for species richness, Shannon diversity, and phylogenetic diversity. Moving beyond a categorical classification of urban and non-urban areas, we also found that frog diversity steadily decreases along a continuous urbanization gradient with little evidence of any thresholds. Although the overall levels of frog diversity vary considerably across ecoregions (e.g., Table 1), our main finding that urban areas had significantly less frog diversity was consistently supported both across and within ecoregions. The strongest effect of urban areas consistently occurred within the Deserts & Xeric Shrublands and Tropical and Subtropical Moist Broadleaf Forests ecoregion types, whereas the weakest effect was consistently observed in Temperate Broadleaf & Mixed Forests. This is likely at least partially a result of increased area of urban environments, and therefore increased sampling, in some ecoregions compared with others (cf. Temperate & Mixed Broadleaf Forests and Deserts & Xeric Shrublands in Fig. 1). Clearly, urban environments are negatively impacting frog diversity at macroecological scales, supporting small-scale studies which have found negative impacts of urban land use on frog diversity, abundance, and reproduction (Knutson, Sauer, & Olsen, 1999; Pillsbury &Miller 2008; Westgate et al. 2015). Urban areas are not placed randomly throughout the landscape, and the environmental conditions in these areas (regardless of whether the area is urban) would also likely influence frog diversity. However, we found support of decreased frog diversity at multiple spatial scales — the continental, regional, and city-specific scales — providing strong evidence that frog diversity is decreased as a result of urbanization.

Frogs are at significant risk to anthropogenic threats. Life-history traits of frogs, such as their often specific physiological and breeding habitat requirements (Hamer &McDonnell 2008) makes most species susceptible to habitat modification (Nowakowski, Watling, & Thompson, 2018). More broadly, species-specific traits (e.g., body size, mating strategy, parental investment) likely moderate, to an extent, a species' ability to persist and tolerate urban environments acting as an ecological filter (Webb, Hoeting, Ames, Pyne, & Poff, 2010). Other threats likely act synergistically with urbanization, such as disease (Vanacker, Lambert, Schmitz, & Skelly, 2019), introduced species (Gaertner, Wilson, & Cadotte, 2017), and pollution (Gallagher et al., 2014). Importantly, we found a steady decrease in frog diversity along an urbanization gradient (Fig. 4), contrasting with other taxa where there are sometimes peaks of biodiversity at intermediate levels along urbanization gradients (Batary et al. 2018; Callaghan et al., 2019). This is likely a result of frogs being more susceptible to the processes of urbanization due to their lack of mobility compared with other taxa (e.g., birds) that can readily move in and out of urban environments, possibly benefitting from urban resources when needed. Additionally, the size and quality of varied habitat needed to support high diversity of frogs (Parris, 2006) is less likely to occur within the most urbanized parts of a city (i.e., remnant or constructed wetlands are rare within central business districts of cities), whereas other taxa may have high diversity even within small patches of urban green areas (Carbó-Ramírez & Zuria, 2011). Species-specific analyses incorporating the role of species-specific traits are necessary to advance our understanding of the mechanisms leading to the steady decline in frog diversity along an urbanization gradient.

Although we found significantly negative impacts of urbanization on frog diversity, it is important to highlight that many frog species were detected in urban areas (Fig. 1). In particular, 14 threatened frog species were recorded within urban areas, highlighting the need to treat urban environments as functioning ecosystems that can support a subset of frog diversity (e.g., Dearborn & Kark, 2010; Ives et al. 2016), although the health of frog populations in urban areas was not tested here. The fact that we found a slight, but not significant relationship, between the area of a SUA and the species richness (Appendix A: Fig. 6) supports the notion that there are macro- and micro-ecological habitat attributes within these SUAs that are influencing frog diversity more than the relative area of the SUA. For example, habitat management at small scales within urban areas can lead to increased frog diversity, if appropriately managed (Hodgkison, Hero, & Warnken, 2007). Unsurprisingly, the retention of natural habitat throughout the urban matrix (Ostergaard, Richter, & West, 2008) can positively influence frog diversity in urban areas. However, constructed wetlands can provide suitable habitat for frog populations and reproduction of wetland breeding species (Babbitt & Tanner, 2000). The size of urban wetlands can influence frog species richness (Parris, 2006), as can the heterogeneity of available frog habitats within urban parks (Li et al., 2018). Other important planning features include the connectivity of green areas throughout the urban matrix (e.g., corridors and buffer zones) which support the mobility of frogs, and thus increase frog diversity in urban areas (Pope, Fahrig, & Merriam, 2000; Semlitsch & Bodie 2003). Future research should thus focus on understanding the influence of various habitat attributes that promote greater frog diversity in urban areas, and the continental scale citizen science data used here can provide an excellent dataset to accomplish this.

Beyond overall diversity of frogs, frog responses to urbanization are species-specific (e.g., Davidson, Shaffer, & Jennings, 2001) and we found consistent evidence that phylogenetic diversity was decreased in urban environments compared with non-urban environments. This suggests that specific taxa or lineages are differentially affected by urbanization. Thus, future work should look to highlight which frog species are most at-risk of urbanization, identify traits that make species particularly sensitive to urbanization, and recommend mitigation mechanisms that are best-suited for specific species. For example, while our citizen science dataset provided macroecological comparisons, we are unable to say whether the populations of frogs in urban areas are successfully reproducing. It is possible that the impact of urbanization on frog species is even greater than we document here, because urban populations of frogs may in fact be sink populations (e.g., Sievers et al., 2018). Therefore, in order to understand the overall impact of urbanization on frogs, future research should work to incorporate local-scale field work examining reproductive success with broad-scale citizen science data to document the impacts of urban environments on frogs.

We provide overwhelming evidence of the negative impacts of urbanization on frog diversity throughout Australia, using both a categorical classification of urban and non-urban areas and a continuous classification of an urbanization gradient. Our knowledge of the impacts of urbanization on frog diversity has traditionally lagged behind our understanding of other taxa (e.g., birds), but with the relatively recent surge of broad-scale citizen science data there now exists data to inform generalizable patterns for the ecology and conservation of many taxa (Chandler, See, & Copas, 2017). Our work here highlights the validity to use citizen science data in informing our knowledge of frogs throughout Australia (e.g., Callaghan et al., 2020). Such citizen science data will be critical to understand the aspects of urban areas which best promote frog diversity. Lastly, given the significant impact of urban areas on frog diversity, we highlight that there should be a concerted effort to incorporate frog diversity in future urban planning and development decisions.

Data availability

All data cannot be made Open Access due to data sensitivity/privacy of the underlying recordings and localities of threatened or otherwise sensitive species (see Rowley & Callaghan, 2020), but most data (i.e., with exact localities of sensitive species buffered) are made available to the public on an annual basis (Rowley & Callaghan, 2020). However, in order to make our analysis reproducible, we provide data and code to reproduce our analyses using only the publicly available data that does not have data generalizations (i.e., removing those species that are sensitive or threatened). The subset of data and the code are available here: https://doi.org/10.5281/zenodo.4686884. Further data can also be requested from the Australian Museum.

Declaration of Competing Interest

The authors declare no conflict and did not receive any specific funding dedicated to this work.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.baae.2021.04.003.

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