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

Corey T. Callaghan[a, b, c, *], Gracie Liu[a,d], Brittany A. Mitchell[a,d], Alistair G. B. Poore[b], Jodi J. L. Rowley[a,d]

[1]Centre for Ecosystem Science; School of Biological, Earth and Environmental Sciences; UNSW Sydney; Sydney, NSW, Australia

[2]Ecology & Evolution Research Centre; School of Biological, Earth and Environmental Sciences; UNSW Sydney; Sydney, NSW, Australia

[3]Czech University of Life Sciences Prague; Faculty of Environmental Sciences; Prague, Czech Republic

[4]Australian Museum Research Institute; Australian Museum; Sydney, NSW, Australia

*Corresponding author.
E-mail address: c.callaghan@unsw.edu.au.

***Note: This is a pre-print and the published version is available here:**
https://doi.org/10.1016/j.baae.2021.04.003

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 & Sansur 2006; Francis 2011; Liu et al. 2016), generally leads to negative impacts on local biodiversity (McKinney 2006). Species richness (Concepción et al. 2015), species diversity (Wang et al. 2001), functional diversity (Nock et al. 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 et al. 2020) or threatened species (Ives et al. 2016) and diversity can even be increased within urban areas compared with non-urban areas (Callaghan et al. 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 et al. 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 et al. 2012). Amphibians have characteristics that are likely to make them more susceptible to urban environments compared with other taxa (Hopkins 2007; Hamer & McDonnell 2008). 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 2017; Anderson 2019). Urban environments reduce available breeding habitat (Westgate et al. 2015) and can inadvertently create ecological traps (Sievers et al. 2018), reducing both juvenile and adult survival due to poor water quality (Hamer & McDonnell 2008; Snodgrass et al. 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 et al. 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 et al. 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 volunteer citizen scientists 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 centre with an urban population of at least 7,000 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 ASGA 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 et al. 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 et al. 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 unique 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 et al. 2020). Phylogenetic diversity — a measure incorporating the phylogenetic difference among species (Faith 1992) — was calculated using the picante package version 1.8.2 (Kembel et al. 2010) 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 & 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 et al. 2019).

This random sampling approach was repeated 1,000 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 1,000 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 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 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 buffer 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 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 night-time lights (Elvidge et al. 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 1km 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 2006), 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 vitelline*) 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 biodiversity. 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 et al. 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 et al. 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 et al. 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 et al. 2010). Other threats likely act synergistically with urbanization, such as disease (VanAcker et al. 2019), introduced species (Gaertner et al. 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 with 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 2011; 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 greater 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 et al. 2007). Unsurprisingly, the retention of natural habitat throughout the urban matrix (Ostergaard et al. 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 et al. 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 et al. 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 recent advent of broad-scale citizen science data there now exists data to inform generalizable patterns for the ecology and conservation of many taxa (Chandler et al. 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.

Acknowledgments

We would like to thank the Citizen Science Grants of the Australian Government for providing funding for the FrogID project; the Impact Grants program of IBM Australia for providing the resources to build the FrogID App; Bunnings, Fyna Foods for supporting FrogID as project partners; the generous donors who provided funding for the project including John T Reid Charitable Trusts; the Museum and Art Gallery of the Northern Territory, Museums Victoria, Queensland Museum, South Australian Museum, Tasmanian Museum and Art Gallery, and Western Australian Museum as FrogID partner museums; the many Australian Museum staff and volunteers who make up the FrogID team; and, most importantly, the thousands of citizen scientists across Australia who have volunteered their time to record frogs.

References

Anderson RB (2019) Human traffic and habitat complexity are strong predictors for the distribution of a declining amphibian. Plos One. doi: 10.1371/journal.pone.0213426

ASGS Volume 4 (2016) Significant Urban Areas, Urban Centres and Localities, Section of State, July 2016. Available from: https://www.abs.gov.au/ausstats/abs@.nsf/mf/1270.0.55.004. Accessed on June 4th, 2020.

Babbitt KJ, Tanner GW (2000) Use of temporary wetlands by anurans in a hydrologically modified landscape. Wetlands 20:313–322. doi: 10.1672/0277-5212(2000)020[0313:uotwba]2.0.co;2

Baillie JEM, Hilton-Taylor C, Stuart SN (2004) A global species assessment. International Union for Conservation of Nature (IUCN).

Batáry P, Kurucz K, Suarez-Rubio M, Chamberlain DE (2017) Non-linearities in bird responses across urbanization gradients: A meta-analysis. Global Change Biology 24:1046–1054. doi: 10.1111/gcb.13964

Callaghan CT, Roberts JD, Poore AGB, et al (2020) Citizen science data accurately predicts expert-derived species richness at a continental scale when sampling thresholds are met. Biodiversity and Conservation 29:1323–1337. doi: 10.1007/s10531-020-01937-3

Callaghan CT, Bino G, Major RE, et al (2019) Heterogeneous urban green areas are bird diversity hotspots: insights using continental-scale citizen science data. Landscape Ecology 34:1231–1246. doi: 10.1007/s10980-019-00851-6

Carbó-Ramírez P, Zuria I (2011) The value of small urban greenspaces for birds in a Mexican city. Landscape and Urban Planning 100:213–222. doi: 10.1016/j.landurbplan.2010.12.008

Chandler M, See L, Copas K, et al (2017) Contribution of citizen science towards international biodiversity monitoring. Biological Conservation 213:280–294. doi: 10.1016/j.biocon.2016.09.004

Concepción ED, Obrist MK, Moretti M, et al (2015) Impacts of urban sprawl on species richness of plants, butterflies, gastropods and birds: not only built-up area matters. Urban Ecosystems 19:225–242. doi: 10.1007/s11252-015-0474-4

Davidson C, Shaffer HB, Jennings MR (2001) Declines Of The California Red-Legged Frog: Climate, Uv-B, Habitat, And Pesticides Hypotheses. Ecological Applications 11:464–479. doi: 10.1890/1051-0761(2001)011[0464:dotcrl]2.0.co;2

Dearborn DC, Kark S (2010) Motivations for Conserving Urban Biodiversity. Conservation Biology 24:432–440. doi: 10.1111/j.1523-1739.2009.01328.x

