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# REVIEW

## and Diversity

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# A systematic review and meta-analysis on urban arthropod diversity

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## Abstract

- 1. Urbanization is rapidly expanding at the global level, a phenomenon often reported to exert negative effects on biodiversity. However, many important knowledge gaps about the effect of urbanization on biodiversity remain, posing important conservation challenges.
- 2. This is especially true for certain taxonomic groups like arthropods, despite being the most diverse and abundant animal group on Earth. Here, we conduct an exhaustive systematic literature review and meta-analysis to assess whether and how urbanization is negatively associated with arthropod diversity.
- We explored potential geographic, temporal and taxonomic biases in the availability of evidence. In addition, we make use of meta-analysis of variance to investigate whether urban areas across the world show similar patterns of arthropod diversity change.
- 4. Our results support previous studies; urbanization and arthropod diversity are negatively associated. However, not all arthropod groups seem to respond similarly (e.g., Odonata) potentially suggesting the importance of implementing taxa-specific conservation actions in urban areas.
- 5. On the other hand, our meta-analysis of variance showed higher variance in arthropod diversity in urban compared to non-urban habitats, suggesting great potential for the implementation of certain city conservation practices or attributes to promote arthropod communities.
- 6. Last, we identified several key taxonomic and geographic biases that require additional scientific attention as well as strong evidence for negative-effects publication bias in the literature.
- 7. Our results highlight the importance of urban ecology research for helping design more diverse urban ecosystems.

## KEYWORDS

biodiversity, conservation, insects, urbanization, variance

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Urban areas are rapidly growing on the planet paralleling the rapid human population increase (United Nations 2019). The numerous studies analysing the impact of urbanization on biodiversity show a clear negative effect at a global scale, which is expected to worsen in the coming years (McKinney, 2006; Seto et al., 2012; Simkin et al., 2022). Therefore, the reconciliation between urban development and biodiversity conservation is key to avoid further species extinctions (Soga et al., 2014). The relevance of this trade-off between urban development and biodiversity conservation is embedded within the 17 Sustainable Development Goals (United Nations, 2015), concretely goals 11 (sustainable cities and communities), 14 (life below water) and 15 (life on land). The main drivers of this negative impact of urbanization on biodiversity have been shown to be the loss of natural habitats as well as habitat fragmentation (Hermansen et al., 2017: Wagner et al., 2021), both of which are often associated with the expansion of invasive species (Borden & Flory, 2021; Li et al., 2014; Santana Margues et al., 2020).

The phylum Arthropoda is the most diverse animal group, currently representing 80% of all described animal species (ca. 1.5 million species) and constituting the largest abundance in terms of animal biomass (Zhang, 2013). Arthropods are also key components of ecosystems, playing a fundamental role in the food web and participating in multiple ecological processes such as parasitism, pollination and nutrient recycling among others (Seastedt & Crossley, 1984; Theodorou, 2022). Because of this huge diversity of species and lifestyles, arthropods are ubiquitous and can be found in numerous habitats on Earth: from the sea bottom to the shore, from land to fresh water and from rainforests to deserts. The urban habitat is not an exception. In fact, their relevance in cities has motivated an increasing interest in studying the impact of urbanization on the diversity of some arthropod groups such as insects (Fenoglio et al., 2020, 2021; Mcintyre, 2002), especially after recent studies have suggested that they are declining worldwide (Hallmann et al., 2017; van Klink et al., 2020). The consequences of such reported massive reduction of insect populations could be catastrophic for the whole planet, with a cascading impact on many other organisms (Cardoso et al., 2020; Kehoe et al., 2021) and huge economic costs (Goulson, 2019). However, despite the relevance of arthropods also for urban ecosystems and the fact that urbanization and housing development are among the main causes of conservation concern for this animal group (IUCN, 2023), the number of studies on the urban entomofauna is proportionally small compared to other animal taxa such as birds or mammals (Beninde et al., 2015; McDonnell & Hahs, 2008; Rega-Brodsky et al., 2022). This important lack of information makes it very difficult to apply appropriate conservation efforts to these organisms even though this conservation aspect is a relevant topic within urban arthropod studies, corresponding to 30.7% of published papers (Collins et al., 2021). Further, many of the studies on urban arthropods are biased towards only a few groups, mainly bees, butterflies and beetles (Brown, 2018; Vaz et al., 2023), while spiders would be the most studied non-insect group (in 19% of urban arthropod studies

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according to Fenoglio et al., 2020). In addition, these studies have been conducted using a wide range of methodological approaches (e.g., urban gradients, urban-rural comparisons and temporal changes), making it difficult to identify any general pattern that would help make clear conservation measures. To our knowledge, no study has investigated the potential influence of urbanization on the diversity of the Phylum Arthropoda as a whole. Some very recent reviews have explored the effect of urbanization on insects (Vaz et al., 2023) or terrestrial arthropod diversity (Fenoglio et al., 2020, 2021) leaving the potential effects on aquatic arthropod taxa virtually unexplored.

Furthermore, these previous studies focused on either taxonomic diversity (species richness and abundance) or some functional traits. but did not consider other important diversity components such as phylogenetic diversity. Analysing several biodiversity components simultaneously is essential as they may not be similarly affected by the urbanization process (Ibáñez-Álamo et al., 2020; Morelli et al., 2021) and thus identifying potential biases in this respect is particularly relevant for the conservation of urban biodiversity (Birkhofer et al., 2015; Devictor et al., 2010). Other important but neglected sources of contrasting results in previous reviews concern the different geographical scales and the taxonomic levels considered. In this sense, no previous information exists on whether city-level studies are more likely to find negative urban biodiversity impacts than largerscale studies (e.g., country or continental-wide approaches). This information on the effect of scale is crucial for understanding biodiversity changes induced by urbanization (Spotswood et al., 2021) and the combination of multiple-scale studies would be especially useful for designing conservation strategies (Lennon et al., 2001; Vimal et al., 2012). Finally, regarding the taxonomic levels considered, the interesting and previously highlighted reviews on the topic focused exclusively on exploring potential urban effects at the Order level, while higher (e.g., class) or lower (e.g., family) taxonomic levels have not been previously investigated even though they could offer valuable information for biodiversity conservation (Kallimanis et al., 2012; Puppim de Oliveira et al., 2022).

Here, we investigate the effect of urbanization on the diversity of all arthropod groups by performing a systematic review and metaanalysis to provide a nuanced and detailed analysis to better understand if there is a worldwide effect. Concretely, we investigated the following two main questions: (i) Does urbanization associate with a lower mean arthropod diversity? and (ii) Does urbanization lead to a reduction in arthropod diversity variance across locations? Given the high levels of heterogeneity among effect sizes found, we tested several methodological research parameters that could explain such heterogeneity (e.g., geographical scale, diversity component analysed, taxon studied, method for urban comparison, etc.) as well as to test and adjust for publication bias. For the first time, we test whether urbanization is not only associated with changes in mean arthropod diversity but also in the range of possible species. Since cities are habitats that are expected to favour generalist and opportunistic species (Fragkias et al., 2013; New, 2015), we predicted a smaller variance in arthropod diversity across urban arthropod communities compared to non-urban environments. We explore this hypothesis both in

## MATERIALS AND METHODS

## Literature search

We conducted a systematic review following the Preferred Reporting Items for Systematic Review and Meta-Analysis (PRISMA) in ecology and evolutionary biology (see checklist in Appendix S1; O'Dea et al., 2021). Literature searches were conducted on the 1st of June. 2022, in Scopus and Web of Science Core Collection (see PRISMA flow diagram in Appendix S2). The databases covered in our search from the Web of Science Core Collection were: Journal Citation Indexes (SCI-EXPANDED 1900-2022, SSCI 1900-2022, A&HCI 1975-2022 and ESCI 2015-2022). Conference Proceedings (CPCI-S 1990-2022 and CPCI-SSH 1990-2022) and Book Citation Indexes (BKCI-S 2005-2022, BKCI-SSH 2005-2022). We performed a topic (TS) search in Web of Science Core Collection and obtained 29,752 results. In Scopus, we used the equivalent search string and searched in the Title, Abstract and Keywords of records published since 1960 (the oldest date possible in Scopus) to 2022, obtaining 30,302 results. Our search string contained a combination of the keywords "\*urban\*", "\*diversit\*", "richness", "\*invertebrate\*", "arthropod\*" and a list of arthropod sub-phyla, classes orders and common names (see Appendix S3 for the exact keyword search strings used).

