

Wealth, water and wildlife: Landscape aridity intensifies the urban luxury effect

Dan Chamberlain¹  | Chevonne Reynolds^{2,3}  | Arjun Amar³  | Dominic Henry^{4,5}  | Enrico Caprio¹  | Péter Batáry⁶ 

¹Department of Life Sciences and Systems Biology, University of Turin, Turin, Italy

²Animal, Plant and Environmental Sciences, University of the Witwatersrand, Braamfontein, South Africa

³Fitzpatrick Institute of African Ornithology, DST-NRF Centre of Excellence, University of Cape Town, Rondebosch, South Africa

⁴Statistics in Ecology, Environment and Conservation, Department of Statistical Sciences, University of Cape Town, Rondebosch, South Africa

⁵Endangered Wildlife Trust, Johannesburg, South Africa

⁶Lendület Landscape and Conservation Ecology, Institute of Ecology and Botany, Centre for Ecological Research, Alkotmány u. 2-4, Vácrátót, 2163, Hungary

Correspondence

Dan Chamberlain, Department of Life Sciences and Systems Biology, University of Turin, Via Accademia Albertina 13, Turin 10123, Italy.

Email: dan.chamberlain99@gmail.com

Editor: Brian McGill

Abstract

Aim: Urban biodiversity, and its associated ecosystem services, is an important component of the quality of life of urban residents. The "luxury effect" posits a positive association between biodiversity and socioeconomic status in urban areas, and is thus reflective of environmental injustice, as the benefits associated with biodiversity are not equitably shared across society. We aimed to determine the generality of the luxury effect, and to identify the factors causing its variation across published studies.

Location: Urbanized landscapes globally.

Time period: Current.

Major taxa studied: Terrestrial animals and plants.

Methods: We tested the luxury effect across a sample of 337 estimates of the relationship between biodiversity measures and socioeconomic status from 96 studies via a meta-analysis, addressing three hypotheses: (a) the luxury effect is more pronounced where water availability is limited, (b) the luxury effect is more pronounced in developing than developed countries, (c) the luxury effect is stronger in exotic compared to native species.

Results: There was a significant overall luxury effect: there was a positive association between terrestrial biodiversity measures and socioeconomic status. The strength of the luxury effect was greater in arid areas. There was limited support for a stronger luxury effect in exotic species, but no support for any association with development status.

Main conclusions: Many key and emerging climate impacts are concentrated in urban areas. Therefore, the degree of environmental injustice represented by the luxury effect may be amplified in the future, especially in arid regions. The objective to increase urban biodiversity through more equitable management and provision of water resources could form part of a wider strategy for sustainable development of cities to promote environmental justice, enhancing the quality of life of urban residents across all sectors of society. Challenges remain to ensure that any such strategy prioritizes conservation goals for native biodiversity.

KEYWORDS

biodiversity, climate change, environmental justice, luxury effect, meta-analysis, non-native species, socioeconomic status, urbanization, water availability

1 | INTRODUCTION

Urban biodiversity is an important component of the quality of life of urban dwellers and is associated with a range of ecosystem services, such as cooling effects through shade provision, flood prevention and pollination services (Belaire, Westphal, Whelan, & Minor, 2015; Dearborn & Kark, 2009), although there can also be negative impacts of urban biodiversity for the human population (so-called 'ecosystem disservices'; Lyytimäki & Sipilä, 2009). There is mounting evidence, however, that the benefits of urban biodiversity are not equitably distributed across all levels of society, as wealthier areas within cities often have higher levels of biodiversity (e.g., Chamberlain, Henry, Reynolds, Caprio, & Amar, 2019; Hope et al., 2003; Leong, Bertone, Bayless, Dunn, & Trautwein, 2016; Leong, Dunn, & Trautwein, 2018; Luck, Smallbone, & O'Brien, 2009). The positive spatial relationship between biodiversity measures and socioeconomic status has been termed the luxury effect (Hope et al., 2003). Hypotheses for the underlying cause of the luxury effect include that wealthier individuals or municipalities have more resources to invest in management promoting biodiversity, or that higher biodiversity areas are more attractive places to live, and hence property prices are elevated (Leong et al., 2018). In terms of the sustainable development of cities, it is important to understand the luxury effect in the context of environmental justice, that is, the right of all urban residents to have access to, and to be able to benefit from, biodiversity and the ecosystem services it provides (e.g., Kinzig, Warren, Martin, Hope, & Katti, 2005). The existence of a luxury effect implies environmental injustice, and hence gives an indication of social division. Urban development plans that aim for social inclusion should, therefore, have the objective of attenuating any such luxury effect.

Much evidence exists for the luxury effect, especially in plants (e.g., Baldock et al., 2019; Gerrish & Watkins, 2018; Hope et al., 2003; Martin, Warren, & Kinzig, 2004), but there is also evidence in birds (e.g., Chamberlain et al., 2019; Lerman & Warren, 2011) and other taxa (e.g., lizards, Ackley, Wu, Angilletta, Myint, & Sullivan, 2015; arthropods, Baldock et al., 2019; Leong et al., 2016). However, such relationships are not universal (Kuras et al., 2020; Leong et al., 2018), with several studies finding no significant associations between socioeconomic status and diversity measures (e.g., Figueroa, Castro, Reyes, & Teillier, 2018; MacGregor-Fors & Schondube, 2011; Walker, Flynn, Ovando-Montejo, Ellis, & Frazier, 2017), or even finding negative associations (e.g., Davis et al., 2012; Ewers, Didham, Wratten, & Tylianakis, 2005). The range of responses, therefore, suggests that the presence of a luxury effect may be more likely under certain socioeconomic and environmental conditions. Leong et al. (2018) proposed a range of factors that could influence the strength of the luxury effect, including climate, socioeconomic context (in particular, the degree of income inequality) and species provenance (i.e., differential responses of native and exotic species).

Plant and animal diversity is positively correlated with water availability at large geographic scales (Hawkins et al., 2003), and this

may be especially marked in arid regions (Brito et al., 2014). There is evidence that diversity in urban areas correlates positively with the area covered by open water (Beninde, Veith, & Hochkirch, 2015; Ferenc, Sedláček, & Fuchs, 2014). The expectation that the luxury effect is stronger when local climatic conditions are more arid (Kuras et al., 2020; Leong et al., 2018) may arise when wealthier areas have more water resources in conditions where this resource may be otherwise limiting for biodiversity (Hope et al., 2003; Jenerette et al., 2013), for example, through irrigation of lawns, and more water features (e.g., garden ponds) in more wealthy areas. Understanding the extent to which the luxury effect may be modified by water availability, in particular across different countries with differing income levels, is important as both climate change and human population growth are predicted to increase the severity and frequency of water shortages in many cities in the future (McDonald et al., 2011; Revi et al., 2014).

The luxury effect might be dependent on the degree of income inequality at the city level, but may also be influenced by socioeconomic status at regional and national levels. First, more equitable societies may be more likely to invest in city resources at all income levels, including features that are important to biodiversity such as public green spaces (Leong et al., 2018). Second, greater overall wealth may allow richer societies to address environmental problems, including biodiversity loss, compared to poorer societies (Stern, 2004). Both income inequality and overall wealth are strongly linked to development status, where developing countries have greater income inequality and lower overall wealth compared to developed countries (United Nations, 2018a).