Dixon P (2003) VEGAN, a package of R functions for community ecology. Journal of Vegetation Science 14:927–930. doi: 10.1111/j.1654-1103.2003.tb02228.x

Edzer, P (2018) Simple features for R: standardized support for spatial vector data 10:439-446. doi: 10.32614/RJ-2018-009

Elvidge CD, Baugh K, Zhizhin M, et al (2017) VIIRS night-time lights. International Journal of Remote Sensing 38:5860–5879. doi: 10.1080/01431161.2017.1342050

Enquist BJ, Feng X, Boyle B, et al (2019) The commonness of rarity: Global and future distribution of rarity across land plants. Science Advances 5:eaaz0414. doi: 10.1126/sciadv.aaz0414

Fahrig L, Pedlar JH, Pope, SE, Taylor PD, Wegner JF (1996) Effect of road traffic on amphibian density. Biological Conservation 75:312. doi: 10.1016/0006-3207(96)90065-8

Faith DP (1992) Conservation evaluation and phylogenetic diversity. Biological Conservation 61:1–10. doi: 10.1016/0006-3207(92)91201-3

Francis CD, Ortega CP, Cruz A (2011) Noise Pollution Filters Bird Communities Based on Vocal Frequency. PLoS ONE. doi: 10.1371/journal.pone.0027052

Gaertner M, Wilson JR, Cadotte MW et al. (2017) Non-native species in urban environments: patterns, processes, impacts and challenges. Biological Invasions 19:3461–3469. doi: 10.1007/s10530-017-1598-7

Gagné SA, Fahrig L (2010) Effects of time since urbanization on anuran community composition in remnant urban ponds. Environmental Conservation 37:128–135. doi: 10.1017/s0376892910000421

Gallagher MT, Snodgrass JW, Brand AB, Casey RE, Lev SM, Van Meter RJ (2014) The role of pollutant accumulation in determining the use of stormwater ponds by amphibians. Wetlands Ecology and Management 22:551–564.

Gorelick N, Hancher M, Dixon M, et al (2017) Google Earth Engine: Planetary-scale geospatial analysis for everyone. Remote Sensing of Environment 202:18–27. doi: 10.1016/j.rse.2017.06.031

Hamer AJ, McDonnell MJ (2008) Amphibian ecology and conservation in the urbanising world: A review. Biological Conservation 141:2432–2449. doi: 10.1016/j.biocon.2008.07.020

Hodgkison S, Hero J-M, Warnken J (2007) The efficacy of small-scale conservation efforts, as assessed on Australian golf courses. Biological Conservation 135:576–586. doi: 10.1016/j.biocon.2006.11.001

Hopkins WA (2007) Amphibians as Models for Studying Environmental Change. ILAR Journal 48:270–277. doi: 10.1093/ilar.48.3.270

Houlahan JE, Findlay CS (2003) The effects of adjacent land use on wetland amphibian species richness and community composition. Canadian Journal of Fisheries and Aquatic Sciences 60:1078–1094. doi: 10.1139/f03-095

IUCN 2020. The IUCN Red List of Threatened Species. Version 2020-1. https://www.iucnredlist.org. Downloaded on 8 June 2020.

Ives CD, Lentini PE, Threlfall CG, et al (2015) Cities are hotspots for threatened species. Global Ecology and Biogeography 25:117–126. doi: 10.1111/geb.12404

Jetz W, Pyron RA (2018) The interplay of past diversification and evolutionary isolation with present imperilment across the amphibian tree of life. Nature Ecology & Evolution 2:850–858. doi: 10.1038/s41559-018-0515-5

Kaczmarski M, Benedetti Y, Morelli F (2020) Amphibian diversity in Polish cities: Taxonomic diversity, functional diversity and evolutionary distinctiveness. Basic and Applied Ecology 44:55–64. doi: 10.1016/j.baae.2020.02.006

Kembel SW, Cowan PD, Helmus MR, et al (2010) Picante: R tools for integrating phylogenies and ecology. Bioinformatics 26:1463–1464. doi: 10.1093/bioinformatics/btq166

Knapp S, Winter M, Klotz S (2016) Increasing species richness but decreasing phylogenetic richness and divergence over a 320-year period of urbanization. Journal of Applied Ecology 54:1152–1160. doi: 10.1111/1365-2664.12826

Knutson MG, Sauer JR, Olsen DA, et al (1999) Effects of Landscape Composition and Wetland Fragmentation on Frog and Toad Abundance and Species Richness in Iowa and Wisconsin, U.S.A. Conservation Biology 13:1437–1446.

Li B, Zhang W, Shu X, Pei E, Yuan X, Wang T, Wang Z (2018) Influence of breeding habitat characteristics and landscape heterogeneity on anuran species richness and abundance in urban parks of Shanghai, China. Urban Forestry & Urban Greening 32:56-63.

Liu X, Huang Y, Xu X, et al (2020) High-spatiotemporal-resolution mapping of global urban change from 1985 to 2015. Nature Sustainability. doi: 10.1038/s41893-020-0521-x

Liu Z, He C, Wu J (2016) The Relationship between Habitat Loss and Fragmentation during Urbanization: An Empirical Evaluation from 16 World Cities. PLoS One. doi: 10.1371/journal.pone.0154613

Magle SB, Hunt VM, Vernon M, Crooks KR (2012) Urban wildlife research: Past, present, and future. Biological Conservation 155:23–32. doi: 10.1016/j.biocon.2012.06.018

Mckinney ML (2006) Urbanization as a major cause of biotic homogenization. Biological Conservation 127:247–260. doi: 10.1016/j.biocon.2005.09.005

Nock CA, Paquette A, Follett M, et al (2013) Effects of Urbanization on Tree Species Functional Diversity in Eastern North America. Ecosystems 16:1487–1497. doi: 10.1007/s10021-013-9697-5

Nowakowski AJ, Watling JI, Thompson ME, et al (2018) Thermal biology mediates responses of amphibians and reptiles to habitat modification. Ecology Letters 21:345–355. doi: 10.1111/ele.12901

Oksanen J, Blanchet FG, Friendly M, et al (2020) vegan: Community Ecology Package. R package version 2.5-7. https://CRAN.R-project.org/package=vegan

Olson DM, Dinerstein E, Wikramanayake ED, et al (2001) Terrestrial Ecoregions of the World: A New Map of Life on Earth. BioScience 51:933.

