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SYNTHESIS

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The effects of urbanization on pollinators and pollination: A meta-analysis

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Abstract

Urbanization is increasing worldwide, with major impacts on biodiversity, species interactions and ecosystem functioning. Pollination is an ecosystem function vital for terrestrial ecosystems and food security; however, the processes underlying the patterns of pollinator diversity and the ecosystem services they provide in cities have seldom been quantified. Here, we perform a comprehensive meta-analysis of 133 studies examining the effects of urbanization on pollinators and pollination. Our results confirm the widespread negative impacts of urbanization on pollinator richness and abundance, with Lepidoptera being the most affected group. Furthermore, pollinator responses were found to be trait-specific, with below-ground nesting and solitary Hymenoptera, and spring flyers more severely affected by urbanization. Meanwhile, cities promote non-native pollinators, which may exacerbate conservation risks to native species. Surprisingly, despite the negative effects of urbanization on pollinator diversity, pollination service measured as seed set is enhanced in non-tropical cities likely due to abundant generalists and managed pollinators therein. We emphasize that the richness of local flowering plants could mitigate the negative impacts of urbanization on pollinator diversity. Overall, the results demonstrate the varying magnitudes of multiple moderators on urban pollinators and pollination services and could help guide conservation actions for biodiversity and ecosystem function for a sustainable future.

KEYWORDS
floral resources, functional traits, plant reproductive success, pollinator diversity, urban

INTRODUCTION

Urbanization is one of the most profound drivers of anthropogenic change with major impacts on global biodiversity (Seto et al., 2012; Van Klink et al., 2020). Urban development results in habitat loss and fragmentation, increase in impervious surfaces, introduction of non-native species, heat-island effects and environmental contaminants (e.g. artificial light, noise, soil and air pollution) with largely negative effects on wildlife (Beninde et al., 2015; Grimm et al., 2008; McKinney, 2008; Piano et al., 2020). Urbanization can affect individual fitness, life-history traits, population dynamics, species interactions, community structure and ecosystem functioning (e.g. Buchholz & Egerer, 2020; Gaston, 2010; Theodorou, 2022). As urban areas continue to expand worldwide, especially in tropical and developing regions (Huang et al., 2019; United Nations, 2018), there

has been an increase in scientific, public and political interest in how cities should be managed to promote biodiversity conservation, food production and ecological restorations for a sustainable future. Pollinators are an important component of biodiversity due to the vital pollination services they provide to wild flowers (Ollerton et al., 2011) and crops (Klein et al., 2007). Currently, pollinator populations are declining worldwide (reviewed by Ollerton, 2017), and the study of pollinators in urban areas has received much attention due to the potential role of cities as refugia for pollinator species (Baldock, 2020; Baldock et al., 2015; Hall et al., 2017; Theodorou, Radzeviciute, et al., 2020), as well as the great social and economic benefits of urban agriculture for food security, especially in low-income communities of developing countries (Wenzel et al., 2020). It is estimated that globally, 25–30% of urban dwellers are involved in the agriculture food industry, and 15–20% of the food production comes from urban and peri-urban agriculture (Orsini et al., 2013; van Veenhuizen, 2006).

In general, urban development has predominantly negative effects on pollinators (Fenoglio et al., 2020; Millard et al., 2021). However, recent studies have also shown that urbanization can have neutral or even positive effects on pollinator abundance and richness (Millard et al., 2021; Theodorou, Radzeviciute, et al., 2020; Wenzel et al., 2020). These varying effects are hypothesized to be due to differences at multiple levels (Faeth et al., 2011; McKinney, 2008). Firstly, taxonomic group, life-history and functional traits could influence how a pollinator species responds to urbanization. Previous studies have shown that Hymenoptera insects may be more resilient to urbanization compared to Diptera and Lepidoptera (Baldock et al., 2015; Fenoglio et al., 2020) and urbanization seems to benefit large-bodied, social, cavity-nesting, generalist and non-native species (Buchholz & Egerer, 2020; Fitch et al., 2019). Secondly, the effects of urbanization on pollinators could vary between climatic and geographic regions due to differences in land-use history and practices, socioeconomics and geographic variation in pollinator communities (Faeth et al., 2011; Fenoglio et al., 2020). Due to the overall higher levels of urbanization and the more strictly seasonal activity of plant–pollinator interactions in temperate regions (Elmqvist et al., 2013), the effects of urbanization on pollinators might be more severe in temperate compared with tropical regions. Thirdly, pollinators respond to the availability of local resources often irrespective of land-use change (Murray et al., 2012; Theodorou, Herbst, et al., 2020; Winfree et al., 2011). In moderately disturbed urban areas with abundant and continuous floral resources, it is not surprising to document high pollinator diversity (Baldock et al., 2015; Theodorou, Radzeviciute, et al., 2020). Fourthly, the contrasting effects of urbanization on pollinator diversity might be due to methodological differences in the design of the studies, for example within city limits urbanization gradient or rural–urban or natural–urban comparisons (Fenoglio et al., 2020; Wenzel et al., 2020). All the above factors suggest that summarizing a global pattern of the effects of urbanization on pollinators is challenging and multiple moderators should be considered when attempting to do so.