To exclude records outside our field of interest, we only included the following categories from the Web of Science (number of included studies in brackets): Ecology (9780), Environmental Sciences (6729), Biodiversity Conservation (4385), Marine Freshwater Biology (2921), Entomology (1530), Environmental Studies (1527), Urban Studies (1363), Multidisciplinary Sciences (1361), Zoology (1119), Biology (652), Limnology (504), Parasitology (301). Similarly, the subject areas considered from Scopus were: Agricultural and Biological Sciences (16398), Environmental Science (14543), Multidisciplinary (976). The final number of records that remained after those filters were applied was 21,400 and 23,417 for Web of Science and Scopus, respectively.

Subsequently, we excluded 23,442 duplicates by manually finding them in Excel and by using the deduplication tool built into the software Rayyan (Ouzzani et al., 2016). One observer performed the titleand-abstract screening of the remaining 21,375 records using the software Rayyan to select urban ecology records with original data (not retrieved from another paper). For the 1363 records that passed the title-and-abstract screening, one observer (EB-U) performed fulltext screening following the inclusion criteria: (1) full text of the paper available, (2) written in English or Spanish, (3) the study included empirical data, (4) there is a clearly defined arthropod taxonomic

group (e.g., official taxonomical categories or common names), (5) diversity index type provided, (6) testing whether urbanization affects biodiversity, (7) valid proxy of urbanization (i.e., excluding human infrastructures out of the urban landscape such as mines, industrial areas or roads) and (8) provided information about the method used and the area covered (i.e., single or multiple city approach, if suburban areas were included, etc.). The 646 records that remained were additionally screened by the same observer to select only those providing complete/usable data for the meta-analysis, which reduced our dataset to a total of 216 studies. Finally, we included data from 5 additional studies identified by another ongoing literature search that was performed on the 13th of May. 2019, in Web of Science Core Collection and Scopus using the same keywords and selection criteria previously described but not restricted to arthropods. Our final database for the meta-analysis contained 511 effect sizes extracted from a total of 221 studies (see PRISMA flow diagram for the exclusion criteria with the number of articles in Appendix S2 and the list of all studies in Appendix S4).

## Data extraction and preparation

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We provide a summary of the moderators tested and the methodological approaches conducted in Figure 1. Each study was classified into one of the following categories depending on the 'methodological approach' used to study the impact of urbanization on arthropod diversity: (1) 'Temporal Urban Gradient' refers to data collected from the same location through a period of time (e.g., Ball-Damerow et al., 2014; Braby et al., 2021). This method is mostly used for urban areas for which the level of urbanization has changed over time; however, some studies compared biodiversity values from the same area and after being urbanized (e.g., Buczkowski before & Richmond, 2012). The method assumes that communities change through time due to progressive urban development in the area. (2) 'Spatial Urban Gradient' compares different locations with different urbanization intensities. This category was subdivided into three subgroups according to the specific spatial comparisons performed: (2a) 'Urban-Rural Paired Comparison' is a method in which two locations along the previously described Urban Gradient (typically the extremes) are compared to each other (e.g., Lundquist & Zhu, 2019; Shochat et al., 2008); (2b) 'City Comparison' restricts the comparison to urban areas and specifically tests whether cities with different levels of urbanization show contrasting biodiversity patterns (e.g., Baena et al., 2020; Fattorini et al., 2016; Varet et al., 2014); (2c) 'Urban Gradient' compares different locations of different urbanization intensities, which typically involves comparing several points of decreasing urbanization intensity from the city centre to the nearby rural areas (e.g., Argañaraz & Gleiser, 2017; Honchar, 2020; Pignataro et al., 2020). The initial concept proposed by McDonnell & Pickett (1990) assumes that urbanization decreases linearly and continuously as the distance from the city centre increases. However, given that urban landscapes can be multi-centric with non-linear gradients of



FIGURE 1 Moderators and analytical approaches conducted to test for the association between urbanization and arthropod diversity.

urbanization (McDonnell & Hahs, 2008; Seress et al., 2014), recent studies have started to implement a non-linear gradient concept (e.g., Zhang et al., 2016).

Data extraction was performed by one observer (EB-U) and from each study, we extracted: (1) 'Year of publication'; (2) 'Continent' in which the study was conducted; (3) arthropod 'Taxa' studied, subdivided into 3 moderators: Class, Order and Family; (4) Component of biodiversity analysed (i.e., Taxonomic, Functional or Phylogenetic diversity); and (5) 'Taxonomic diversity index' used (i.e., Species richness vs. Other indices such as Shannon and Simpson). Furthermore, we also collected information on (6) the spatial 'Scale' studied using the following classification: (i) 'City', if the study was conducted in a single city and its surroundings (0-100 km<sup>2</sup> approx.); (ii) 'Local', if the study analysed a greater area, generally encompassing more than one city (101-10,000 km<sup>2</sup> approx.); (iii) 'Regional', when the area of study was larger than the previous one up to the continental size (10001–1 million km<sup>2</sup> approx.); and (iv) 'Continental' for studies with sites distributed throughout a continent. We also extracted all necessary statistical information to estimate the effect size for the association between urbanization and biodiversity. Some studies reported more than one effect size, when that was due to the use of different statistical methods on the same data, we chose a single one based on the following order of preference: (1) Means, standard deviations (or equivalent, e.g., SE) and sample sizes of comparisons between more urbanized and less urbanized areas either from the

text or from figures using the R package "metaDigitise" v.1.0.1 (Pick et al., 2019); (2) Pearson's correlation coefficients (r); (3)  $R^2$  values from simple or multiple regression; and (4) Inferential statistics (i.e., t, F and  $\chi^2$  values). Any study not reporting all the statistical information necessary to be included in the meta-analysis was ultimately excluded. Effect sizes were coded so that a negative effect size would reflect a negative association between urbanization and biodiversity throughout the dataset. To combine all estimates in the analyses, r values were kept unchanged, whereas  $R^2$  values and inferential statistics were transformed to r using equations from Nakagawa and Cuthill (2007) and Lajeunesse (2013). The variance in r was calculated as:  $(1-r^2)^2/(n-1)$ , where n refers to the total number of sampling areas studied. Following the recommendations in Jacobs and Viechtbauer (2017), means, standard deviations and sample sizes of comparisons between two areas (e.g., more urbanized vs. less urbanized) were transformed to biserial correlations and their variance was calculated using the R package "metafor" v.3.4-0 (Viechtbauer, 2010). Note that (1) although effect sizes in metaanalyses using r as the single effect size of interest are often transformed into Fisher's Zr before the analyses, meta-analyses combining both r and biserial correlations need to be based on the raw coefficients, this is why we did not use Fisher's r-to-Zr transformation (Jacobs & Viechtbauer, 2017); and (2) in some extreme cases, biserial correlations can reach values smaller than -1 or larger than 1 (Jacobs & Viechtbauer, 2017).