Ostergaard EC, Richter KO, West SD (2008) Amphibian use of stormwater ponds in the Puget lowlands of Washington, USA. In: Mitchell JC, Jung Brown RE, Bartholomew B (eds) Urban herpetology. Society for the Study of Amphibians and Reptiles, Salt Lake City, pp 259–270

Parris KM (2006) Urban amphibian assemblages as metacommunities. Journal of Animal Ecology 75:757–764. doi: 10.1111/j.1365-2656.2006.01096.x

Pillsbury FC, Miller JR (2008) Habitat And Landscape Characteristics Underlying Anuran Community Structure Along An Urban–Rural Gradient. Ecological Applications 18:1107–1118. doi: 10.1890/07-1899.1

Pope SE, Fahrig L, Merriam HG (2000) Landscape complementation and metapopulation effects on leopard frog populations. Ecology 81:2498–2508

Rowley JJ, Callaghan CT (2020) The FrogID dataset: expert-validated occurrence records of Australia’s frogs collected by citizen scientists. ZooKeys 912:139–151. doi: 10.3897/zookeys.912.38253

Scheffers BR, Paszkowski CA (2011) The effects of urbanization on North American amphibian species: Identifying new directions for urban conservation. Urban Ecosystems 15:133–147. doi: 10.1007/s11252-011-0199-y

Semlitsch, RD (2000) Principles for management of aquatic-breeding amphibians. Journal of Wildlife Management 64:615-631.

Sievers M, Parris KM, Swearer SE, Hale R (2018) Stormwater wetlands can function as ecological traps for urban frogs. Ecological Applications 28:1106–1115. doi: 10.1002/eap.1714

Simmons AM, Narins PM (2018) Effects of Anthropogenic Noise on Amphibians and Reptiles. Effects of Anthropogenic Noise on Animals Springer Handbook of Auditory Research 179–208. doi: 10.1007/978-1-4939-8574-6_7

Snodgrass JW, Casey RE, Joseph D, Simon JA (2008) Microcosm investigations of stormwater pond sediment toxicity to embryonic and larval amphibians: Variation in sensitivity among species. Environmental Pollution 154:291–297. doi: 10.1016/j.envpol.2007.10.003

Spellerberg IF, Fedor PJ (2003) A tribute to Claude Shannon (1916–2001) and a plea for more rigorous use of species richness, species diversity and the ‘Shannon–Wiener’ Index. Global Ecology & Biogeography 12:177-179.

Staab M, Pereira-Peixoto MH, Klein AM (2020) Exotic garden plants partly substitute for native plants as resources for pollinators when native plants become seasonally scarce. Oecologia 194:465-480

Stuart SN, Chanson JS, Cox NA, et al (2004) Status and Trends of Amphibian Declines and Extinctions Worldwide. Science 306:1783–1786. doi: 10.1126/science.1103538

Swaileh KM, Sansur R (2006) Monitoring urban heavy metal pollution using the House Sparrow (Passer domesticus). J Environ Monit 8:209–213. doi: 10.1039/b510635d

Vanacker MC, Lambert MR, Schmitz OJ, Skelly DK (2019) Suburbanization Increases Echinostome Infection in Green Frogs and Snails. EcoHealth 16:235–247. doi: 10.1007/s10393-019-01427-1

Villaseñor NR, Driscoll DA, Gibbons P, et al (2017) The relative importance of aquatic and terrestrial variables for frogs in an urbanizing landscape: Key insights for sustainable urban development. Landscape and Urban Planning 157:26–35. doi: 10.1016/j.landurbplan.2016.06.006

Vliet JV (2019) Direct and indirect loss of natural area from urban expansion. Nature Sustainability 2:755–763. doi: 10.1038/s41893-019-0340-0

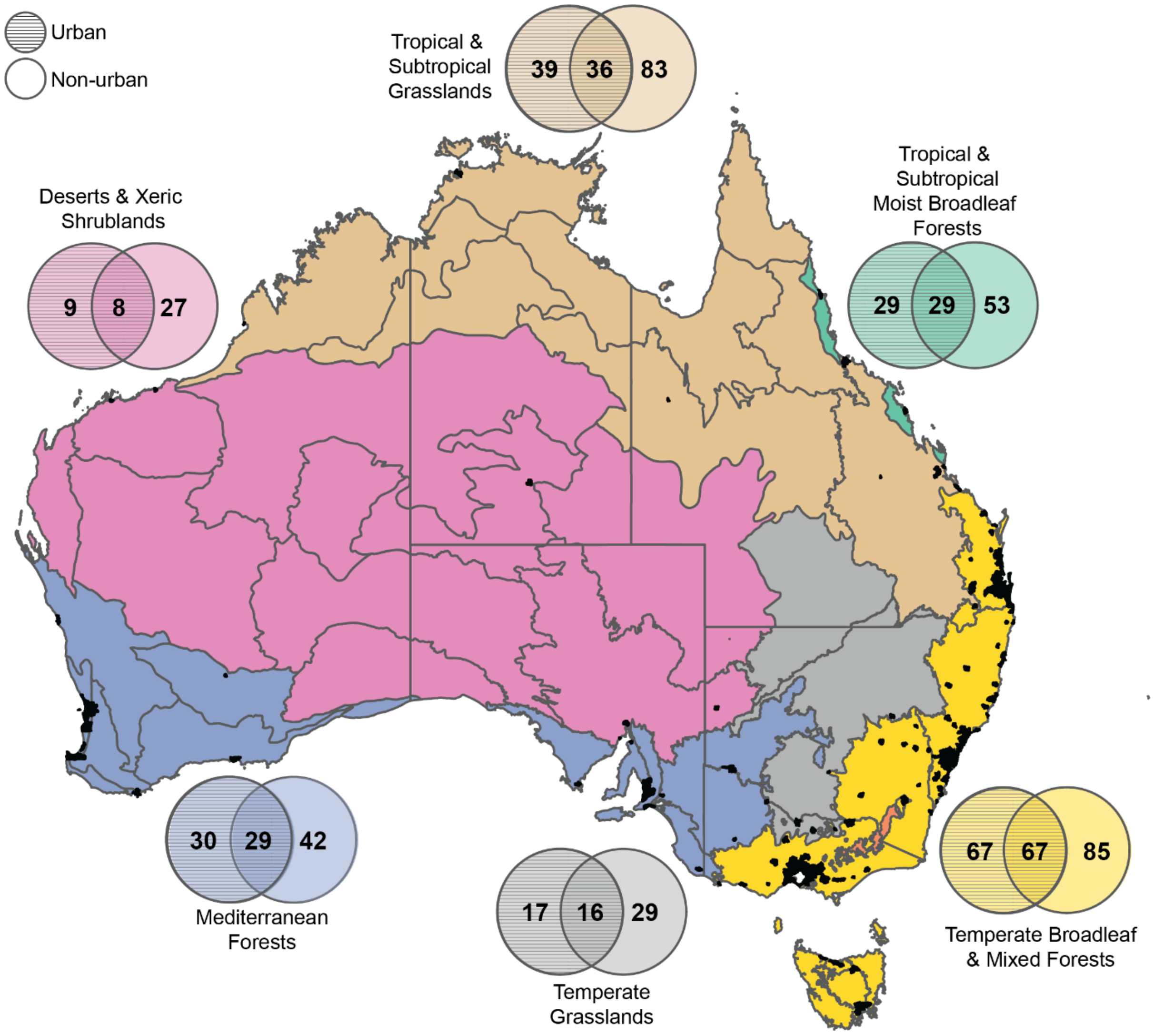
Wang L, Lyons J, Kanehl P, Bannerman R (2001) Impacts of Urbanization on Stream Habitat and Fish Across Multiple Spatial Scales. Environmental Management 28:255–266. doi: 10.1007/s0026702409