Urban areas are often characterized by non-native species (Gaertner et al., 2017). For plants, there is little doubt that humans act directly on urban vegetation through planting and management (Leong et al., 2018), and that private gardens and urban parks very commonly hold many non-native species, in addition to managed native species and cultivars. Introduction and management of non-native species is likely to have a relatively higher economic cost, thus the luxury effect is expected to be stronger for exotic plant species. The extent to which either native or exotic bird species are more closely tied to socioeconomic status is less clear (Leong et al., 2018), but may in part depend on the level of native vegetation within a given urban environment (Kinzig et al., 2005; Lerman & Warren, 2011).

We undertook a systematic literature review to derive data on the strength of the luxury effect across different studies. Using these data, we first tested for evidence of an overall luxury effect on urban terrestrial biodiversity by quantifying the strength of the relationship between biodiversity and socioeconomic status from each included study. We then tested three separate hypotheses: (a) the luxury effect is more pronounced where water availability is limited in the landscape (as proposed by Leong et al., 2018), that is, we predicted that the luxury effect would be stronger in areas that are naturally more arid; (b) the luxury effect is more pronounced in developing rather than developed countries as the former have greater income inequality (United Nations, 2018a); (c) there is a greater response in exotic compared to native species, as they are especially associated

with urban areas and may be more closely linked to anthropogenic resources that may be more prevalent in wealthier areas (Loss, Ruiz, & Brawn, 2009). In addition, we explored if the strength of the luxury effect was influenced by other potential drivers, including taxonomic group, and which of these drivers (e.g., aridity, development status, native/exotic species), or combination of drivers, best explained variation in the strength of the luxury effect across our sample.

2 | METHODS

2.1 | Literature search

We conducted a systematic review of studies investigating the luxury effect using the Web of Science Core Collection database over all citation indices except chemical, all document types, all years and all languages (initial database query 27 April 2018, final database query 31 December 2018). This procedure was carried out for separate taxa (birds, mammals, reptiles, arthropods and plants) divided amongst the authors for ease of management (as per Winter et al., 2018). Titles and abstracts were initially screened to remove clearly inappropriate references. In addition to those references that were obviously irrelevant, a series of exclusion criteria were also applied. Studies were excluded that: (a) were at the species-level only, as the luxury effect is relevant to species communities; (b) were not based, at least partially, in suburban or urban landscapes (defined as per Batáry, Kurucz, Suarez-Rubio, & Chamberlain, 2018) as the luxury effect concerns urban socioeconomic status and biodiversity; (c) were non-terrestrial (freshwater or marine); and, (d) were only at the level of the whole city, region or country, as we were interested in how socioeconomic status correlates with biodiversity within, rather than between, urbanized areas. The above search procedures were tested amongst the authors in a preliminary phase. Tests of inter-rater agreement between authors showed a good level of repeatability of study selection using the specified criteria. Further details of the search procedure and the repeatability analysis are given in Supporting Information Appendix S1.

Studies that were selected for the next stage were urban, but included both studies carried out within metropolitan areas (i.e., dominated by artificial surfaces and usually referred to as urban or suburban areas) and those that considered a longer gradient, which extended to rural and (semi-)natural habitats. A comparison of these gradients (defined respectively as short and long urbanization gradients as per Batáry et al., 2018) showed no significant difference in response (Supporting Information Appendix S2), so both were included in the analysis. All studies analysed some measure of biodiversity in relation to socioeconomic status. The luxury effect is primarily concerned with wealth status, which is commonly measured by household income (Leong et al., 2018). We included any variable that described the wealth of a given sample location (e.g., income or property prices), as well as proxy measures that were clearly shown to be related to wealth status of a given sample location in a particular study, typically indices of social deprivation (e.g., prosperity

index, MacGregor-Fors & Schondube, 2011; social welfare index, Paz Silva, Garcia, Estay, & Barbosa, 2015). Biodiversity not only included both 'diversity measures' (including species richness and diversity indices) and 'abundance measures', including count and density, but also measures likely to be correlated with absolute abundance, such as percent plant cover and the normalized difference vegetation index (NDVI). Measures of plant cover and NDVI, usually from remote-sensing data (e.g., Ossola & Hopton, 2018; Schwarz, Berland, & Herrmann, 2018), and true measures of abundance (i.e., based on counts of individual plants) were highly consistent in their effect sizes when considered separately (Supporting Information Appendix S2), and were thus pooled for the main analysis of abundance measures. Whilst the luxury effect typically considers diversity measures, we also consider abundance measures as they may be equally important to the human population in terms of ecosystem service provision (Belaire et al., 2015; Dearborn & Kark, 2009; Gerrish & Watkins, 2018; Jenerette, Harlan, Stefanov, & Martin, 2011).

Following screening of each paper, key meta-data for relevant papers were extracted (location, socioeconomic measure used, gradient length, whether native or exotic species were specified). At this stage there were a number of studies that could not be used for the final analysis due to lack of information regarding the data or the analyses (e.g., inadequate presentation of results). Authors of studies published in the last 10 years ($n = 18$) were contacted to provide missing information, which yielded further usable data from 10 studies.

2.2 | Effect size calculation

Test statistics that described the link between measures of diversity or abundance and socioeconomic status were converted to Pearson's r using standard conversion formulas (Lajeunesse, 2013). Pearson's r was calculated for any comparison within a study (i.e., it was possible to have more than one value of Pearson's r per study in the analysis), such as when different taxonomic groups were analysed (e.g., animals and plants, or native versus exotic organisms), or different urban habitats or locations were subsampled (e.g., private gardens and parks). Pearson's r is expressed so that the strength of a given linear association between diversity/abundance and socioeconomic status ranges between 1.0 (i.e., very strong support for the luxury effect) and -1.0 (diversity/abundance decreases with socioeconomic status), where 0 signifies no association. The luxury effect has primarily considered linear associations between wealth status and biodiversity, and here we considered only linear associations. Studies showing significant nonlinear associations were not included, although they were rare (Supporting Information Appendix S1).

2.3 | Meta-analysis

The standardized estimates of Pearson's r were analysed using the *metafor* package (Viechtbauer, 2010) within the R environment (R version 3.5.1, R Development Core Team, 2019). Prior to modelling,

Pearson's r was converted to Fisher's z to better approximate a normal distribution (Rosenberg, Rothstein, & Gurevitch, 2013). Fisher's z values and their 95% confidence intervals (CIs) were back-transformed to Pearson's r for data visualization, since its interpretation is more straightforward (Batáry et al., 2018). We refer to model-derived estimates of Pearson's r as the strength of the luxury effect, which was considered significant when the 95% CIs of the back-transformed estimate did not overlap zero.

We performed hierarchical meta-analyses separately for diversity and abundance measures, allowing for the specification of nesting factors, in order to calculate the mean overall effect size (the 'overall model'). In other words, we assessed the extent to which the luxury effect was supported across the whole sample. As there were often multiple estimates from the same publication (mean = 3.51 estimates per publication), a publication-level nesting factor was specified (Batáry et al., 2018).

To test our hypothesis that the luxury effect would be stronger in more arid conditions, we extracted the cumulative annual precipitation (mm) for a 50-km buffer around each location in the database, calculated as a 20-year average (1999–2019) from the Terraclimate data set (Abatzoglou, Dobrowski, Parks, & Hegewisch, 2018) and available at a 2.5 arc-minute resolution (c. 5 km). In instances where single effect sizes were based on more than one location, the mean precipitation was used. Precipitation was scaled and centred prior to analysis and fitted as a continuous moderator to the model specified above, that is, we performed a meta-regression specifying a publication-level nesting factor.

We then tested the influence of other moderators (i.e., variables that condition the effect size in meta-analyses) on the luxury effect, and assessed the extent to which different moderators, or combinations of moderators, explained the strength of the luxury effect across the sample by comparing model performance (see below). We ran further hierarchical models that tested for differences between levels of a moderator within a given model (between-group heterogeneity). We considered cases where between-group heterogeneity was significant as evidence of a moderator effect.