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## Statistical analyses

First, we graphically explored the percentage of studies that used each of the four methodological approaches previously described (i.e., Temporal Urban Gradient, Urban Gradient, Urban-Rural Paired Comparison and City Comparison) and the use of these methodologies in relation to time, geography, focal taxa, spatial scale and the component of biodiversity investigated. Due to the low sample sizes for certain category levels, we performed the following recategorizations before the analyses: (i) for the "Diversity component" moderator, Shannon (57 effect sizes) and Simpson (5 effect sizes) indices were grouped into "Other taxonomic diversity". (ii) For studies using an 'Urban Gradient' approach and for which we had to extract means, standard deviations and sample sizes to calculate biserial correlations (347 effect sizes), we did so for the most urbanized and least urbanized areas from the provided gradient, and we, therefore, recategorized these comparisons as 'Urban-Rural Paired Comparison' rather than the original 'Urban Gradient'. (iii) For the moderator "Order", we grouped non-insect orders into "Non-Insect Orders" (56 effect sizes) and Ephemeroptera (5 effect sizes). Plecoptera (3 effect sizes) and Trichoptera (15 effect sizes) into "EPT", as it is commonly found in the literature (e.g., Valente-Neto et al., 2018). (iv) For the moderator "Family", we grouped families with less than 10 effect sizes into "Other Families" (58 effect sizes). (v) Finally, for the moderator "Continent", Africa (12 effect sizes) and Oceania (15 effect sizes) were grouped into "Other".

Second, we conducted a multilevel (intercept-only) meta-analysis to estimate the overall effect size for the association between urbanization and arthropod diversity, and several multilevel meta-regressions to test methodological moderators potentially affecting this association (e.g., spatial scale), and thus, potentially explaining some of the heterogeneity among effect sizes that we found (see Results). All models included the following random effects: (1) "observationID" to account for within-study/residual heterogeneity, (2) "studyID" to account for among-study heterogeneity (i.e., estimates reported by the same study, although not necessarily using the same data), (3) "comparisonID" to account for different biodiversity indices calculated using the same data and (4) "locationID" to account for data extracted from the same sampling sites. For all models, we specified sampling variance as a variance-covariance matrix that assumed a 0.5 correlation between the effect size sample variances with the same "studyID" (Noble et al., 2017). All multilevel meta-analyses and meta-regressions were fitted using the function "rma.mv()" from the R package "metafor" v.3.4–0 (Viechtbauer, 2010).

Third, we calculated absolute and relative heterogeneity among effect sizes in the multilevel (intercept-only) meta-analysis using the Q test and by estimating  $I^2_{total}$  (Nakagawa & Santos, 2012), respectively. Cochran's corresponds to a test statistic to determine whether the true effects are heterogeneous and thus, functions as a metric for assessing absolute heterogeneity among effect sizes in meta-analyses (Cochran, 1954).  $I^2$  is a variance-standardised metric that estimates relative heterogeneity by providing a value for the percentage of variance among effect sizes that is not due to statistical noise, thus,

providing information about the sources of heterogeneity (Higgins & Thompson, 2002). Additionally, we assessed publication bias both for small-study and decline effects following Nakagawa et al. (2022). To test for small-study effects, we first ran extended Egger's regressions using the square root of the inverse of the sample size of each study as a moderator in a multilevel meta-regression following Nakagawa et al. (2022). This approach tests for the existence of funnel plot asymmetry due to missing effect sizes of small size (i.e., small-study effects) while accounting for the random effects described above (Nakagawa et al., 2022). Then, we explored temporal patterns in the data that could highlight the existence of decline effects (i.e., effect sizes decreasing over time; Trikalinos & loannidis, 2005) by running a multilevel meta-regression where year of publication was included as a mean-centred moderator (Nakagawa et al., 2022).

Fourth, we fitted multilevel uni-moderator meta-regressions to test if and how much heterogeneity was explained by the following moderators: Methodological approach (4 levels: Urban Gradient, City Comparison, Urban-Rural Paired Comparison, Temporal Urban Gradient), Continent (5 levels: North America, South America, Europe, Asia, Others), Scale (4 levels: City, Local, Regional, Continental-Global), Taxonomic diversity index (4 levels: Richness, Other Diversity Indexes, Functional Diversity, Abundance) and the three Taxa moderators (i.e., Class, Order and Family), each with several levels. For all metaregressions, we calculated post-hoc Wald tests to detect statistical differences between levels for moderators with more than two levels and also estimated the percentage of heterogeneity explained by each moderator as  $R^2_{marginal}$  (Nakagawa & Schielzeth, 2013). We present 95% confidence intervals (hereafter 95% CI) and 95% prediction intervals (hereafter 95% PI) throughout.

Fifth, we performed a meta-analysis of variance to test if urbanization is not only associated with lower mean biodiversity values but also lower variance in biodiversity values across habitats. To do so, we calculated the effect size InCVR (i.e., the natural logarithm of the ratio between the coefficients of variation; Nakagawa et al., 2015; Senior et al., 2020) using the function "escalc()" from the R package "metafor" v.3.4–0 (Viechtbauer, 2010) and fitted the same meta-regression and meta-analytic models described above. The number of effect sizes available for the meta-analysis of variance was smaller because only studies from which we could extract means, standard deviations and sample sizes could be used, and thus, some moderator levels are not represented in these analyses.

Finally, we performed several sensitivity analyses to assess the robustness of our results. To test whether the effect sizes obtained through biserial correlations and inferential statistics differed from the correlation coefficients directly extracted from the original studies, we ran all the analyses using the data subset only including correlation coefficients (*r*). To test if results remained similar when comparing mean biodiversity between the two habitats with different levels of urbanization (e.g., more urbanized vs. less urbanized sites) instead of calculating biserial correlations (see above), we reran all the analyses twice, once using lnRR (the natural logarithm of the ratio between the two means; Hedges et al., 1999) as effect size, and another time using SMDH (standardized mean difference with



**FIGURE 2** Effect of urbanization on mean arthropod diversity depending on (a) the continent where the study was conducted ('Others' refers to both Africa and Oceania), (b) the methodological approach used, (c) the scale of the study and (d) the diversity component analysed ('others' refers to both Shannon and Simpson indices). For each moderator, mean, 95% CI and 95% PI are provided. *k* corresponds to the number of effect sizes and the number of studies is shown in brackets.

heteroscedastic population variances in the two groups; Bonett, 2008, 2009) as effect size. Both effect sizes were calculated using the function "escalc" from the R package "metafor" v.3.4–0 (Viechtbauer, 2010). Last, the reason to choose InCVR for our metaanalysis of variance was because of the observed mean-variance relationship (often known as Taylor's Law; Appendix S11; more in Sánchez-Tójar et al., 2020). To test for any potential hidden effect, the meta-analysis of variance was repeated using InVR (the logarithm of the ratio of the standard deviations), which does not account for the differences in the means of the two groups.