Webb CT, Hoeting JA, Ames GM, Pyne MI, Poff NL (2010) A structured and dynamic framework to advance traits-based theory and prediction in ecology. Ecology Letters 13:267-283.

Westgate MJ, Scheele BC, Ikin K, et al (2015) Citizen Science Program Shows Urban Areas Have Lower Occurrence of Frog Species, but Not Accelerated Declines. Plos One. doi: 10.1371/journal.pone.0140973

Wood SN (2006) Generalized Additive Models. doi: 10.1201/9781420010404

605 Figures



606

607 **Fig. 1**. Our study area of continental Australia, stratified by ecoregion, and the significant 608 urban areas (SUAs) are illustrated in black. For each ecoregion, we summarized the total 609 species richness of frogs in urban and non-urban areas using a venn diagram. The gray lines 610 represent the bioregions of Australia.

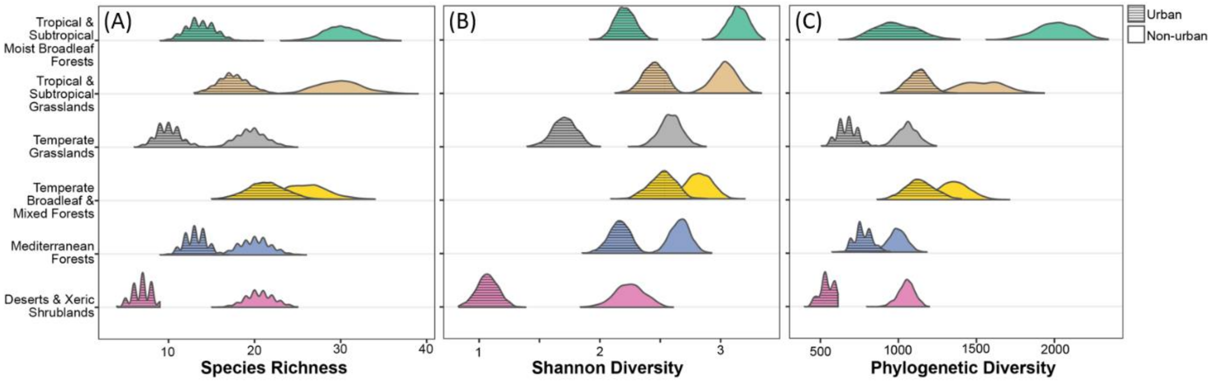


Fig. 2. Resampled measures of (A) species richness, (B) Shannon diversity, and (C) phylogenetic diversity for urban and non-urban areas within each ecoregion. Non-urban areas consistently had greater biodiversity than non-urban areas when using a resampling approach.

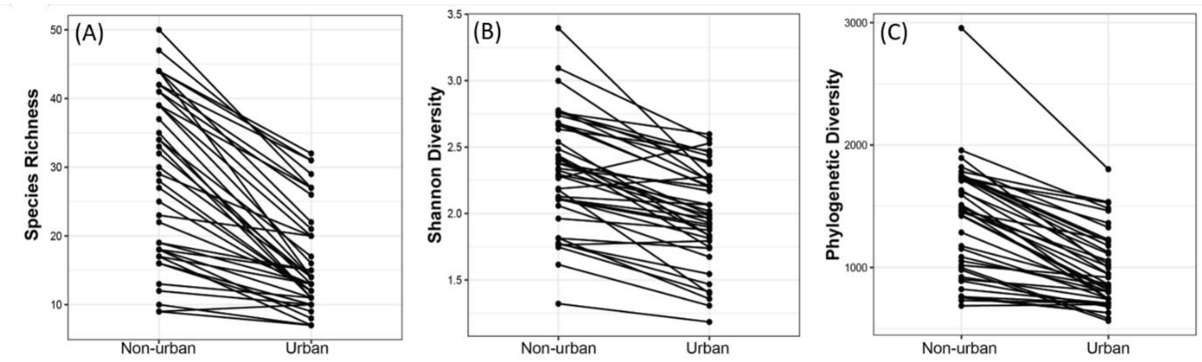


Fig. 3. The total (i.e., among all samples) species richness (A), Shannon diversity (B), and phylogenetic diversity (C) stratified by each significant urban areas (SUA). Each line in the plot above corresponds to a single SUA, connecting a SUA's measure with its corresponding buffer measure of biodiversity.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