Although we have a growing understanding of how urbanization impacts different taxonomic and functional groups of pollinators, it is unclear whether these changes translate into shifts in pollination service provision (Theodorou, 2022). The effects of urbanization on the community structure and functional diversity of pollinators could reduce the efficiency or frequency of pollen transfer and could lead to pollen limitation (Irwin et al., 2018). In addition, urbanization can affect abiotic and landscape features, the abundance of conspecific flowers and the diversity of flowering plants in an area (de Barros Ruas et al., 2022). These factors may have an impact on pollinator foraging patterns, visitation rates, conspecific pollen deposition and consequently influence plant reproduction (Pellissier et al., 2012). Similarly, to pollinators, the origin of the plant species, its functional traits and pollinator specialization may influence its reproductive success in cities. Native plants are generally preferred by pollinators (Chrobock et al., 2013); plants with open radial flowers attract more flower visitors (Ollerton et al., 2007; Willmer, 2011) and therefore flower symmetry could mediate the effects of urbanization on pollination. Recent studies have investigated the effects of urbanization on plant reproductive success by estimating fruit set and/or seed set or by using visitation rates and visit duration as proxies, and many studies have shown an increase in pollination service provision in non-tropical cities driven by the high abundance of managed and generalist pollinator species (Theodorou, 2022; Theodorou et al., 2021).

Although there are some qualitative reviews on the effects of urbanization on pollinators and pollination (Ayers & Rehan, 2021; Baldock, 2020; Brant et al., 2022; Buchholz & Egerer, 2020; Harrison & Winfree, 2015; Maruyama et al., 2021; Prendergast et al., 2022; Rahimi et al., 2022; Silva et al., 2021; Wenzel et al., 2020), only two meta-analyses investigated the overall effects of urbanization on pollinator diversity (Fenoglio et al., 2020; Millard et al., 2021). In our study, we extend the research in this field by performing a hierarchical meta-analysis to assess how dependent the effects of urbanization are on the taxonomic group and origin (native vs. non-native) of the pollinator species, climatic region of the study, local floral food resource availability and study design. Furthermore, we assess how urbanization influences the activity length, seasonality, sociality, nesting behaviour, diet and body size of pollinator communities. Finally, we investigate the potential effects of urbanization on pollination service provision and test if the effects differ between climate regions, pollinator group and origin, flower symmetry, plant origin and reproductive success index.

METHODS

Literature search and inclusion criteria

We conducted a literature search in the ISI Web of Science and Scopus databases (until 28 December 2021), using a combination of different keywords depending on our research questions. To find publications investigating the effects of urbanization on pollinator abundance and richness, we used the keywords [urban* OR city OR cities OR town] AND [pollinat*] AND ["species richness" OR "species diversity" OR abundance OR density OR assemblage]. We replaced the last combination with [trait OR phenology OR "body size" OR nest* OR sociality OR diet] to find publications on the effects of urbanization on pollinator functional traits. To search for studies that investigate the effects of urbanization on pollination, we changed the last combination to ["pollinat* service" OR "plant reproduc*" OR seed OR fruit]. This search yielded 719, 708 and 504 publications on the Web of Science, and 454, 366 and 348 in Scopus, respectively. In addition, we also surveyed recent reviews (e.g. Fenoglio et al., 2020; Wenzel et al., 2020) for relevant publications.