## RESULTS

In all, we included 511 effect sizes from 221 studies for the systematic review and meta-analysis. From a global point of view, 62% of studies on urban arthropods were conducted in North America and Europe in contrast with Africa and Oceania, which together only represented 6% of all studies (Figure 2a). Most studies (55%) compared urban versus rural areas ("Urban-Rural Paired Comparison" method), whereas only 1% compared cities ("City Comparison" method; Figure 2b). We also detected a noticeable

preference for performing studies at the "City" scale (67%) in contrast to the "Local" (25%) and "Regional" scales (8%; Figure 2c). Note that for these calculations, the sum of percentages can be higher than 100 due to some studies having multiple moderator levels. We did not find any study using the continental scale, that is, comparing sites from more than a single continent (global range or continental scale). More than half of the studies (59%) focused on taxonomic richness, almost triple the number of studies analysing abundance (21%; Figure 2d). Insects were much more often studied (80% of studies) than any other arthropod group, with the order Hymenoptera (23%) and the family Apoidea (23%) being the most often investigated group (Figure 3). When considering the number of studies conducted on Arthropods, we observed a clear bias towards insects regardless of the continent where the study was conducted (Figure 4). For example, in Africa and Oceania only another Class other than Insecta was studied (Myriapoda and Arachnida, respectively).

## Urbanization effects on biodiversity

We found a statistically significant and strong negative effect of urbanization on arthropod diversity (mean r [95% CI] {95% PI} = -0.48



**FIGURE 3** Effect of urbanization on mean arthropod diversity depending on the taxonomic (a) Class, (b) Order and (c) Family. EPT stands for the grouping of Ephemeroptera, Plecoptera and Trichoptera insect orders. For each moderator, mean, 95% CI and 95% PI are provided. *k* corresponds to the number of effect sizes, and the number of studies is shown in brackets.



FIGURE 4 Continental distribution of all studies testing the effect of urbanization on the diversity of taxonomic classes of arthropods.

[-0.55, -0.41]  $\{-1.60, 0.64\}$ ; n = 221 studies, k = 511 effect sizes), but total relative heterogeneity was high ( $l_{total}^2 = 97.4\%$ ; see Table 1), with comparison ID accounting for most of this heterogeneity ( $l_{comparisonID}^2 = 63.8\%$ ). The  $l_{total}^2$  value shows that only 2.6% of the

variance among effect sizes is due to statistical noise, or, said differently, that heterogeneity is 37 times larger than that of statistical noise.

The negative impact of urbanization on arthropod diversity was present in all continents (Table 2; Figure 2a). Post-hoc Wald tests

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Effect size	k	Meta-analytic mean [95% CI; 95% PI]	l <sup>2</sup> total (%)	l <sup>2</sup> <sub>studyID</sub> (%)	2 <sub>comparisonID</sub> (%)	l <sup>2</sup> locationID (%)	l <sup>2</sup> observationID (%)
Correlation and biserial	511	-0.48 [-0.55, -0.41; -1.60, 0.64]	97.4	0.0	63.8	6.1	27.4
InRR	345	-0.44 [-0.54, -034; -1.83, 0.95]	98.4	0.0	67.7	0.0	30.7
SMDH	342	-0.96 [-1.17, -0.76; -3.55, 1.63]	85.41	0.0	58.82	0.0	26.58
InCVR	343	0.25 [0.16, 0.35; -0.61, 1.12]	52.3	0.0	6.4	17.3	28.6
InVR	343	-0.19 [-0.31, -0.07; -1.65, 1.27]	81.5	0.0	43.3	0.0	38.2

**TABLE 1** Results of the meta-analyses testing the effect of urbanization on mean arthropod diversity (correlation, InRR and SMDH) and its variance (InCVR and LnVR). k represents the number of estimates and  $l^2$  the heterogeneity.

revealed no statistically significant differences between continents (p > 0.11 in all cases) and the moderator continent explained 1.4% of heterogeneity ( $R^2_{marginal} = 0.014$ ). As for the methodological approach, we found that all methods provided similar results (Table 2; Figure 2b), with no statistically significant differences detected between them (all post-hoc p > 0.09) and the heterogeneity explained by the moderator being only 1.4% ( $R^2_{marginal} = 0.014$ ). The negative effects of urbanization on arthropod diversity were present regardless of the scale considered (City, Local and Regional; all post-hoc p > 0.32; Table 2; Figure 2c) and the moderator only explained 0.5% of the heterogeneity ( $R^2_{marginal} = 0.005$ ). On the other hand, more urban arthropod communities showed lower levels of diversity compared to less urban communities regardless of the component analysed (Table 2; Figure 2d). Post-hoc Wald tests detected statistically significant differences between the categories Abundance and "Other diversity components" (p = 0.04), with the later showing a more intense effect of urbanization (Figure 2d), but the biodiversity component moderator only explained 1.1% heterogeneity of  $(R^2_{\text{marginal}} = 0.011).$ 

If we consider the arthropod taxonomic class studied, all but Entognatha showed a statistically significant negative estimate (Table 2; Figure 3a), although the post-hoc Wald tests only detected statistically significant differences between the classes Crustacea and Arachnida (p = 0.03), with the latter having a less intense negative effect than the former (Table 2; Figure 3a). Taxonomic Class explained 1.9% of the heterogeneity ( $R^2_{marginal} = 0.019$ ). Within insects, urbanization had a statistically significant negative impact on all orders except for Hemiptera and Odonata (Table 2; Figure 3b), but the posthoc Wald tests evidenced statistically significant differences between several orders (see Appendix S5). Note that for calculating these differences, the orders Hemiptera and Orthoptera had to be removed due to the low number of studies (n < 10 each). The moderator Taxonomic Order explained a considerable amount of heterogeneity (10.7%,  $R^2_{marginal} = 0.107$ ). Last, all insect families were statistically negatively affected by urbanization (Table 2; Figure 3c), and there were no statistically significant differences between them (all post-hoc p > 0.05). Taxonomic Family explained 4.7% of the total heterogeneity ( $R^2_{marginal} = 0.047$ ).

## Meta-analysis of variance

The variance in arthropod diversity in more urbanized areas was on average around 28% higher than in less urbanized areas (mean InCVR [95% CI] {95% PI} = 0.25 [0.16, 0.35] {-0.61, 1.12}; n = 154 studies, k = 343 effect sizes). Overall heterogeneity was moderate ( $l^2_{total} = 52.3\%$ ; see Table 1) with an important contribution of within-study/residual variation ( $l^2_{observationID} = 28.6\%$ ). The  $l^2_{total}$  value shows that 47.7% of the variance among effect sizes is due to statistical noise, or said differently, that heterogeneity is only around 1.1 times larger than that of statistical noise.

Urbanization had a statistically significant and positive effect on arthropod diversity variance in Europe, North and South America (Table 3; Figure 5a). Post-hoc Wald tests showed statistically significant differences between North America and the level "Others" (Oceania and Africa together; p = 0.02), and this moderator explained 6.8% of heterogeneity ( $R^2_{marginal} = 0.068$ ). Regarding the methodological approach used (Table 3), we found statistically non-significant results for city comparison but an increase in variance associated with urbanization for studies comparing more urbanized to less urbanized areas and for those using a temporal urban gradient (Table 3; Figure 5b). No statistically significant differences were detected between methods though (all post-hoc p > 0.27), and the moderator only explained 0.7% of heterogeneity ( $R^2_{marginal} = 0.007$ ). Similarly, statistically significant and positive effects on variance associated with urbanization were detected for both city and local geographical scales, with the results for the regional scale being inconclusive (Table 3; Figure 5c). We found no statistically significant differences between scales (all post-hoc p > 0.47) and the moderator only explained 0.8% of heterogeneity ( $R^2_{marginal} = 0.008$ ). Regarding the different diversity components, we found a statistically significant positive effect on variance for abundance, richness and other diversity metrics, but not for functional diversity (Table 3; Figure 5d), but no statistically significant differences between them were observed (all post-hoc p > 0.61) and only explained 0.2% this moderator of heterogeneity  $(R^2_{marginal} = 0.002).$ 

Regarding taxonomic class, the class Insecta was the only arthropod group for which variance was statistically significant and

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**TABLE 2** Meta-regressions testing moderators potentially affecting the effect of urbanization (*r*) on arthropod diversity. *k* corresponds to the total number of effect sizes.