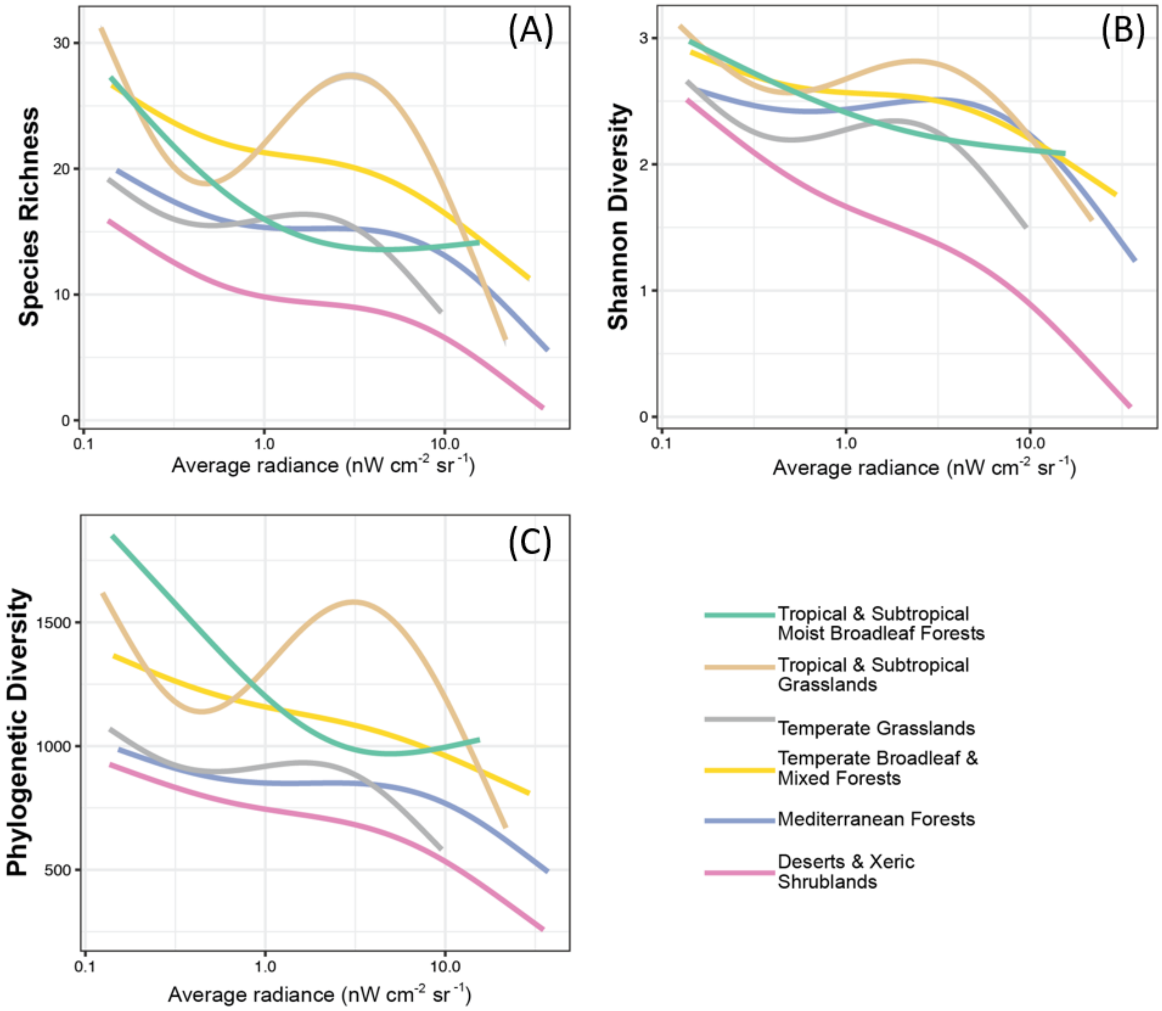


Fig. 4. The relationship between frog diversity and a continuous urbanization gradient, showing the general decreasing trends along an urbanization gradient within each ecoregion. Lines represent a generalized additive model fit where the response variable is (A) species richness, (B) Shannon diversity,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

Tables

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	10875
Temperate Broadleaf & Mixed Forests	Non-urban	85	23843
Temperate Broadleaf & Mixed Forests	Urban	67	38856
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