The following factorial moderators were tested: species provenance (i.e., native or exotic), development status and taxonomic group. To test the hypothesis that the luxury effect would be more pronounced in developing countries (i.e., where income inequality is greater), we specified development status as a simple two-level classification of developed or developing countries defined according to United Nations (2018a), although for brevity we use 'rich' or 'poor' countries, respectively. This classification was representative of income inequality: the Gini coefficient derived from the World Inequality Report 2018 (wir2018.wid.world) for each country in the meta-analysis was much higher for poor (mean \pm SE = 46.7 ± 1.9 , $n = 9$) than rich (mean \pm SE = 31.5 ± 1.3 , $n = 8$) countries. To test the hypothesis that the luxury effect would vary according to species provenance, we tested the difference in response between native and exotic species (for studies where this was specified). We then tested for different effects of precipitation on the strength of the luxury effect according to taxonomic group, species provenance and

development status, by testing the interaction between precipitation and each factorial moderator in turn.

In addition to the three hypotheses detailed above, we also tested for a difference in response between different taxonomic groups. The majority of studies were based on plants and birds, with very few that assessed other animal groups (see Results), hence two taxonomic groups, plants and animals, were defined. For diversity measures, there were some studies that considered composite indices of biodiversity and included multiple measures (e.g., both animals and plants) as well as some other structural habitat elements (e.g., Belaire, Westphal, & Minor, 2016; Hand, Freeman, Seddon, & van Heezik, 2016). These were classified as a third 'taxonomic' grouping, termed 'All'.

Akaike's information criterion adjusted for small sample size (AICc) was used as a measure of model performance (Burnham & Anderson, 2002) to compare different models derived from the same data set and hence rank the support for effects of different moderators. Lower AICc values indicate better model performance when the difference in AICc between models (Δ AICc) is greater than 2 (Burnham & Anderson, 2002). Otherwise, models were considered of equivalent performance.

2.4 | Publication bias

Publication bias typically arises when studies finding significant effects, or supporting a particular hypothesis, are more likely to be published than those that find no supportive evidence. Whilst there are several tests for publication bias in meta-analyses, no single test is conclusive (Jennions, Lortie, Rosenberg, & Rothstein, 2013). We therefore used four separate methods to assess publication bias in our sample (following Winter et al., 2018). There was no evidence of publication bias in any analysis (Supporting Information Appendix S3). Furthermore, we identified potential influential outliers using graphical methods, and their effects were assessed by comparing model parameter estimates with and without these outliers. There were few outliers identified, and their inclusion in the model did not have a large influence on the overall patterns (Supporting Information Appendix S3).

3 | RESULTS

3.1 | Literature search

We identified 3,206 studies in the initial literature search, of which 139 were deemed to be relevant for testing the luxury effect, and a subset of 96 satisfied the necessary inclusion criteria for the meta-analysis (see Supporting Information Appendix S1 for a full details of the selection procedure). There were 38 studies that considered diversity measures in relation to socioeconomic status, 72 that considered abundance measures and 14 studies that considered both types of measure. Plant communities were studied in 80% of these

papers (Figure 1). The only other group that constituted a reasonable proportion of the total sample was birds (15%). There were only 13 studies in total that explicitly considered native and/or exotic species. There was a clear geographic bias in the sample where 60.4% of studies were carried out in North America (Figure 1). The only other region that contributed more than 10% was Australia/New Zealand (14.6%). Only 15.6% of the sample was carried out in poor countries. Mean annual precipitation ranged from 116 to 2,535 mm across the sample (mean \pm SE = 869 \pm 11 mm, n = 337).

3.2 | Meta-analysis

There were 337 separate standardized effect sizes calculated from the 96 studies (99 for diversity measures, 238 for abundance measures). All model results are shown in Supporting Information Appendix S2.

There was a significant positive overall relationship between socioeconomic status and diversity measures (Figure 2a), showing general support for the luxury effect across our sample of 38 papers. There was a significant moderator effect of precipitation on the relationship with diversity measures. In contrast, there was

no indication that the relationship with diversity measures was influenced by either taxonomic group or development status. There was a significant moderator effect of species provenance, with no overall association observed for native species, but a positive association observed for exotic species (Figure 2a). However, these results were based on small sample sizes (n = 20 standardized estimates from 10 studies). Results for abundance measures were consistent with those for diversity measures: there was a significant positive relationship between socioeconomic status and abundance measures, and a significant negative moderator effect of precipitation on abundance measures (Figure 2b). There were insufficient data to test for a moderator effect of species provenance on abundance measures (n = 7 standardized estimates from 4 studies).

The relationships between precipitation, and diversity and abundance measures, are shown in Figure 3. For diversity measures, the negative influence of precipitation was somewhat more evident in rich countries (Figure 3a) as shown by a weak interaction with development status (Pearson's r = 0.102, 95%CI = -0.001 to 0.204) that approached significance (p = 0.053; Supporting Information Appendix S2). The precipitation-only model, and the model including the interaction between precipitation and development status,