After removing duplicates, non-English papers and review papers, our survey resulted in a total of 1,205 publications. The publications were filtered by reading the title, abstract and full text according to two criteria: (1) studies that reported any of the following: pollinator abundance, pollinator richness, activity length, seasonality, nesting behaviour, diet specialization, body size, sociality, fruit set, seed set, visitation duration, number of visits and visitation rates along urbanization gradients or comparisons of urbanization intensity within-urban, urban–rural or urban–natural land-use categories; and (2) provided numerical data and reported means, measures of variance and sample sizes for different categories of comparison or regression or correlation coefficients for urbanization gradient studies. A total of 133 publications met our criteria (Appendix S1.1–9).

Data extraction and effect size calculation

When two different landscape categories were compared; natural or rural versus urban sites, we selected the most extreme category comparison (natural versus urban; Fenoglio et al., 2020). We obtained mean values, sample sizes and standard deviation from texts or tables (*mean value*-type data), for each of the two contrasting ecosystems: control (i.e. natural, forest, rural or suburban sites) versus urban (i.e. urban sites). A meta-analysis may produce spurious results and further exacerbate publication bias when excluding studies with missing information. Therefore, we converted or imputed data from relevant studies that report incomplete information on means, correlations, variances and sample sizes (Koricheva et al., 2013).

When the effect of urbanization was measured using a continuous variable (i.e. impervious surfaces, distance to the city centre or green area), we extracted Pearson's correlation coefficients (r) or the coefficients of determination (R^2; *r*-type data). When none of these values was reported, we used the statistical values of parametric tests (e.g. ANOVAs, Chi-square, *t*-tests; *statistic values*-type data). If these parameter values were only presented in graphs, we estimated the values from the figures using WebPlotDigitizer (Burda et al., 2017). If the standard deviation was not shown in graphs; but instead using a boxplot of minimum, maximum, first quartile or third quartile, we estimated it using the Excel spreadsheet with formulas provided by Wan et al. (2014). Moreover, when all the above information was not available in the main text, we calculated means and standard deviation or correlation coefficients from the supporting material and/or original datasets (47.6% of all cases).

If a publication reported the results of several taxonomic groups or cities separately, each was considered a separate observation (Aguilar et al., 2006). When abundance, species richness, traits or plant reproductive success were reported at multiple time points (months or years), we selected the time point with the highest sample size. If multiple time points had equal sample sizes, we chose the most recent period of sampling, or if possible, we chose the sampling period of maximum pollinator activity, which we estimated based on the data of each study (Fenoglio et al., 2020). For pollination services, we collected information on fruit and seed set, as they are the two best indicators of plant reproductive success. However, due to the limited number of cases ($N=8$ for fruit set and $N=17$ for seed set), whenever possible, we additionally extracted the number, rate and duration of visits and used them as proxies for plant pollination service delivery (Kleijn et al., 2015).

Moderator variables

Pollinator taxonomic group

The abundance of pollinators and the number of pollinator species (or families when species richness was not available) were extracted and used as response variables. To assess whether the effects of urbanization differ between pollinator groups, we classified them according to taxonomic affiliation; Aves, Mammalia and Insecta (Hymenoptera, Lepidoptera, Diptera and Coleoptera). As Hymenoptera insects were studied most frequently, we further divided them into *Apis* (honey bees), *Bombus* (bumble bees) and other Hymenoptera.

Climatic region

We classified each study as tropical or non-tropical according to its latitude (tropical <23°26′13.4", non-tropical >23°26′13.4"). We used the coordinates of each sampled city (a study could have multiple cities) to assess the geographical and climatic distribution of the studies. When the data were sampled in different cities (e.g. Baldock et al., 2015; Harrison et al., 2018), we took only the centroid of the respective region for simplicity and to avoid overplotting (Maruyama et al., 2021).

Plant and pollinator origin

We extracted information on the origin (native or non-native) of the pollinator and plant 'pollinometer' species studied. If a species name is given, but its origin is not available in the publication, we filled in this information using Google Scholar and other online databases (for references, see Appendix S1.1–2 and 5, Appendix S2).

Study design

We classified the studies into three types according to their design: within-urban (green spaces with different degrees of impervious surfaces), urban–rural comparison and urban–natural comparison (Appendix S1.1–2). Given the inconsistent classifications of land-use types in the literature, we standardized definitions as follows: 'Natural'—natural or semi-natural areas with little or no human disturbances, for example natural reserves; 'Rural'—farmland landscapes with low density of housing; 'Urban'—human settlements with relatively high impervious surfaces (Batáry et al., 2018; Fenoglio et al., 2020). According to our definitions, we re-classified three studies by the predominant land-use type they described in the text (shown with '*' in Appendix S1.1–2) and four studies were excluded as they did not have clear information on the land-use comparison (shown with 'NA' in Appendix S1.1–2).