		Estimate	SE	t value	p value	95% CI lower bound	95% CI upper bound
Continent	Europe	-0.45	0.06	-7.58	<0.01	-0.56	-0.33
<i>k</i> = 511	North America	-0.47	0.06	-7.84	<0.01	-0.59	-0.35
	South America	-0.57	0.09	-6.69	<0.01	-0.74	-0.40
	Asia	-0.59	0.10	-5.77	<0.01	-0.79	-0.39
	Others	-0.31	0.14	-2.17	0.03	-0.59	-0.03
Methodological approach $k = 511$	Urban Gradient	-0.40	0.07	-6.13	<0.01	-0.53	-0.27
	Temporal Urban Gradient	-0.44	0.16	-2.75	<0.01	-0.76	-0.13
	Urban-Rural	-0.51	0.04	-12.26	<0.01	-0.59	-0.43
	City Comparison	-0.95	0.26	-3.65	<0.01	-1.47	-0.44
Scale	City	-0.45	0.04	-11.04	<0.01	-0.54	-0.37
<i>k</i> = 511	Local	-0.54	0.07	-7.50	<0.01	-0.68	-0.40
	Regional	-0.58	0.12	-4.87	<0.01	-0.81	-0.34
Diversity component	Taxonomic diversity: richness	-0.51	0.04	-14.17	<0.01	-0.58	-0.44
<i>k</i> = 511	Taxonomic diversity: others	-0.49	0.06	-8.57	<0.01	-0.60	-0.38
	Functional diversity	-0.43	0.14	-2.98	<0.01	-0.71	-0.15
	Abundance	-0.36	0.05	-7.48	<0.01	-0.46	-0.27
Taxonomic class $k = 504$	Insecta	-0.50	0.04	-13.32	<0.01	-0.57	-0.42
	Arachnida	-0.30	0.11	-2.77	<0.01	-0.51	-0.09
	Crustacea	-0.74	0.18	-4.04	<0.01	-1.11	-0.38
	Myriapoda	-0.50	0.20	-2.53	0.01	-0.89	-0.11
	Entognatha	-0.27	0.26	-1.05	0.29	-0.78	0.24
Taxonomic order k = 459	Coleoptera	-0.48	0.08	-6.01	<0.01	-0.64	-0.33
	Diptera	-0.48	0.09	-5.07	<0.01	-0.67	-0.29
	EPT	-0.79	0.08	-10.59	<0.01	-0.94	-0.65
	Hemiptera	-0.04	0.31	-0.12	0.91	-0.64	0.57
	Hymenoptera	-0.28	0.07	-3.87	<0.01	-0.43	-0.14
	Lepidoptera	-0.66	0.11	-6.18	<0.01	-0.87	-0.45
	Odonata	-0.24	0.16	-1.49	0.14	-0.55	0.08
	Orthoptera	-0.64	0.26	-2.45	0.01	-1.15	-0.13
	Non-Insect orders	-0.36	0.10	-3.81	<0.01	-0.55	-0.18
Taxonomic family $k = 227$	Apoidea	-0.24	0.11	-2.16	0.03	-0.45	-0.02
	Calliphoridae	-0.61	0.31	-1.98	0.05	-1.22	-0.00
	Carabidae	-0.58	0.12	-4.71	<0.01	-0.82	-0.33
	Culicidae	-0.38	0.21	-1.79	0.08	-0.79	0.04
	Drosophilidae	-0.37	0.29	-1.26	0.21	-0.95	0.21
	Formicidae	-0.32	0.13	-2.52	0.01	-0.57	-0.07
	Other families	-0.50	0.10	-4.97	<0.01	-0.70	-0.30

positively affected by urbanization (Table 3; Figure 6a) although no statistical differences among classes were detected (all post-hoc p > 0.32). Taxonomic class explained 2.6% of heterogeneity ( $R^2_{margin-al} = 0.026$ ). Regarding taxonomic order, there was a statistically significant positive effect of urbanization on variance for the order Coleoptera, the EPT group and Lepidoptera (Table 3; Figure 6b). Post-

hoc Wald tests revealed statistically significant differences for Diptera, Hymenoptera, Odonata and Non-insect orders (see Appendix S5) and explained a relatively high (15.5%) amount of heterogeneity ( $R^2_{marginal} = 0.155$ ). Finally, regarding taxonomic Family, no statistically significant effects on variance were detected except for the category "Other families" This category was also statistically significantly

**TABLE 3** Meta-regressions testing moderators potentially affecting the effect of urbanization on arthropod diversity variance (InCVR). *k* corresponds to the total number of effect sizes.

		Estimate	SE	t value	p value	95% CI lower bound	95% CI upper bound
Continent	Europe	0.18	0.09	2.03	0.04	0.01	0.3
<i>k</i> = 343	North America	0.39	0.08	4.76	<0.01	0.23	0.55
	South America	0.28	0.10	2.91	<0.01	0.09	0.47
	Asia	0.21	0.13	1.62	0.11	-0.04	0.46
	Others	-0.06	0.17	-0.32	0.75	-0.39	0.28
Methodological approach $k = 343$	Temporal Urban Gradient	0.45	0.18	2.50	0.01	0.10	0.80
	Urban-Rural	0.25	0.05	5.01	<0.01	0.15	0.34
	City Comparison	0.14	0.34	0.40	0.69	-0.54	0.82
Scale $k = 343$	City	0.23	0.06	4.00	<0.01	0.12	0.34
	Local	0.31	0.10	3.20	<0.01	0.12	0.50
	Regional	0.32	0.16	1.95	0.05	-0.00	0.64
Diversity component	Taxonomic diversity: richness	0.26	0.05	5.01	<0.01	0.16	0.36
k = 343	Taxonomic diversity: others	0.26	0.08	3.08	<0.01	0.09	0.42
	Functional diversity	0.11	0.27	0.42	0.67	-0.42	0.64
	Abundance	0.25	0.08	3.18	<0.01	0.09	0.40
Taxonomic class $k = 339$	Insecta	0.26	0.05	5.17	<0.01	0.16	0.36
	Arachnida	0.17	0.13	1.31	0.19	-0.09	0.43
	Crustacea	0.24	0.22	1.09	0.28	-0.19	0.68
	Myriapoda	0.49	0.30	1.62	0.11	-0.11	1.09
	Entognatha	-0.32	0.75	-0.43	0.67	-1.79	1.16
Taxonomic order k = 308	Coleoptera	0.27	0.12	2.16	0.03	0.02	0.51
	Diptera	0.16	0.11	1.54	0.13	-0.05	0.37
	EPT	0.62	0.11	5.69	<0.01	0.41	0.83
	Hemiptera	0.02	0.75	0.02	0.98	-1.45	1.48
	Hymenoptera	0.12	0.09	1.40	0.16	-0.05	0.30
	Lepidoptera	0.37	0.18	2.08	0.04	0.02	0.71
	Odonata	-0.03	0.17	-0.19	0.85	-0.38	0.31
	Orthoptera	0.39	0.82	0.48	0.63	-1.22	2.00
	Non-Insect orders	0.23	0.12	1.89	0.06	-0.01	0.46
Taxonomic family $k = 163$	Apoidea	0.088	0.125	0.706	0.48	-0.16	0.34
	Calliphoridae	0.538	0.322	1.669	0.10	-0.10	1.17
	Carabidae	0.067	0.170	0.391	0.70	-0.27	0.40
	Culicidae	0.088	0.223	0.393	0.70	-0.35	0.53
	Drosophilidae	-0.237	0.298	-0.795	0.43	-0.83	0.35
	Formicidae	0.181	0.134	1.355	0.18	-0.08	0.45
	Other families	0.407	0.126	3.237	< 0.01	0.16	0.66

different from Drosophilidae (post-hoc test p < 0.05). The moderator explained a relatively high (16.1%) amount of heterogeneity ( $R^2_{marginal} = 0.161$ ).