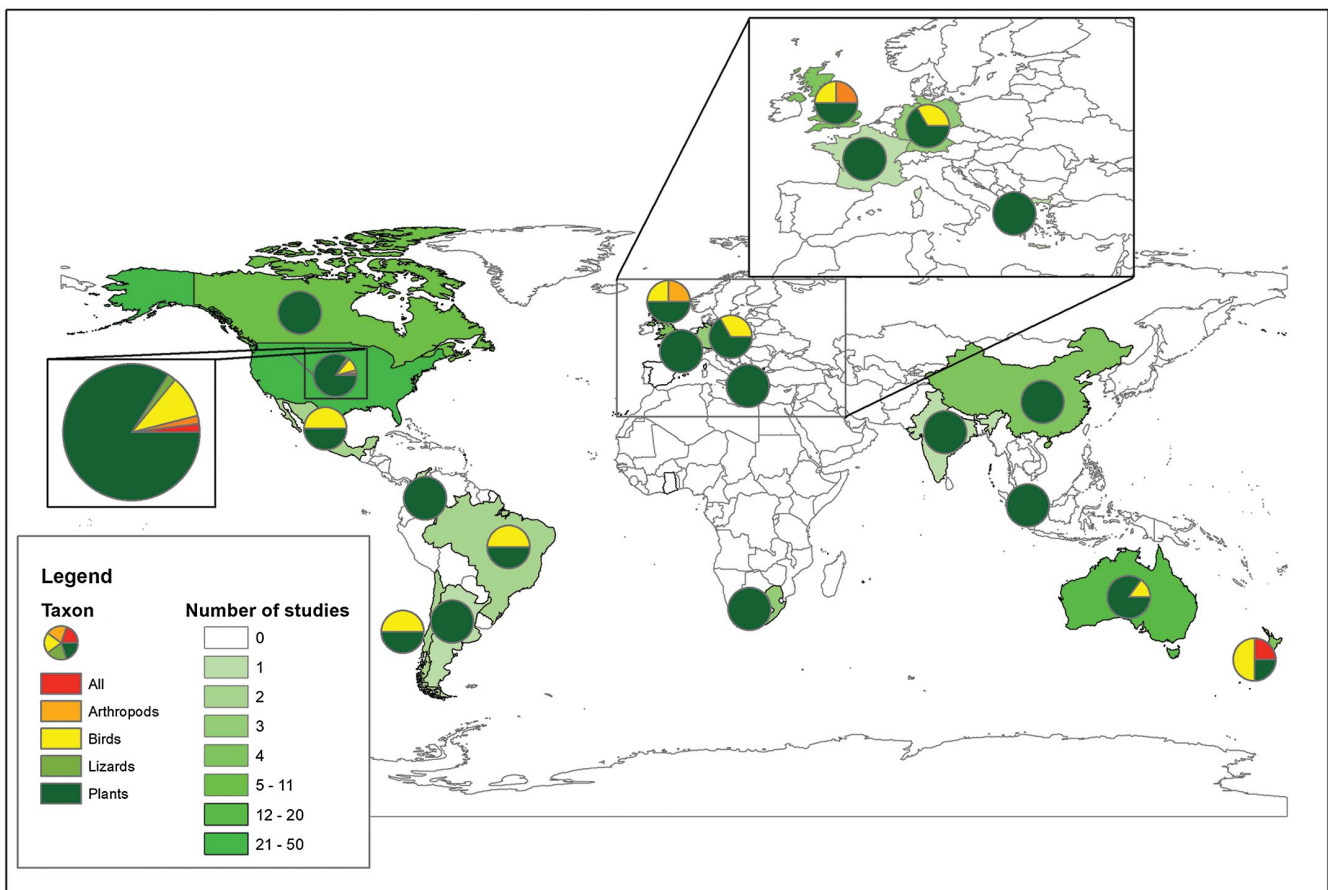
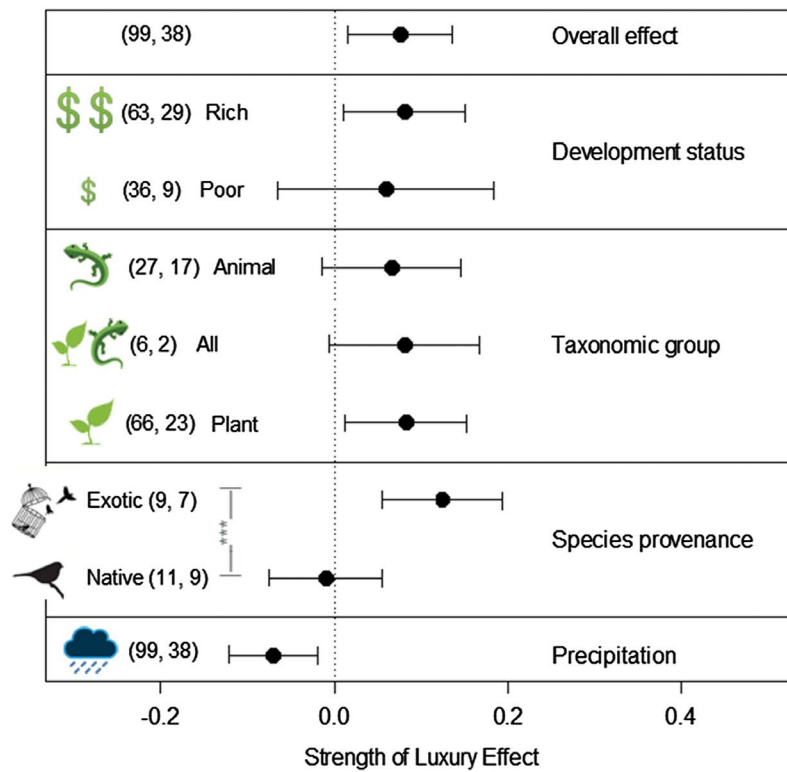


FIGURE 1 Geographic distribution of studies in the meta-analysis, and the proportion of studies per region analysing different categories of taxonomic group. Countries where at least one study was carried out are shaded according to the number of studies. Proportions were recalculated based on n = 96 studies overall, and n = 101 studies for the number of taxa (there were five studies that considered two taxa each). Insets show enlarged portions of the figure to aid visual assessment

(a) Diversity measures



(b) Abundance measures

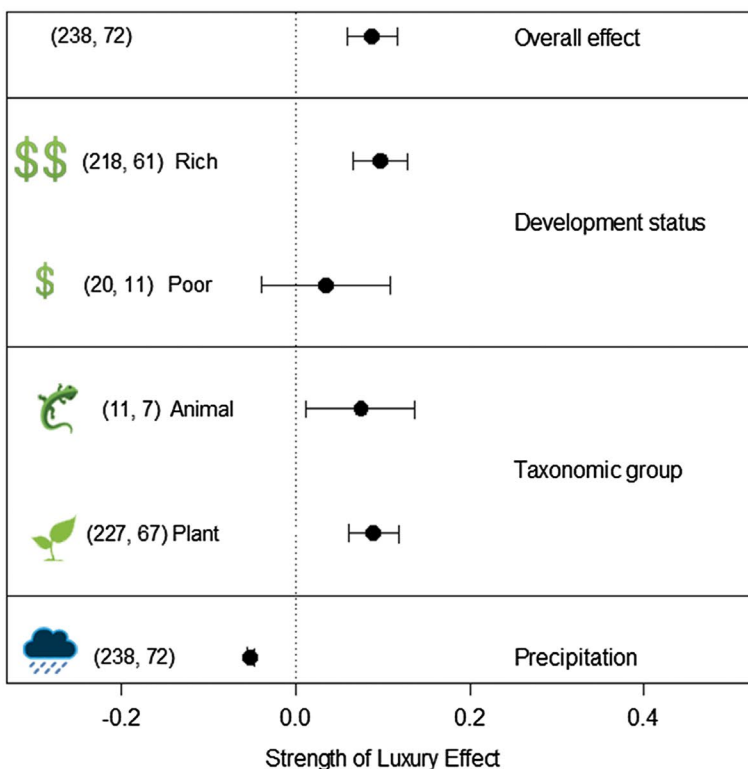
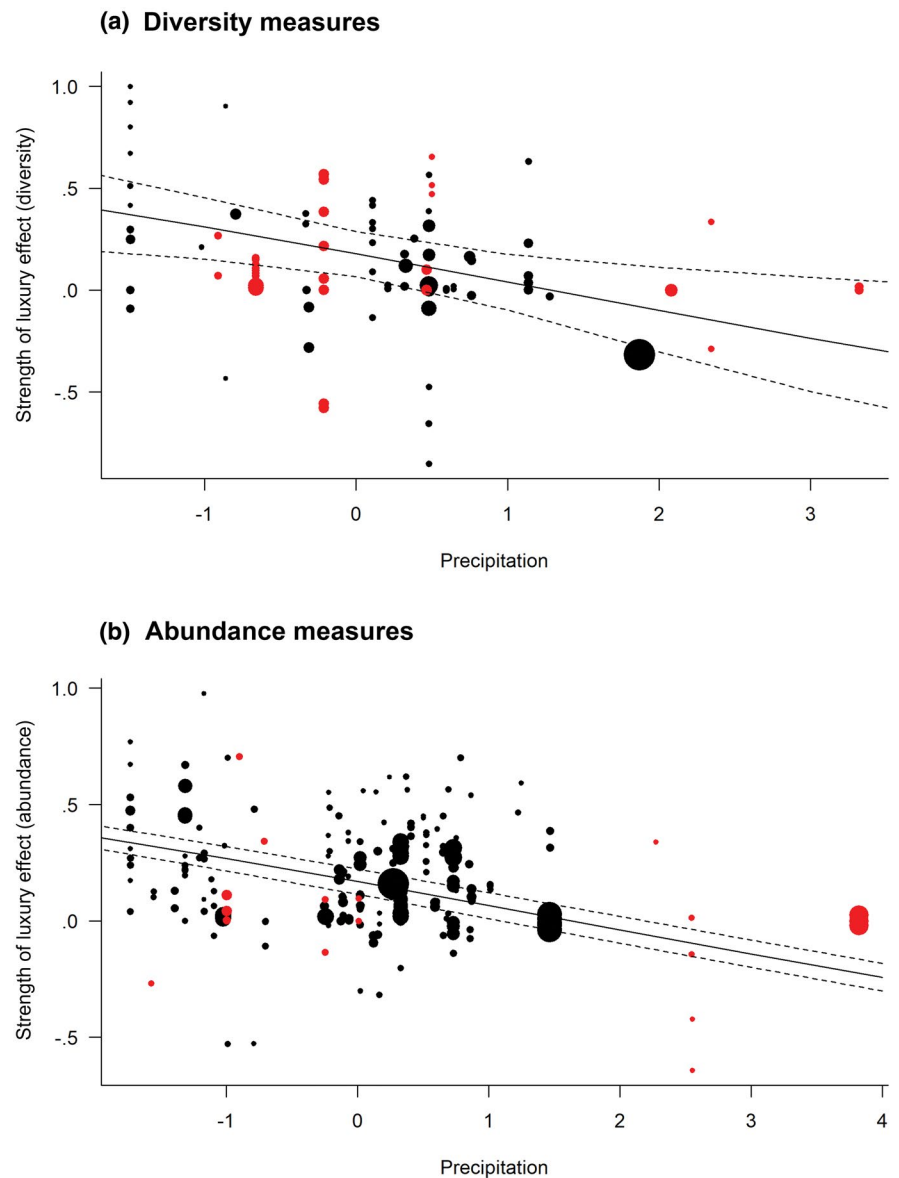