Pollinator and plant traits

For pollinators, we collected several functional trait data (Table 1). Activity length and seasonality (i.e. abundance and richness at different seasons) data were collected for all pollinator groups. For body size, we used the inter-tegular distance (ITD) for bees and the wingspan for Lepidoptera. Hymenoptera pollinators were further categorized based on (1) their nesting behaviour: above ground (tree, wood, stem, above ground cavity) or below ground (within existing tunnels or excavators), (2) sociality: social, solitary or parasitic and (3) diet specialization; polylectic or oligolectic depending on if they feed on various or a particular plant taxon (Michener, 2007). Activity length and body size are continuous traits, while all the other traits are categorical. We used the abundance and richness of pollinators as response variables for categorical traits (i.e. seasonality, sociality, nesting behaviour, diet), to assess whether the effects of urbanization on pollinator communities depend on trait guild. All traits were extracted directly from original studies or from additional references when the species' scientific names were given (for trait references see Appendix S1.3–4, Appendix S2). Due to data limitations, functional traits were collected mainly for Hymenoptera and Lepidoptera (Table 1).

We categorized each flower as non-radial (e.g. *Lotus* spp.) or radial (e.g. Asteraceae) to test whether flower morphology mediates the effects of urbanization on plant reproductive success.

Effect size calculation and hierarchical meta-analysis

We used Hedges' *d*, weighted by sample size, as our effect size. An individual effect size of Hedges' *d* was calculated either by using packages in R statistical software (R Core Team, 2021) or by standard mathematical formulas (Borenstein et al., 2021; Koricheva et al., 2013). For the *mean-value*-type data and regression coefficient data, effect sizes were calculated using the R packages '*metafor*'

TABLE 1 Description of pollinator and plant traits used in our meta-analysis.

	Traits	Data type	Classification	Groups
Pollinator	Seasonality	Categorical	Early spring/spring summer/autumn	A, D, H, L
	Activity length	Continuous	—	H, L
	Body size	Continuous	—	H, L
	Sociality	Categorical	Social/ solitary/ parasitic	H
	Nesting	Categorical	Above ground/below ground	H
	Diet	Categorical	Polylectic/oligolectic	H
Plant	Flower symmetry	Categorical	Radial/non-radical	—

Note: A-Aves; D-Diptera; H-Hymenoptera; L-Lepidoptera.

(Viechtbauer, 2010) and '*esc*' (Lüdecke, 2019), respectively (see R codes in Appendix S3). For *r*-type data, effect sizes were transformed into Cohen's *d* and then into Hedges' *d* using standard mathematical formulas (Koricheva et al., 2013; Borenstein et al., 2021; Table S1). Chi-square data were first transformed into *r* using the formulas in Table S1, and then into Hedges' *d*. In all cases, a negative value of Hedges' *d* reflects the negative effects of urbanization on pollinators or pollination.

Some publications provided more than one effect size, which may result in pseudoreplication, so we carried out a hierarchical meta-analysis that allows nesting effects within papers/studies (Tuck et al., 2014). We included a publication-level random effect as a nesting factor to incorporate this non-independency. We first performed a random effects meta-analysis to calculate the overall mean effect size of urbanization on pollinator abundance and richness, flower abundance and richness, functional traits and pollination separately. Effect sizes were considered statistically significant if their 95% bias-corrected bootstrap confidence intervals (CI) did not overlap with zero (Borenstein et al., 2021; Koricheva et al., 2013). Secondly, we incorporated moderators, including the climatic region of the study, the origin of the species, the taxonomic group of pollinators, study design and flower symmetry. To assess the levels of heterogeneity of effect sizes, we calculated the *P*-value of the Q_t statistics. When they were statistically significant ($p<0.05$), the influence of moderators on the effects of urbanization was examined using Q_m.

To test whether a change in floral diversity (Hedges' *d* for flower abundance and richness) could predict a change in pollinator diversity (Hedges' *d* for pollinator abundance and richness), we fitted maximum likelihood meta-regression models (Filazzola et al., 2020). The adjustment of Knapp and Hartung was then used to account for uncertainty in the variance between studies, with overall model significance against an F-distribution (Knapp & Hartung, 2003). All analyses were conducted in R statistical software using the *metafor* package (R Core Team, 2021; Viechtbauer, 2010).