# Publication bias

We found clear evidence suggesting the existence of small-study effects in our dataset (Appendices S6 and S7; mean slope value [95%

CI] = -0.97 [-1.66, -0.29];  $R^2_{marginal} = 2.7\%$ ) but inconclusive evidence for decline effects (Appendix S6; mean slope [95% CI] = 0.01 [-0.00, 0.02];  $R^2_{marginal} = 1.3\%$ ). Although the overall evidence for the negative association between urbanization and arthropod diversity remains statistically significant after accounting for small-study effects, our analysis suggests an average reduction of 50% in such evidence (small-study effects intercept = -0.24 [-0.42, -0.06] compared to -0.48 [-0.55, -0.41] in the main model; Appendix S6 and Table 1). The all-in model performed to test if such evidence remained



**FIGURE 5** Effect of urbanization on arthropod diversity variance (InCVR) depending on (a) the continent where the study was conducted ('Others' refers to both Africa and Oceania), (b) the methodological approach used, (c) the scale of the study and (d) the diversity component analysed ('others' refers to both Shanon and Simpson indices). For each moderator, mean, 95% CI and 95% PI are provided. *k* corresponds to the number of effect sizes and the number of studies is shown in brackets.

after accounting for all the heterogeneity explained by our moderators confirmed such conclusions (Appendix S6; small-study effects slope [95% CI] = -1.98 [-4.14, 0.17]; decline effects slope [95% CI] = 0.02 [-0.00, 0.05]), and all the moderators together explained up to 18% of the heterogeneity ( $R^2_{marginal} = 0.180$ ).

## Sensitivity analyses

Our sensitivity analyses using lnRR and SMDH as effect sizes led to qualitatively similar results, that is, urbanization and arthropod diversity are negatively associated (mean lnRR [95% CI] {95% PI} = -0.44 [-0.54, -0.34] {-1.83, 0.95}, n = 153 studies, k = 345 effect sizes; mean SMDH = -0.96 [-1.17, -0.76] {-3.552, 1.630}, n = 153 studies, k = 342 effect sizes) and, like our main analyses, the negative effect was present across the moderator levels (Appendices S8 and S9). Post-hoc Wald tests for lnRR yielded statistically significant differences between Asia and both South and North America (p < 0.01 and 0.03 respectively). At the taxonomic level of order, we also found statistically significant differences for Diptera (all post-hoc p < 0.01), Hymenoptera ( $p \le 0.01$ ), Odonata ( $p \le 0.01$ ) and non-insect orders ( $p \le 0.05$ ). As for SMDH, post-hoc tests showed significant differences for abundance compared with other diversity components (p = 0.03), between taxonomic classes Arachnida and Crustacea

(p = 0.02), and several orders (see Appendix S5). Total relative heterogeneity among effect sizes remained high for both lnRR ( $l^2_{total} = 98.4\%$ ) and SMDH ( $l^2_{total} = 85.4\%$ ), and, similarly to our main meta-analytic model using *r*, most of this heterogeneity was accounted by comparison ID (lnRR  $l^2_{comparisonID} = 67.7\%$ ; SMDH  $l^2_{comparisonID} = 58.8\%$ ; Table 1).

Our complementary meta-analysis of variance using InVR, which tested for raw differences in variance between urban and non-urban areas without accounting for mean differences between them, highlighted the majority of factors determining the variation of mean diversity of urban arthropod communities based on our main metaanalysis of variance (i.e., InCVR) but with opposite effects (Table 1 and Appendix S10). According to InVR, urbanization leads to an average reduction of 21% in total variation in arthropod diversity (mean InVR [95%CI]  $\{95\%PI\} = -0.19$  [-0.31, -0.07]  $\{-1.65, 1.27\}$ ; n = 153studies, k = 343 effect sizes), but heterogeneity was high and mostly accounted for by comparison ID and observation ID ( $l_{total}^2 = 81.5\%$ ,  $I^2_{\text{comparisonID}} = 43.3\%$ ,  $I^2_{\text{observationID}} = 38.2\%$ ; see Table 1). Insects were the only taxonomic class statistically significantly and negatively affected by a reduction in total variance, and at the order level, Coleoptera, EPT, Hemiptera and Lepidoptera showed statistically significant negative differences. Meta-regressions are shown in Appendix S10 and post-hoc Wald tests at the taxonomic order in Appendix S5. The orders Hemiptera and Orthoptera had to be



**FIGURE 6** Effect of urbanization on arthropod diversity variance (InCVR) depending on the taxonomic (a) class, (b) order and (c) family. EPT stands for the grouping of Ephemeroptera, Plecoptera and Trichoptera insect orders. For each moderator, mean, 95% CI and 95% PI are provided. *k* corresponds to the number of effect sizes and the number of studies is shown in brackets.

removed from post-hoc analyses due to the low number of data points (for mean diversity k = 5 for each order and for variance k = 1).

## DISCUSSION

We tested the association of urbanization with arthropod diversity by integrating the existing published scientific literature and investigated multiple methodological factors that could explain the disagreement observed across these studies. To our knowledge, our meta-analysis is the first one adhering to the PRISMA reporting guidelines within the topic, including a number of studies (N = 221) that is well beyond the average in ecological meta-analyses (e.g., media n = 41 studies in plant ecology: Koricheva & Gurevitch, 2014); or 44 studies in evolutionary ecology: table S6 from (Pollo et al., 2024, as well as those involving arthropods in some way: Fenoglio et al., 2020), (N = 162studies, Korányi et al., 2022), (N = 36, 24 and 16 studies for each subset analysed, Szabó et al., 2023), (N = 103 studies, Martinson & Raupp, 2013), (N = 18 studies and Saari et al., 2016), (N = 20 and 26 studies). Moreover, our exhaustive systematic literature review is the first one to focus on the entire Arthropod phylum and, to the best of our knowledge, the first one investigating the effect of urbanization not only on mean diversity but also on its variance. Our synthesis shows that urbanization is strongly linked with a reduction in

arthropod diversity, but also that urban areas can differ in their levels of arthropod diversity. This information is an essential step towards urban biodiversity conservation because it highlights the importance of considering urbanization as a conservation threat to arthropod populations (IUCN, 2023) and thus to life on Earth (UN Sustainable Development Goals 11, 14 and 15; United Nations, 2015). Furthermore, the variance results are particularly interesting as they show how variability in arthropod diversity can differ between different levels of urbanization, which can provide insights into what urbanization features might be better for preserving arthropod communities.