FIGURE 2 Estimates of the strength of the luxury effect (expressed as standardized Pearson's $r \pm 95\%$ confidence limits) based on associations between (a) diversity measures and socioeconomic status, and (b) abundance measures and socioeconomic status. The overall effect is the strength of the luxury effect without moderators. For taxonomic group (a), 'All' refers to studies that considered multi-taxa diversity measures. Significant ($p < .001$) differences in between-group heterogeneity of moderators are indicated by vertical whiskers and asterisks. Sample sizes are given in parentheses (number of standardized estimates, number of studies). In some cases, observations were included for different levels of a given moderator from the same paper (e.g., a paper may have analysed both animals and plants, or both native and exotic species). Note the estimate for precipitation in (b) has a very narrow 95% confidence interval

were the best performing models for diversity measures (Supporting Information Appendix S4). For abundance measures, the precipitation model was also the best performing model. The only equivalent

model was that including the interaction between precipitation and gradient length ($\Delta AICc = 0.38$; Supporting Information Appendix S2, Table S4), although the interaction in this latter model, in common

FIGURE 3 The strength of the luxury effect (expressed as standardized Pearson's r) in relation to the standardized precipitation of each study location, where negative values indicate more arid conditions. Lines were fitted from a meta-regression model, specifying study identity as a nesting factor. Dotted lines indicate 95% confidence limits. Symbol size is inversely proportional to the standard error of the estimate (i.e., larger sizes are associated with higher precision and larger sample sizes). Black symbols are from rich countries, red symbols from poor countries. (a) Diversity measures, $n = 99$ estimates derived from 38 studies. (b) Abundance measures, $n = 237$ estimates derived from 72 studies



with others that included interactions between precipitation and any factorial moderators, was not significant (Supporting Information Appendix S4).

4 | DISCUSSION

Our meta-analysis supported the existence of the luxury effect, with significant positive associations between both diversity and abundance measures and socioeconomic status. The effect sizes were not strong for either diversity measures ($r = 0.076$, 95%CI = 0.015 to 0.137) or abundance measures ($r = 0.088$, 95%CI = 0.058 to 0.117). Nevertheless, the luxury effect was consistent (i.e., no significant between-group heterogeneity) amongst different taxonomic groups and between different urbanization gradient lengths, and was robust to outliers. Additionally, there was strong support for the hypothesis that the luxury effect is more pronounced in drier cities. The strength of the luxury effect was higher where

there was less precipitation for both diversity and abundance measures, thus supporting Leong et al.'s (2018) contention that the luxury effect would be amplified in more arid cities. There was no support for the hypothesis that the luxury effect is more pronounced where income inequality is greater, but there was some support for an influence of species provenance, where the luxury effect was evident in exotic, but not native, species. It should, however, be noted that there was a fair degree of unexplained variation in these analyses. There are many potential underlying drivers of the luxury effect (Kuras et al., 2020; Leong et al., 2018) that may have accounted for this unexplained variation. Such drivers include land use history, social history and the age of urban settlements (so-called 'legacy effects'), as well as how socioeconomic status is measured. Indeed, using income-based measures to assess links between socioeconomic status and urban biodiversity may be an over-simplification, as there is evidence that social status may also be important (i.e., 'the ecology of prestige'; Grove, Locke, & O'Neil-Dunne, 2014).

Our results suggest that socioeconomic status has a greater influence on urban biodiversity in more arid regions, likely through greater investment in the provision of water resources (irrigation of gardens and parks, public and private water features), and also possibly because areas with water are more desirable, thus, inflating property prices (Mahan, Polasky, & Adams, 2000). Our results suggest that water availability is an important component driving urban biodiversity in drier areas, likely through enhanced vegetation cover and species richness, and subsequent cascading effects on animal diversity. Our findings also agree with previous research showing that the link between socioeconomic status, biodiversity (Kuras et al., 2020) and vegetation cover (Jenerette et al., 2013) is more pronounced in arid cities. There is evidence that socioeconomic status is linked to greater ecosystem service provision of vegetation, in particular in terms of cooling effects of canopy cover (Jenerette et al., 2011). On this basis, the effect of precipitation found in our study demonstrates environmental injustice in arid cities in that poorer areas will have greater exposure to the deleterious effects of higher temperatures, which will be exacerbated in the future by the effects of climate change.

We found no evidence that the luxury effect differed between countries defined according to development status, thus there was no support for the hypothesis that it would be stronger where income inequality is greater (Leong et al., 2018). There was some evidence of an interaction between precipitation and development status, the influence of precipitation being more evident in rich countries. We therefore expect the luxury effect to be most evident in drier, richer countries. Indeed, the effect size for studies with precipitation levels lower than the overall median and which were carried out in rich countries was 0.204 (95%CI = 0.051 to 0.357, $n = 31$ observations from 12 studies), considerably more than the overall effect size of 0.076. The influence of development status represented by this interaction with precipitation, though weak, may suggest that the luxury effect is more associated with rich countries because a certain level of wealth needs to be attained before negative impacts of urbanization can be ameliorated, whereas this threshold may not be reached in poorer countries. This has parallels with the concept of the environmental Kuznets' curve, where the damaging consequences of economic growth on the environment (e.g., Donald, Pisano, Rayment, & Pain, 2002) can only be ameliorated when a certain level of wealth is reached (Stern, 2004), although the evidence for such an effect is equivocal (e.g., Czech, 2008). Nevertheless, increased urbanization may actually have several potential societal benefits, which may lead to wider biodiversity benefits (Sanderson, Walston, & Robinson, 2018), as long as urban planning and management is driven by ideas of sustainability and social equity.