Publication bias

Publication bias was evaluated graphically by inspecting the asymmetry of the funnel plots and statistically using Egger's regression tests (Sterne & Egger, 2005). Significantly asymmetric results were then augmented using the Trim and Fill method (Duval & Tweedie, 2000). The Trim and Fill method estimates the number of missing studies due to publication biases, calculates their effect sizes and standard errors and adds them to the meta-analysis dataset. In addition, the Rosenberg's fail-safe number was calculated. The Rosenberg's fail-safe number represents the number of non-significant, unpublished studies that must be added to a meta-analysis to change the result from significant to non-significant (Rosenberg, 2005). A fail-safe number that is larger than $5n+10$, where n is the number of studies used in the meta-analysis, is considered robust (Rosenthal, 1986).

RESULTS

We identified 133 (n_p) publications and 799 observations (n_o) reporting the effects of urbanization on pollinator abundance ($n_p=78$, $n_o=228$, Appendix S1.1), richness ($n_p=87$, $n_o=147$, Appendix S1.2), functional traits ($n_p=53$, $n_o=436$, Appendix S1.3–4, 6–7), floral resources ($n_p=38$, $n_o=58$, Appendix S1.8–9) and plant reproductive success ($n_p=28$, $n_o=116$; Appendix S1.5). The geographical distribution of the studies was clearly uneven (Figure 1). More than three quarters of the studies were carried out in two continents (Europe: $n=52$, 39.1% and North America: $n=49$, 36.8%), and the remaining studies were carried out in Asia ($n=17$, 12.8%), South America ($n=8$, 6%), Oceania ($n=4$, 3%) and Africa ($n=3$, 2.3%). Furthermore, 114 (85.7%) studies were conducted in non-tropical regions and only 19 (14.3%) were conducted in tropical regions. Most studies focused on Insecta, especially Hymenoptera and Lepidoptera, while a small number of studies involved Aves and Mammalia (Appendix S1.1–9).

Pollinator abundance and richness

Overall, urbanization had a negative effect on pollinator abundance ($d=-0.42$; 95% CI=[−0.7, −0.15]; $p=0.003$) and richness ($d=-0.66$; 95% CI=[−0.96, −0.36]; $p<0.001$; Figure 2). The heterogeneity of the effect sizes was large and statistically significant for both abundance ($Q_t=1450.11$, df=227, $p<0.001$) and richness ($Q_t=908.31$, df=146, $p<0.001$). Pollinator origin (native or non-native) was an important moderator of the effects of urbanization on pollinator richness (Table 2). Urbanization had a significant negative effect on native pollinator species richness and a significant positive effect on non-native pollinator species richness (Figure 2; Table S2). Similarly, the taxonomic group was an important moderator of the effects of urbanization on pollinator richness (Table 2). Specifically, the richness of Diptera, Hymenoptera and Lepidoptera were negatively influenced by urbanization (Figure 2; Table S2). Furthermore, urbanization had a negative effect on the abundance of Lepidoptera and a negative, although marginally significant, effect on the abundance of Hymenoptera (Figure 2; Table S2). When the Hymenoptera were divided into *Apis* bees, *Bombus* bees and other Hymenoptera, we did not detect an effect of urbanization on the abundance of these subgroups (Figure S1).