## Urbanization and mean diversity values

Two previous meta-analyses have linked urban areas with a decline in insect and terrestrial arthropod diversity, with diversity being measured as mean species richness and abundance (Fenoglio et al., 2020; Vaz et al., 2023). This negative association between urbanization and insect and terrestrial arthropod taxonomic diversity is confirmed by our larger, updated meta-analysis, and we show how this effect also expands to arthropod classes not previously investigated such as Crustacea and Myriapoda. Although in the same direction, this negative effect was, however, inconclusive for Entognatha, likely due to the reduced sample size for this class (n = 4 studies). However, it should be noted that the high levels of heterogeneity among effect

sizes found, which are reflected by the wide prediction intervals of our estimates, also indicate that there are different contexts in which urbanization could lead to an increase in arthropod diversity. This finding is important as there is a debate in urban ecology regarding the generality of the negative association between urbanization and biodiversity, with some studies reporting contrasting effects, such as higher presence and/or abundance of certain species depending on life-history traits or functional groups (e.g., Nagy et al., 2018; Wilson & Jamieson, 2019). Our results confirmed that although urbanization would most often lead to a decrease in arthropod diversity, there are scenarios where such an effect can be reversed. Identifying those scenarios should be a key conservation priority of future studies.

Our synthesis highlights that most studies on urban arthropod diversity so far have analysed taxonomic diversity, with only very few studies focusing on functional (n = 8 studies) and none on phylogenetic diversity. Investigating urban functional diversity is important from a conservation point of view because functional diversity estimates the ecological functions and interactions taking place (i.e., through trophic guilds, morphological traits, etc.; Wong et al., 2019; Buchholz & Egerer, 2020; Theodorou, 2022), which would help us understand how sustainable or resilient an ecological community is, and thus, would be key to elaborating adequate conservation strategies. In addition, phylogenetic diversity provides an evolutionary perspective of the species relationships and thus can help us make predictions also valuable for conservation measures (Knapp et al., 2008). Future studies should focus on filling this important knowledge gap, particularly regarding phylogenetic diversity, which remains unexplored despite previous recommendations (Theodorou et al., 2020; Winter et al., 2013). Another relevant conclusion from our review is that all methodological approaches and scales provide similar results. This is particularly interesting as city-level studies using an urban-rural or urban gradient comparison, logistically much easier to perform, can provide equally valid and reliable information than other more complex approaches regarding the impact of urbanization on arthropod diversity. This finding should encourage researchers to carry out additional (local) studies on the topic.

Our meta-analysis also showed evidence for important biases in urbanization research. For example, although the effect of urbanization on arthropods is geographically consistent across continents, there is a substantial lack of studies conducted in Africa and Oceania, which together only represented 6% of all studies. This is especially relevant regarding Africa as it integrates an important proportion of countries from the Global South and where urban areas are expected to grow dramatically in the foreseeable future (United Nations, 2022). In fact, a recent systematic review on urban ecology in Africa also indicated that arthropods are rarely studied in this continent (Awoyemi & Ibáñez-Álamo, 2023). Furthermore, we found clear evidence of publication bias suggesting that the published literature on this topic is biased towards estimates showing a negative association between urbanization and arthropod diversity. This is due to a lack of published estimates based on small sample sizes not showing a clear effect or showing a positive effect of urbanization on mean arthropod diversity. Indeed, although our sensitivity analyses confirmed the robustness of our main analyses, and although the overall evidence for the negative association between urbanization and arthropod diversity remains statistically significant after accounting for such small-study effects, our publication bias tests suggest an average reduction of 50% in such evidence. That is, there is strong evidence that many studies with positive or no effects have not been published. We encourage urban ecologists to make any unpublished estimates available to the scientific community so that we can better understand the nuances and derive more accurate conservation actions.

Our meta-regressions identified important differences between taxonomic groups. Most arthropod orders showed an overall clear reduction in diversity associated with urbanization, with the exception of Hemiptera and Odonata. The lack of studies performed on Hemiptera (n = 3 studies) could explain the lack of a clear effect for this insect order, although Vaz et al. (2023) found a similar effect in their meta-analysis. Our results on Odonata, however, contrast with those obtained by Vaz et al. (2023) who found a negative effect of urbanization on Odonata abundance. This order is particularly interesting because we identified statistically significant differences between Odonata and EPT (Ephemeroptera, Plecoptera and Trichoptera), another category integrating three aquatic insect orders which seem to be more negatively influenced by urbanization. The EPT group is associated with current waters and known to be very sensitive to water quality, whereas odonates typically inhabit lentic waters and are generally more tolerant to pollutants (Rogers, 2014; Tierno de Figueroa et al., 2013). That is, the results for EPT could be directly related to urban water quality as several studies have highlighted the bad conservation status of urban rivers and ponds (Everard & Moggridge, 2012; Hill et al., 2018). However, we need more studies on Odonata, an order that remains relatively unexplored in urban areas (n = 9 studies) and in which it has been shown that species differ in both sensitivity (see Villalobos-Jimenez et al., 2016) and dispersal abilities (Sarremejane et al., 2020). Indeed, our meta-analysis evidences that researchers prefer studying terrestrial rather than aquatic organisms despite the importance of the latter habitat. On the other hand, when we zoom in taxonomically and focus on Families, and despite the more restricted sample size, our meta-analysis offers interesting and previously unknown patterns. Our results suggest that the urban effect might not be homogeneous across families within certain orders. For example, at the order level, our meta-analysis shows similar negative effects of urbanization to those shown by previous reviews for the order Diptera (Fenoglio et al., 2020; Vaz et al., 2023); however, this effect was only statistically clear for the family Calliphoridae. These results also indicate that we need more studies focusing on low taxonomic levels such as families to better understand the influence that urbanization has on this mega-diverse animal phylum (e.g., Wenzel et al., 2022). These findings are important given that previous general conservation actions oriented towards the preservation of certain high taxonomic groups might be misleading or not benefiting all animal groups within it.

## Urbanization and the variance of diversity

Contrary to our initial expectations, once we account for the meanvariance relationship observed in our data, variance in arthropod diversity values was 28% higher across urban habitats compared to less urban ones (i.e., less urbanized or rural habitats). There are several features and management practices that have been proposed to affect urban arthropod diversity and can vary widely across urban habitats, thus potentially leading to higher variance in urban arthropod diversity: (1) urban vegetation can play an important role since many exotic arthropods come along with introduced plants (e.g., Arteaga et al., 2020); (2) the high proportion of impervious surfaces and the associated higher temperatures can favour the presence of certain species through higher reproductive success (e.g., Dale & Frank. 2017): (3) bad urban vegetation management such as practices that weaken plant defences (e.g., intensive pruning) can enhance the presence of herbivorous and sap-feeding arthropods but also decrease those acting in top-down regulation (Korányi et al., 2022); (4) light pollution and water scarcity are usually higher in city centres, where arthropod species more tolerant or specialists to these conditions would be positively selected (Horváth et al., 2012); (5) a high heterogeneity of habitats at short distances that usually characterizes the urban habitat would also allow the presence of a wide array of arthropod species and functional groups (Sattler et al., 2010). These urban characteristics and management practices should be taken into account when designing urban areas as they can deeply enhance or reduce arthropod presence and abundance (Baldock et al., 2019; Smith & Lamp, 2008). In this sense, Kotze et al. (2010) suggested that urban areas could act as a collection of ecological islands or microhabitats for arthropods so that this environmental heterogeneity would allow many different kinds of insects to thrive. Therefore, within each urban habitat, a strategic conservation plan consisting in making the urban landscape more heterogeneous would be desirable to increase urban arthropod diversity (Tam & Bonebrake, 2016; Watson et al., 2020). This strategy of enhancing heterogeneity would be especially evident in the urban core, whereas city edge areas could buffer this effect due to their proximity to surrounding natural areas (Evans et al., 2018; Villalta et al., 2022). However, we should take into account the local climate when designing the urban areas, as a recent meta-analysis on soil fauna (Szabó et al., 2023) concluded that climate-neutral cities could better sustain local biodiversity. In this sense, our results could also be partially associated with the intermediate disturbance hypothesis, for which intermediate levels of disturbance can enhance diversity levels compared to natural environments (Evans, 2010), a similar conclusion drawn from another meta-analysis on urban fauna (Saari et al., 2016).