There was evidence that the luxury effect was stronger in exotic rather than in native species. However, the sample sizes were very small because, in most studies, there was no distinction made between native and exotic species. Previous studies have found differing responses of native and exotic species (Leong et al., 2018), in some cases the luxury effect being more strongly evident in native species (e.g., Lerman & Warren, 2011), whilst in others the overall

relationship was driven by exotic species (Figueroa, Castro, Reyes, & Teillier, 2018; Loss et al., 2009). Our results support the contention that the luxury effect is more strongly associated with exotic species that have established self-sustaining populations and that are typically good exploiters of urban habitats (Gaertner et al., 2017). For plants, many of these populations likely derive from ornamental species, as wealthier households are more likely to be able to buy and manage (e.g., through irrigation) these species. Indeed, it has been shown that the establishment of invasive plants is linked to market conditions in the horticultural trade (Dehnen-Schmutz, Touza, Perrings, & Williamson, 2007). Whilst we have found some intriguing differences, which lend some support to our hypothesis of a more pronounced luxury effect in non-native species, the results highlight the lack of studies that have considered separate tests of the luxury effect according to species provenance, and we would encourage future studies to explicitly explore this aspect.

There was no strong evidence that the standardized effect sizes were subject to publication bias. Nevertheless, there were geographic and taxonomic biases evident. First, there were relatively few (c. 15%) studies carried out in the developing world, and there was a clear bias towards studies carried out in North America. Although some differences in the strength of the luxury effect were shown between poor and rich countries, to some extent this may have been caused by low sample sizes in the former. Given that population growth rates are highest and future rates of urban expansion are forecast to be greatest in the developing world (United Nations, 2018b), and that these regions hold the highest levels of biodiversity and poverty (Fisher & Christopher, 2007), it is essential that more tests of the luxury effect are carried out in poorer countries in order to inform urban development strategies in those regions. Second, with few exceptions, studies linking socioeconomic status and urban biodiversity have been carried out on plants or birds. Further research into the luxury effect should therefore seek to expand our knowledge of urban biodiversity responses to socioeconomic status across a broad range of taxa. In particular, research should be targeted at those underexplored taxa. It would also be of considerable interest to understand whether the effect extends equally to those taxa that are associated with ecosystem services (e.g., pollinators; Baldock et al., 2019) and disservices (e.g., potential disease spread by mammal species such as rats and bats; Lyytimäki & Sipilä, 2009).

5 | CONCLUSION

Our study strongly supports the hypothesis that the luxury effect may be driven by a positive response of urban biodiversity to water availability. Strategies that enhance water provision in poorer urban areas, such as increased irrigation of public spaces or the creation of water features, are therefore likely to promote biodiversity and the benefits with which it is associated, in particular for cities in more arid landscapes. However, while urban biodiversity may have a range of benefits to the human population

(Dearborn & Kark, 2009), not all biodiversity is perceived as 'positive', especially when urban plant and animal communities feature non-native species (Belaire et al., 2015). As within other habitat types, the conservation of native species should be prioritized in urban areas (McKinney, 2006). This clearly can have implications for management approaches that seek to address issues related to the luxury effect. For example, enhanced water provision to poorer areas of arid cities will probably enhance overall biodiversity, but it seems likely that, at least in part, this will be due to the creation of habitats for species that would not otherwise occur there, and could also be detrimental to more arid-adapted native species. Nevertheless, the limited evidence available does suggest that even exotic species can often contribute positively to urban ecosystem services (Ziter, 2016). A remaining challenge in developing sustainable urbanization strategies is therefore to reconcile the potential benefits of non-native species with conservation goals for native biodiversity in an urban context.

Many key and emerging climate risks are likely to be concentrated in urban areas, including reduced precipitation (Revi et al., 2014). Thus, if cities become more arid, the degree of environmental injustice represented by the luxury effect is likely to be amplified in the future. The objective to increase urban, and preferably native, biodiversity through more equitable management and provision of water resources should, therefore, form part of a wider strategy for sustainable development of cities that includes planning for sustainable settlements, targeted construction (i.e., building on biodiversity-poor rather than biodiversity-rich sites), and consideration of social aspects in order to promote environmental justice, and thus enhance the quality of life of urban inhabitants across all sectors of society.

Urbanization undoubtedly has generally negative effects on the native biodiversity of largely intact habitats (Aronson et al., 2014). However, given that the human population is expanding rapidly, and that the proportion living in urban areas is increasing (United Nations, 2015), further urbanization is inevitable. Ultimately, more sustainable ways of urban living need to be found, both to minimize negative impacts on biodiversity and to maximize the quality of life of urban inhabitants (Sanderson et al., 2018; United Nations, 2018b), and thus to enhance the resilience of cities in the face of elevated risks to urban dwellers caused by increasing temperatures (Revi et al., 2014). An understanding of the factors that drive the apparently pervasive luxury effect will facilitate the management of urban areas in a more equitable manner, helping to ensure that the benefits of urban biodiversity are available to both rich and poor alike.

ACKNOWLEDGMENTS

We would like to thank the following for helping us to track down data, and for their encouraging advice: Jeff Ackley, Adam Berland, Katharine Bowgen, K. Arthur Endsley, Javier Alejandro Figueroa Ortiz, Ann Kinzig, Scott Loss, Carmen Paz Silva, Cassondra Walker and Erin Wetherley. PB was supported by the Economic Development and Innovation Operational Programme of Hungary (GINOP-2.3.2-15-2016-00019).

AUTHOR CONTRIBUTIONS

D. Chamberlain designed the study and wrote the paper, with contributions from all authors. P. Batáry led the analysis. C. Reynolds carried out the GIS data extraction. All authors contributed to literature searches and data extraction.

DATA AVAILABILITY STATEMENT

All data used in the meta-analysis are available as an Excel file at: <https://zenodo.org/record/3765225#.XqL9n2j7RnI>

ORCID

Dan Chamberlain  <https://orcid.org/0000-0002-5381-2024>
 Chevonne Reynolds  <https://orcid.org/0000-0002-2345-7017>
 Arjun Amar  <https://orcid.org/0000-0002-7405-1180>
 Dominic Henry  <https://orcid.org/0000-0001-7375-141X>
 Enrico Caprio  <https://orcid.org/0000-0002-5997-5959>
 Péter Batáry  <https://orcid.org/0000-0002-1017-6996>

REFERENCES

- Abatzoglou, J. T., Dobrowski, S. Z., Parks, S. A., & Hegewisch, K. C. (2018). Terraclimate, a high-resolution global dataset of monthly climate and climatic water balance from 1958–2015. *Scientific Data*, 5, 170191. <https://doi.org/10.1038/sdata.2017.191>
- Ackley, J. W., Wu, J., Angilletta, M. J., Myint, S. W., & Sullivan, B. (2015). Rich lizards: How affluence and land cover influence the diversity and abundance of desert reptiles persisting in an urban landscape. *Biological Conservation*, 182, 87–92. <https://doi.org/10.1016/j.biocon.2014.11.009>
- Aronson, M. F. J., La Sorte, F. A., Nilon, C. H., Katti, M., Goddard, M. A., Lepczyk, C. A., ... Winter, M. (2014). A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. *Proceedings of the Royal Society B: Biological Sciences*, 281, 20133330. <https://doi.org/10.1098/rspb.2013.3330>
- Baldock, K. C. R., Goddard, M. A., Hicks, D. M., Kunin, W. E., Mitschunas, N., Morse, H., ... Memmott, J. (2019). A systems approach reveals urban pollinator hotspots and conservation opportunities. *Nature Ecology and Evolution*, 3, 363–373. <https://doi.org/10.1038/s41559-018-0769-y>
- Batáry, P., Kurucz, K., Suarez-Rubio, M., & Chamberlain, D. (2018). Non-linearities in bird responses across urbanization gradients: A meta-analysis. *Global Change Biology*, 24, 1046–1054. <https://doi.org/10.1111/gcb.13964>
- Belaire, J. A., Westphal, L. M., & Minor, E. S. (2016). Different social drivers, including perceptions of urban wildlife, explain the ecological resources in residential landscapes. *Landscape Ecology*, 31, 401–413. <https://doi.org/10.1007/s10980-015-0256-7>
- Belaire, J. A., Westphal, L. M., Whelan, C. J., & Minor, E. S. (2015). Urban residents' perceptions of birds in the neighborhood: Biodiversity, cultural ecosystem services, and disservices. *Condor*, 117, 192–202. <https://doi.org/10.1650/CONDOR-14-128.1>
- Beninde, J., Veith, M., & Hochkirch, A. (2015). Biodiversity in cities needs space: A meta-analysis of factors determining intra-urban biodiversity variation. *Ecology Letters*, 18, 581–592. <https://doi.org/10.1111/ele.12427>
- Brito, J. C., Godinho, R., Martínez-Freiría, F., Pleguezuelos, J. M., Rebelo, H., Santos, X., ... Carranza, S. (2014). Unravelling biodiversity, evolution and threats to conservation in the Sahara-Sahel. *Biological Reviews*, 89, 215–231. <https://doi.org/10.1111/brv.12049>
- Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference. A practical information-theoretic approach* (2nd ed.). Berlin, Germany: Springer-Verlag.