Supplementary Figures & Tables

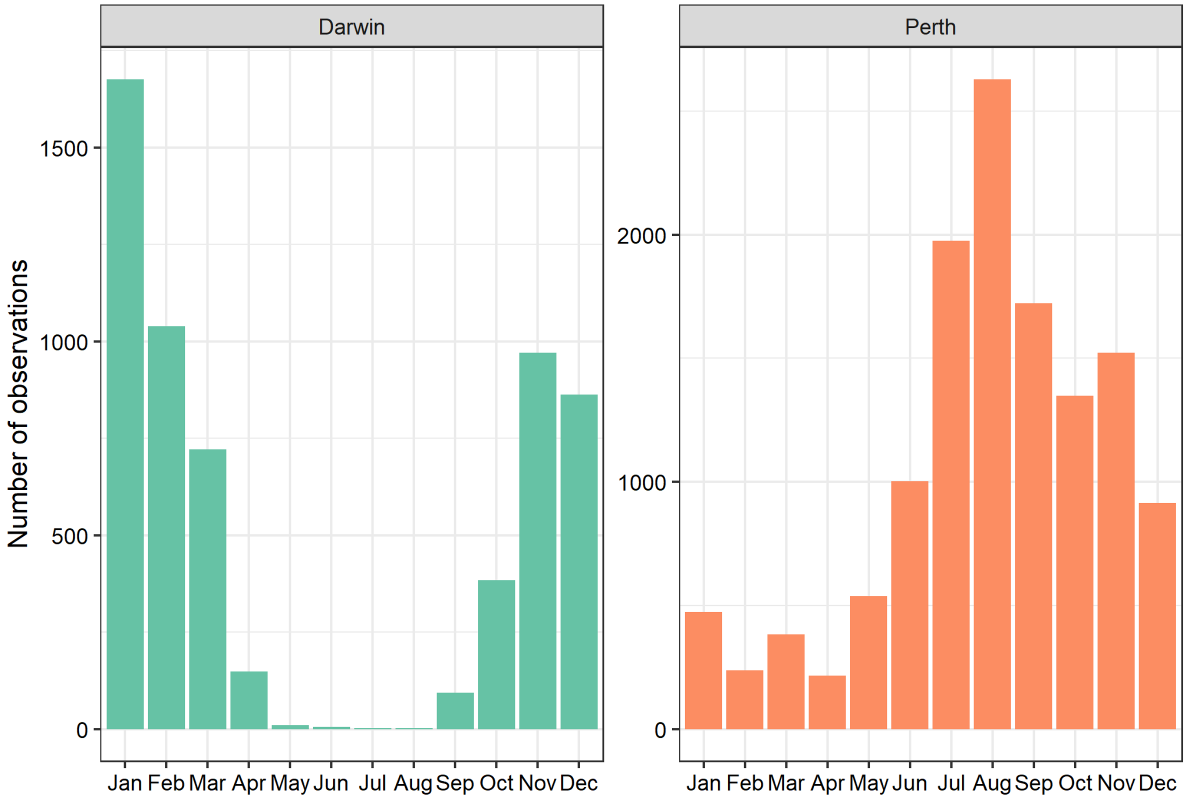


Fig. 1. Temporal sampling by month for two different SUAs in our dataset, Darwin (left) and Perth (right). Darwin has extreme summer bias because there are no frogs calling in the dry season. In contrast, in Perth, where most rain is in winter and most frogs call in winter, the sampling is heavily biased towards winter.

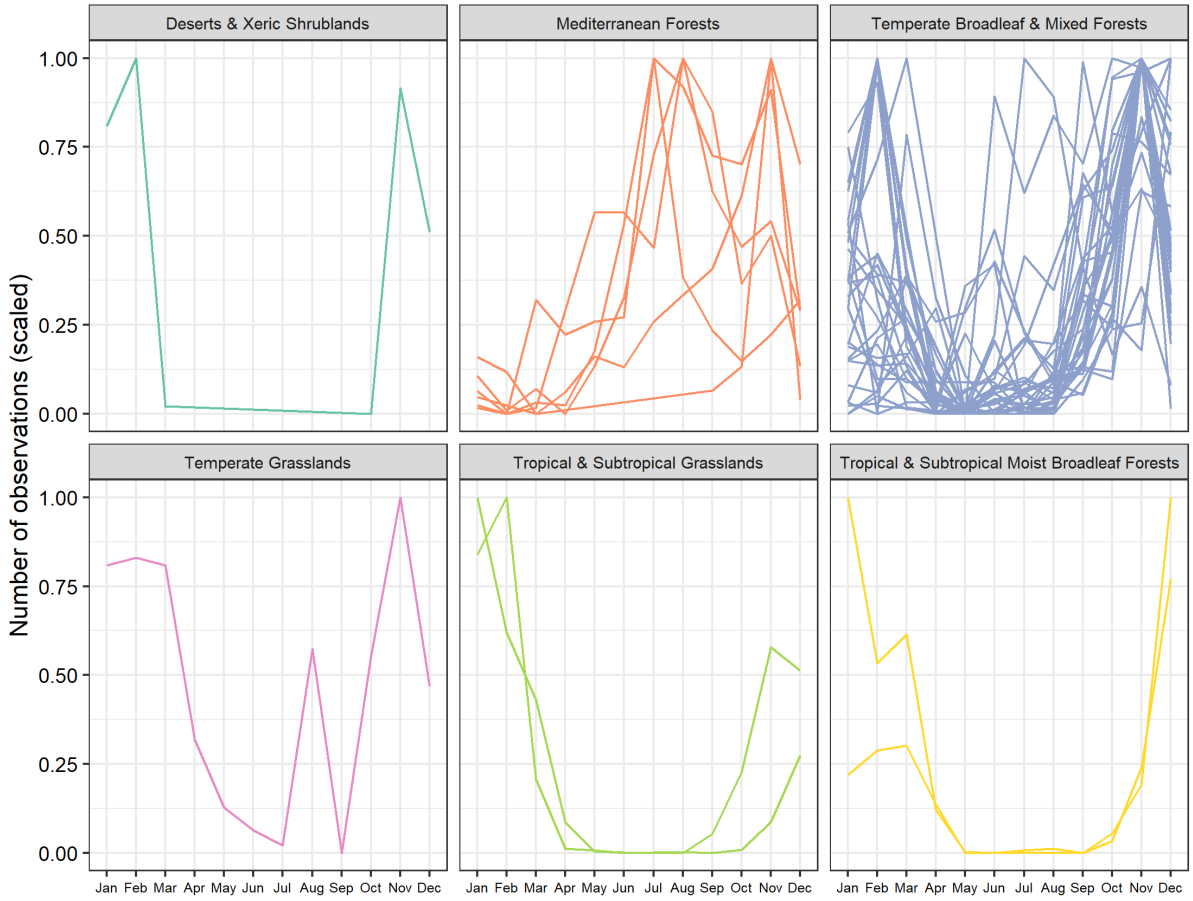


Fig. 2. The number of observations per SUA (each line represents a SUA) stratified by Ecoregion. The number of observations per month are scaled to make the patterns comparable.

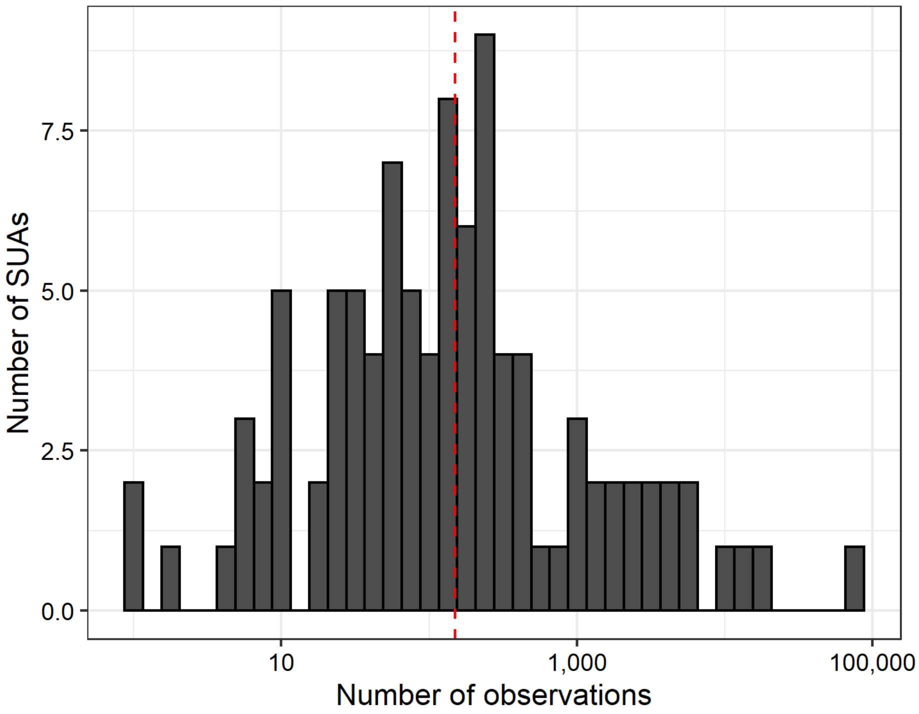


Fig. 3. The number of observations within each of the 101 SUAs considered for analysis. Only SUAs with a minimum of 150 observations, represented by the red dashed line, were considered for further analysis (N=43).