Another factor that could explain our observation of higher variance in biodiversity values in urban habitats is species turnover. Lennon et al. (2001) found a negative association between species richness (alpha diversity) and species turnover (beta diversity), which could also be happening in urban areas. Avoiding species turnover could be key to preventing biotic homogenization through exotic species replacing natural ones in urban areas and therefore leading to similar biotic

composition (McKinney, 2006; McKinney & Lockwood, 1999). This could be especially relevant for non-insect orders, whose studies do not usually look for the nativeness of the specimens (Gaume & Desguilbet, 2023). A recent review on urban biotic homogenization highlighted that there is still much debate about the existence and extent of biotic homogenization in cities (Lokatis & Jeschke, 2022). Our meta-analysis of variance suggests that some urban areas can hold higher levels of species richness than the urban average (potentially preventing species turnover) while other urban areas hold lower diversity levels (promoting community simplification and homogenization). Thus, identifying the cities showing higher levels of arthropod diversity and particularly the urban attributes and/or conservation actions responsible for would be instrumental in minimizing the impact of urban habitats on biodiversity. This consideration is even more important given the lack of arthropod studies on this topic, as the observed taxonomic bias could be behind the observed discrepancies found in the literature (Lokatis & Jeschke, 2022).

The observed higher variance in arthropod diversity across urban areas was clear for all taxonomic diversity proxies but functional diversity, although that is likely because of the small number of studies calculating functional diversity (n = 4 studies). Interestingly, our results suggest that this effect might not be geographically consistent since, although in the same direction, the effect was not statistically significant for Asia, Africa and Oceania. Though this again could be caused by the geographical bias (see references above) and the low number of studies performed in those continents (21 and 11 respectively). A possible explanation for why variance might be similar between urban and less urbanized habitats could be that urban features and management practices are more homogeneous in these continents (i.e., same urban vegetation, similar vegetation managing practices among cities, similar proportion of green areas compared to paved ones, etc.) compared to Europe and America, something that could be further investigated. Our results also suggest that the increase in variance might be restricted to insects only, with Coleoptera, EPT and Lepidoptera leading this effect. This suggests that whatever the cause of such finding, it can affect both the aquatic and terrestrial ecosystems and animals with very different ways of living. Additionally, the Family level analysis shows that other families beyond Carabidae are driving the findings for Coleoptera. Nevertheless, a meta-analysis on this family in urban areas also evidenced that some species responded differently (sensitively or not) to urbanization depending on the city considered (Martinson & Raupp, 2013), so that similar analyses should be performed on other Coleoptera families to confirm our results.

In conclusion, urbanization, despite being associated with lower levels of arthropod diversity, holds a great potential for conservation. This is because we observed not only high heterogeneity across effect sizes suggesting certain scenarios where urbanization might be positively associated with arthropod diversity but also because the higher variance in biodiversity value across urban habitats compared to less urbanized habitats suggests a higher potential success for conservation measures targeted at urbanized environments. We found that although the negative effect of urbanization seems commonplace across arthropod groups, its magnitude seems to differ, suggesting the need for taxa-specific conservation actions in urban areas. Future studies should also focus on identifying the causes of the large differences observed across urban habitats as well as investigating the arthropod groups that we identified as severely underrepresented in the literature (i.e., Entognatha, Myriapoda, Orthoptera). The latter is essential since different taxa are expected to need particular habitat requirements, which would subsequently mean the need for taxonspecific conservation actions. Finally, although the negative effect of urbanization was generally evident across our dataset, we also found strong evidence of publication bias suggesting that the current literature on this topic is likely biased towards negative estimates. Thus, we here call urban ecologists to not only perform further research to fill in the knowledge gaps that we identified (e.g., underrepresented taxa and regions), but to make sure that any existing estimates for the association between urbanization and arthropod diversity are available to the scientific community and beyond. This combined effort becomes essential for finding the balance between urban development and the conservation of a such a hyper-diverse and ecologically relevant animal group as arthropods.

## AUTHOR CONTRIBUTIONS

**Olivia Sanllorente:** Conceptualization; writing – original draft; writing – review and editing; project administration; funding acquisition; supervision; visualization. **Endika Blanco-Urdillo**: Software; formal analysis; data curation; visualization; writing – review and editing; investigation. **Alfredo Sánchez-Tójar**: Methodology; validation; writing – review and editing; software. **Juan Diego Ibáñez-Álamo**: Writing – review and editing; conceptualization; supervision; funding acquisition; project administration.

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### CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

The data and code used for this study are available in https://doi.org/10.5281/zenodo.15131609andnet/10481/94956, respectively.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Checklist of the Preferred Reporting Items for Systematic Review and Meta-Analysis (PRISMA) Statement. https://digibug. ugr.es/handle/10481/85613.

**Appendix S2.** Prisma flow diagram summarizing a systematic literature review performed to find published evidence on the association between urbanization and arthropod diversity.

**Appendix S3.** Search string used in the Web of Science Core Collection and Scopus searches performed on the 1st of June, 2022 for the systematic literature review searching for published evidence on the association between urbanization and arthropod diversity.

**Appendix S4.** List of the 221 articles included in the meta-analysis performed to find published evidence on the association between urbanization and arthropod diversity. https://hdl.handle.net/10481/85617.

**Appendix S5.** Post-hoc Wald tests for categories of factor 'Taxonomic order' potentially affected by the effect of urbanization on arthropod mean diversity (R, InRR and SMDH) and diversity variance (InVCR and InVR). *k* corresponds to the total number of effect sizes.

**Appendix S6.** Meta-regressions testing small study, time-lag and all-in biases in published literature on the association between urbanization and arthropod diversity. *k* corresponds to the number of effect sizes.

**Appendix S7.** Meta-regression showing clear evidence of small-study effects in the published literature testing the association between urbanization and arthropod diversity. *k* corresponds to the number of effect sizes, the continuous bold line represents mean values of arthropod diversity, dashed lines correspond to 95% CI and dotted lines to 95% PI.

**Appendix S8.** Meta-regressions testing factors potentially affecting the effect of urbanization on mean arthropod diversity (InRR). *k* corresponds to the number of effect sizes.

**Appendix S9.** Meta-regressions testing factors potentially affecting the effect of urbanization on mean arthropod diversity (SMDH). *k* corresponds to the number of effect sizes.

**Appendix S10.** Meta-regressions testing factors of the urbanization effect on arthropod diversity variance (InVR). *k* corresponds to the number of effect sizes.

**Appendix S11.** Plots showing the ln(mean)–ln(variance) relationship observed in our data from both rural and urban studies.

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