- Chamberlain, D. E., Henry, D., Reynolds, C., Caprio, E., & Amar, A. (2019). The relationship between wealth and biodiversity: A test of the Luxury Effect on bird species richness in the developing world. *Global Change Biology*, 25, 3045–3055. <https://doi.org/10.1111/gcb.14682>
- Czech, B. (2008). Prospects for reconciling the conflict between economic growth and biodiversity conservation with technological progress. *Conservation Biology*, 22, 1389–1398. <https://doi.org/10.1111/j.1523-1739.2008.01089.x>
- Davis, A. Y., Belaire, J. A., Farfan, M. A., Milz, D., Sweeney, E. R., Loss, S. R., & Minor, E. S. (2012). Green infrastructure and bird diversity across an urban socioeconomic gradient. *Ecosphere*, 3, 105. <https://doi.org/10.1890/ES12-00126.1>
- Dearborn, D. C., & Kark, S. (2009). Motivations for conserving urban biodiversity. *Conservation Biology*, 24, 432–440. <https://doi.org/10.1111/j.1523-1739.2009.01328.x>
- Dehnen-Schmutz, K., Touza, J., Perrings, C., & Williamson, M. (2007). A century of the ornamental plant trade and its impact on invasion success. *Diversity and Distributions*, 13, 527–534. <https://doi.org/10.1111/j.1472-4642.2007.00359.x>
- Donald, P. F., Pisano, G., Rayment, M. D., & Pain, D. J. (2002). The common agricultural policy, EU enlargement and the conservation of Europe's farmland birds. *Agriculture, Ecosystems and Environment*, 89, 167–182. [https://doi.org/10.1016/S0167-8809\(01\)00244-4](https://doi.org/10.1016/S0167-8809(01)00244-4)
- Ewers, R. M., Didham, R. K., Wratten, S. D., & Tylianakis, J. M. (2005). Remotely sensed landscape heterogeneity as a rapid tool for assessing local biodiversity value in a highly modified New Zealand landscape. *Biodiversity and Conservation*, 14, 1469–1485. <https://doi.org/10.1007/s10531-004-9786-z>
- Ferenc, M., Sedláček, O., & Fuchs, R. (2014). How to improve urban greenspace for woodland birds: Site and local-scale determinants of bird species richness. *Urban Ecosystems*, 17, 625–640. <https://doi.org/10.1007/s11252-013-0328-x>
- Figueroa, J. A., Castro, S. A., Reyes, M., & Teillier, S. (2018). Urban park area and age determine the richness of native and exotic plants in parks of a Latin American city: Santiago as a case study. *Urban Ecosystems*, 21, 645–655. <https://doi.org/10.1007/s11252-018-0743-0>
- Fisher, B., & Christopher, T. (2007). Poverty and biodiversity: Measuring the overlap of human poverty and the biodiversity hotspots. *Ecological Economics*, 62, 93–101. <https://doi.org/10.1016/j.ecolecon.2006.05.020>
- Gaertner, M., Wilson, J. R. U., Cadotte, M. W., MacIvor, J. S., Zenni, R. D., & Richardson, D. M. (2017). Non-native species in urban environments: Patterns, processes, impacts and challenges. *Biological Invasions*, 19, 3461–3469. <https://doi.org/10.1007/s10530-017-1598-7>
- Gerrish, E., & Watkins, S. L. (2018). The relationship between urban forests and income: A meta-analysis. *Landscape and Urban Planning*, 170, 293–308. <https://doi.org/10.1016/j.landurbplan.2017.09.005>
- Grove, J. M., Locke, D. H., & O'Neil-Dunne, J. P. M. (2014). An ecology of prestige in New York City: Examining the relationships among population density, socio-economic status, group identity, and residential canopy cover. *Environmental Management*, 54, 402–419. <https://doi.org/10.1007/s00267-014-0310-2>
- Hand, K. L., Freeman, C., Seddon, P. J., Stein, A., & van Heezik, Y. (2016). A novel method for fine-scale biodiversity assessment and prediction across diverse urban landscapes reveals social deprivation-related inequalities in private, not public spaces. *Landscape and Urban Planning*, 151, 33–44. <https://doi.org/10.1016/j.landurbplan.2016.03.002>
- Hawkins, B. A., Field, R., Cornell, H. V., Currie, D. J., Guégan, J.-F., Kaufman, D. M., ... Turner, J. R. G. (2003). Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, 84, 3105–3117. <https://doi.org/10.1890/03-8006>
- Hope, D., Gries, C., Zhu, W., Fagan, W. F., Redman, C. L., Grimm, N. B., ... Kinzig, A. (2003). Socioeconomics drives urban plant biodiversity. *Proceedings of the National Academy of Sciences USA*, 100, 8788–8792. <https://doi.org/10.1080/13549830802522061>
- Jenerette, G. D., Harlan, S. L., Stefanov, W. L., & Martin, C. A. (2011). Ecosystem services and urban heat riskscape moderation: Water, green spaces, and social inequality in Phoenix, USA. *Ecological Applications*, 21, 2637–2651. <https://doi.org/10.1890/10-1493.1>
- Jenerette, G. D., Miller, G., Buyantuev, A., Patakis, D. E., Gillespie, T. W., & Pincetl, S. (2013). Urban vegetation and income segregation in drylands: A synthesis of seven metropolitan regions in the southwestern United States. *Environmental Research Letters*, 8, e044001. <https://doi.org/10.1088/1748-9326/8/4/044001>
- Jennions, M. D., Lortie, C. J., Rosenberg, M. S., & Rothstein, H. R. (2013). Publication and related biases. In J. Koricheva, J. Gurevitch, & K. Mengersen (Eds.), *Handbook of meta-analysis in ecology and evolution* (pp. 207–236). New Jersey: Princeton University Press.
- Kinzig, A., Warren, P., Martin, C., Hope, D., & Katti, M. (2005). The effects of human socioeconomic status and cultural characteristics on urban patterns of biodiversity. *Ecology and Society*, 10, 23. <https://doi.org/10.5751/ES-01264-100123>
- Kuras, E. R., Warren, P. S., Zinder, J. A., Aronson, M. F. J., Cilliers, S., Goddard, M. A., ... Winkler, R. (2020). Urban socioeconomic inequality and biodiversity often converge, but not always: A global meta-analysis. *Landscape and Urban Planning*, 198, 103799. <https://doi.org/10.1016/j.landurbplan.2020.103799>
- Lajeunesse, M. J. (2013). Recovering missing or partial data from studies: A survey of conversions and imputations for meta-analysis. In J. Koricheva, J. Gurevitch, & K. Mengersen (Eds.), *Handbook of meta-analysis in ecology and evolution* (pp. 195–206). NJ: Princeton University Press.
- Leong, M., Bertone, M. A., Bayless, K. M., Dunn, R. R., & Trautwein, M. D. (2016). Exoskeletons and economics: Indoor arthropod diversity increases in affluent neighbourhoods. *Biology Letters*, 12, 20160322. <https://doi.org/10.1098/rsbl.2016.0322>
- Leong, M., Dunn, R. R., & Trautwein, M. D. (2018). Biodiversity and socioeconomics in the city: A review of the luxury effect. *Biology Letters*, 14, 20180082. <https://doi.org/10.1098/rsbl.2018.0082>
- Lerman, S. B., & Warren, P. S. (2011). The conservation value of residential yards: Linking birds and people. *Ecological Applications*, 21, 1327–1339. <https://doi.org/10.1890/10-0423.1>
- Loss, S. R., Ruiz, M. O., & Brawn, J. D. (2009). Relationships between avian diversity, neighborhood age, income, and environmental characteristics of an urban landscape. *Biological Conservation*, 142, 2578–2585. <https://doi.org/10.1016/j.biocon.2009.06.004>
- Luck, G. W., Smallbone, L. T., & O'Brien, R. (2009). Socioeconomics and vegetation change in urban ecosystems: Patterns in space and time. *Ecosystems*, 12, 604–620. <https://doi.org/10.1007/s10021-009-9244-6>
- Lyytimäki, J., & Sipilä, M. (2009). Hopping on one leg – The challenge of ecosystem disservices for urban green management. *Urban Forestry and Urban Greening*, 8, 309–315. <https://doi.org/10.1016/j.ufug.2009.09.003>
- MacGregor-Fors, I., & Schondube, J. E. (2011). Gray vs. green urbanization: Relative importance of urban features for urban bird communities. *Basic and Applied Ecology*, 12, 372–381. <https://doi.org/10.1016/j.baae.2011.04.003>
- Mahan, B. L., Polasky, S., & Adams, R. M. (2000). Valuing urban wetlands: A property price approach. *Land Economics*, 76, 100–113. <https://doi.org/10.2307/3147260>
- Martin, C. A., Warren, P. S., & Kinzig, A. P. (2004). Neighborhood socioeconomic status is a useful predictor of perennial landscape vegetation in residential neighborhoods and embedded small parks of Phoenix, AZ. *Landscape and Urban Planning*, 69, 355–368. <https://doi.org/10.1016/j.landurbplan.2003.10.034>
- McDonald, R. I., Green, P., Balk, D., Fekete, B. M., Revenga, C., Todd, M., & Montgomery, M. (2011). Urban growth, climate change, and freshwater availability. *Proceedings of the National Academy of Sciences USA*, 108, 6312–6317. <https://doi.org/10.1073/pnas.1011615108>