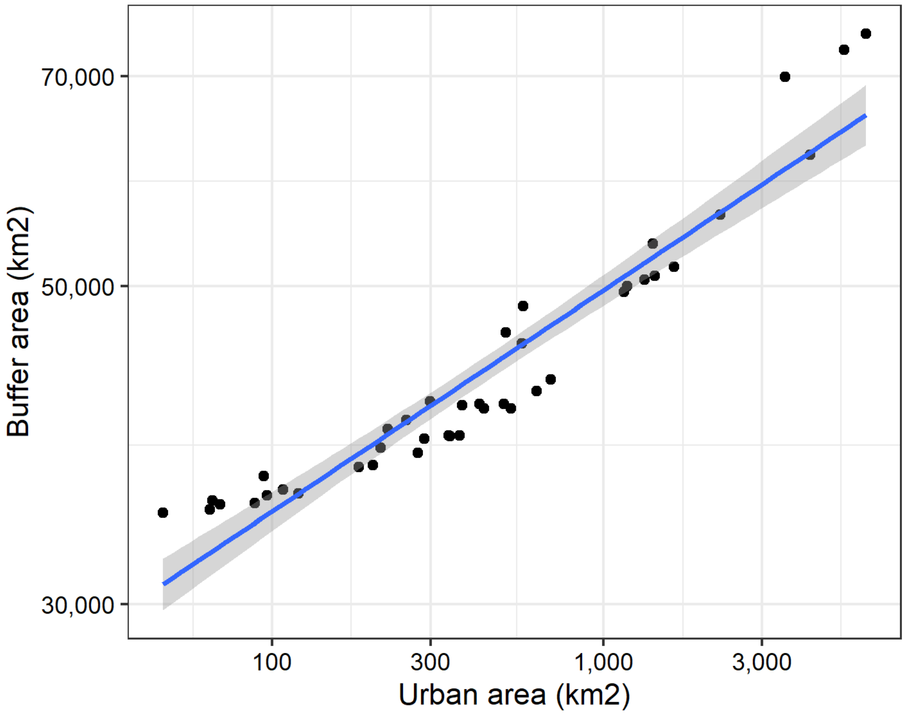


Fig. 4. The relationship between the area of a SUA and the area of the SUA's corresponding buffer. There was a strong positive relationship between these two variables, and thus we did not include area as a predictor in the model because the effect of area would be equal to each paired SUA and buffer.

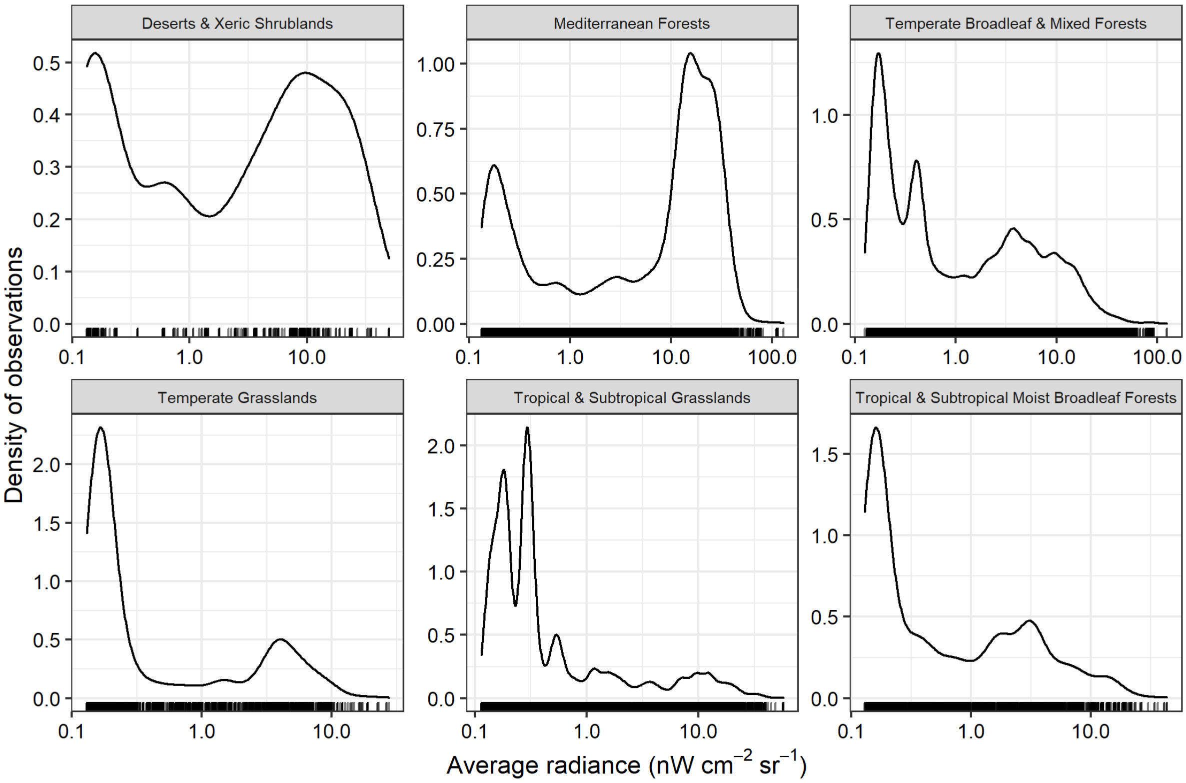


Fig. 5. The distribution of observations in relation to their urbanization level, measured as VIIRS night-time lights, for each ecoregion examined.