- McKinney, M. L. (2006). Urbanization as a major cause of biotic homogenization. *Biological Conservation*, 127, 247–260. <https://doi.org/10.1016/j.biocon.2005.09.005>
- Ossola, A., & Hopton, M. E. (2018). Measuring urban tree loss dynamics across residential landscapes. *Science of the Total Environment*, 612, 940–949. <https://doi.org/10.1016/j.scitotenv.2017.08.103>
- Paz Silva, C. P., Garcia, C. E., Estay, S. A., & Barbosa, O. (2015). Bird richness and abundance in response to urban form in a Latin American city: Valdivia, Chile as a case study. *PLoS ONE*, 10, e0138120. <https://doi.org/10.1371/journal.pone.0138120>
- R Development Core Team. (2019). *R: A language and environment for statistical computing*, version 3.5.3. Vienna, Austria: R Foundation for Statistical Computing.
- Revi, A., Satterthwaite, D. E., Aragón-Durand, F., Corfee-Morlot, J., Kiunsi, R. B. R., Pelling, M., & Solecki, W. (2014). Urban areas. In C. B. Field, V. R. Barros, D. J. Dokken, K. J. Mach, M. D. Mastrandrea, T. E. Bilir, ... L. L. White (Eds.), *Climate change 2014: Impacts, adaptation, and vulnerability. Part A: Global and sectoral aspects. Contribution of Working Group II to the fifth assessment report of the Intergovernmental Panel on Climate Change* (pp. 535–612). UK: Cambridge University Press.
- Rosenberg, M. S., Rothstein, H. R., & Gurevitch, J. (2013). Effect sizes: Conventional choices and calculations. In J. Koricheva, J. Gurevitch, & K. Mengersen (Eds.), *Handbook of meta-analysis in ecology and evolution* (pp. 61–71). NJ: Princeton University Press.
- Sanderson, E. W., Walston, J., & Robinson, J. G. (2018). From bottleneck to breakthrough: Urbanization and the future of biodiversity conservation. *BioScience*, 68, 412–426. <https://doi.org/10.1093/biosci/biy039>
- Schwarz, K., Berland, A., & Herrmann, D. L. (2018). Green, but not just? Rethinking environmental justice indicators in shrinking cities. *Sustainable Cities and Society*, 41, 816–821. <https://doi.org/10.1016/j.scs.2018.06.026>
- Stern, D. I. (2004). The rise and the fall of the Environmental Kuznets Curve. *World Development*, 32, 1419–1439. <https://doi.org/10.1016/j.worlddev.2004.03>
- United Nations. (2015). *World urbanization prospects: The 2014 revision*. New York, NY: United Nations.
- United Nations (2018a). About the Sustainable Development Goals. Accessed 25 July 2018, from www.un.org/sustainabledevelopment/sustainable-development-goals/
- United Nations. (2018b). Goal 11: Make cities inclusive, safe, resilient and sustainable. Accessed 8 August 2019 from www.un.org/sustainabledevelopment/cities/
- Viechtbauer, W. (2010). Conducting meta-analyses in R with the metafor package. *Journal of Statistical Software*, 36, 1–48. <https://doi.org/10.18637/jss.v036.i03>
- Walker, C. M., Flynn, K. C., Ovando-Montejo, G. A., Ellis, E. A., & Frazier, A. E. (2017). Does demolition improve biodiversity? Linking urban green space and socioeconomic characteristics to avian richness in a shrinking city. *Urban Ecosystems*, 20, 1191–1202. <https://doi.org/10.1007/s11252-017-0671-4>
- Winter, S., Bauer, T., Strauss, P., Kratschmer, S., Paredes, D., Popescu, D., ... Batáry, P. (2018). Effects of vegetation management intensity on biodiversity and ecosystem services in vineyards: A meta-analysis. *Journal of Applied Ecology*, 55, 2484–2495. <https://doi.org/10.1111/1365-2664.13124>
- Ziter, C. (2016). The biodiversity–ecosystem service relationship in urban areas: A quantitative review. *Oikos*, 125, 761–768. <https://doi.org/10.1111/oik.02883>

BIOSKETCH

Dan Chamberlain works on impacts of environmental change on animal biodiversity, including impacts of urbanization. He is an Associate Professor in Animal Ecology at the University of Turin.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Chamberlain D, Reynolds C, Amar A, Henry D, Caprio E, Batáry P. Wealth, water and wildlife: Landscape aridity intensifies the urban luxury effect. *Global Ecol Biogeogr*. 2020;00:1–11. <https://doi.org/10.1111/geb.13122>