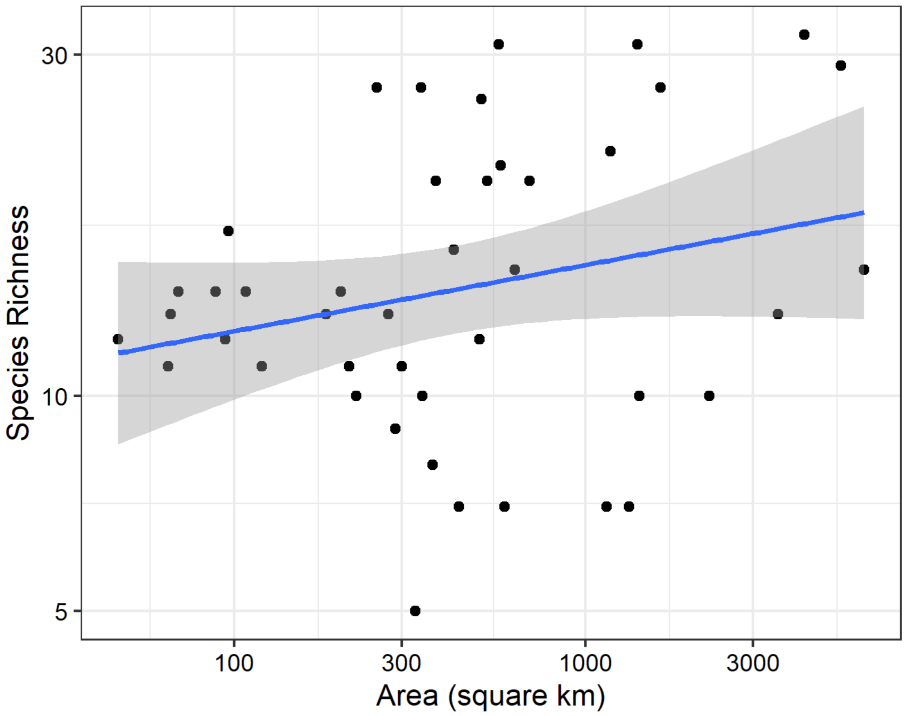


Fig. 6. The relationship between area and species richness within SUAs (N=43) throughout Australia, showing a slightly positive but non-significant relationship.

Table 1. The results of the SUA-buffer analysis, where each SUA received a 100 km buffer as a regional species pool and species richness, Shannon diversity, and phylogenetic diversity.

Significant Urban Area	Species richness		Shannon diversity		Phylogenetic diversity		Number of records	
	Urban	Buffer	Urban	Buffer	Urban	Buffer	Urban	Buffer
Adelaide	10	9	1.31	1.62	698.01	686.69	2253	867
Albany	11	13	2.07	2.13	707.46	760.35	336	783
Albury - Wodonga	15	19	1.88	1.96	847.95	1052.55	3715	1640
Armidale	13	34	2.25	2.77	861.97	1509.74	270	1666
Ballarat	10	16	1.41	1.75	741.18	921.67	526	7879
Batemans Bay	12	27	1.99	2.49	814.65	1422.10	273	5783
Bendigo	9	16	1.79	1.76	678.77	889.54	275	5459
Bowral - Mittagong	16	39	1.97	2.11	947.83	1630.47	401	26254
Brisbane	29	47	2.37	2.78	1481.93	1957.05	4157	13143
Bunbury	10	12	1.90	2.11	708.22	730.47	280	1914
Busselton	10	16	1.98	2.32	708.22	822.37	739	2535
Cairns	27	50	2.28	3.40	1802.53	2955.87	1973	7324
Camden Haven	20	39	2.46	2.76	1111.79	1618.30	252	2671
Canberra - Queanbeyan	12	25	1.75	2.42	799.03	1286.23	1489	5027
Central Coast	31	44	2.28	2.19	1527.58	1716.85	10773	25600
Coffs Harbour	26	41	2.56	3.09	1228.05	1757.12	1740	6285
Darwin	20	23	2.43	2.74	1227.27	1456.03	5915	5126
Dubbo	13	19	1.40	2.18	798.94	1085.94	370	737
Geelong	7	17	1.47	1.78	583.11	998.23	1091	12151
Gisborne - Macedon	8	18	1.36	1.81	563.43	979.50	408	12102
Gold Coast - Tweed Heads	31	42	2.60	2.76	1535.12	1783.30	1255	8992
Goulburn	11	33	2.02	2.38	742.35	1480.85	262	9701

Gympie	14	37	2.20	2.68	1028.15	1722.89	160	9608
Hobart	7	9	1.18	1.32	629.60	753.19	380	709
Launceston	7	10	1.54	1.77	629.60	764.51	195	807
Lismore	14	44	2.24	3.00	994.79	1894.56	265	8419
Lithgow	11	35	1.67	2.06	743.04	1592.86	261	16416
Mackay	11	18	1.83	2.44	746.51	1152.56	171	550
Melbourne	15	18	1.74	1.81	919.27	1017.48	5043	10200
Morisset - Cooranbong	27	42	2.53	2.27	1362.58	1709.25	1131	31026
Mudgee	13	22	1.92	2.11	859.82	1174.69	191	1779
Newcastle - Maitland	22	44	2.20	2.34	1211.85	1744.27	2101	27477
Nowra - Bomaderry	14	32	2.07	2.29	1007.01	1490.37	313	10503
Perth	13	17	1.81	2.11	805.37	902.65	12963	1407
Port Macquarie	17	34	2.39	2.67	1055.69	1450.79	265	2288
St Georges Basin - Sanctuary Point	14	30	2.17	2.38	946.06	1463.46	168	9423
Sunshine Coast	27	39	2.47	2.63	1327.53	1819.92	3628	10015
Sydney	32	44	1.83	2.54	1463.62	1740.97	17192	24376
Townsville	20	29	2.21	2.67	1177.91	1730.19	1083	1168
Ulladulla	12	28	1.96	2.41	832.16	1428.19	296	7872
Wollongong	21	41	1.93	2.29	1125.31	1733.48	3389	33563