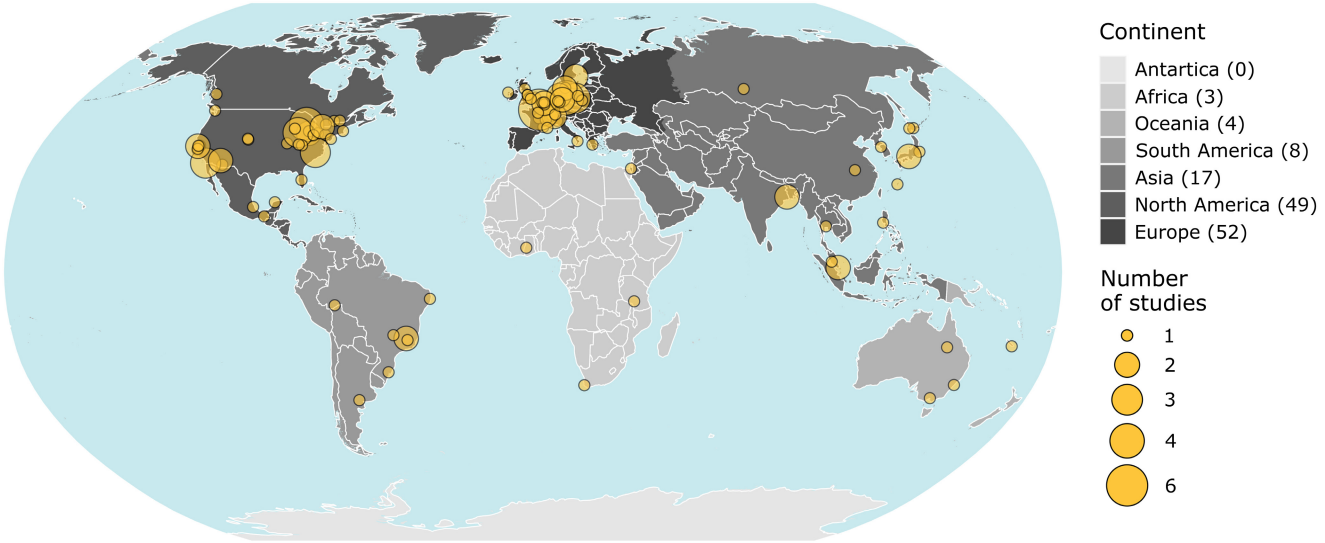

FIGURE 1 Distribution of studies included in the meta-analysis ($N = 133$). The sizes of the yellow circles are proportional to the number of studies in each city.

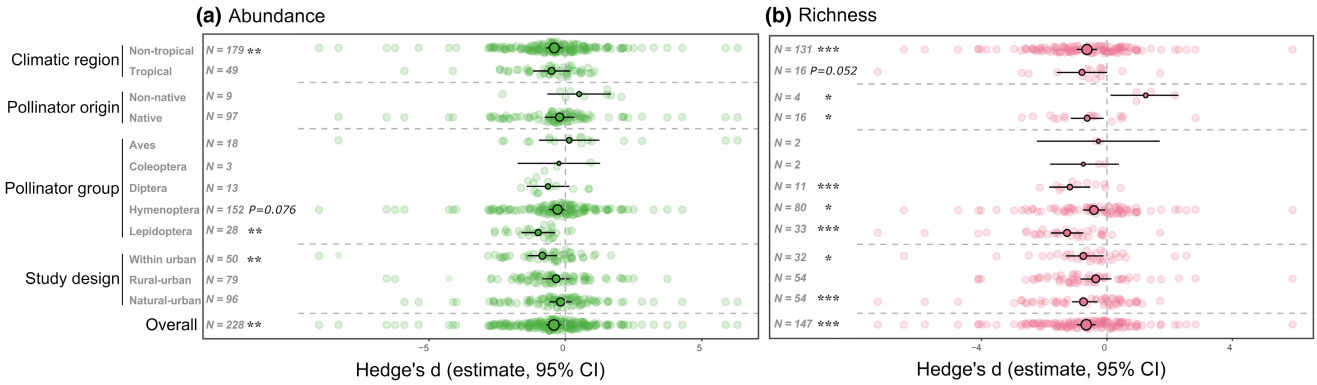

FIGURE 2 Effects of urbanization on (a) pollinator abundance and (b) richness depending on climatic region, pollinator origin, pollinator taxonomic group and study design. Estimated mean effect sizes and 95% confidence intervals are shown. Sample sizes are shown next to each moderator subgroup. *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

The climatic region (tropical vs. non-tropical) did not explain the heterogeneity of the effects of urbanization on pollinator abundance and richness (Table 2). Yet, urbanization had a significant negative effect on pollinator abundance and pollinator richness in non-tropical regions (Figure 2; Table S2), whereas in tropical regions urbanization had a marginally significant negative effect only on pollinator richness (Figure 2; Table S2).

The type of study design did not explain the heterogeneity of the effects of urbanization on pollinator abundance and richness (Table 2). However, urbanization had significant negative effects on pollinator abundance and richness in studies that used a within-urban gradient design, and a negative effect on pollinator richness in studies that compared natural versus urban localities (Figure 2; Table S2). Urbanization had no effect on pollinator abundance and richness in studies that compared rural versus urban localities (Figure 2; Table S2).

Urbanization was not found to influence the richness and abundance of flowering plant species (Figure S2; Table S3). However, flowering plant richness had a positive effect on pollinator richness ($F = 5.838$; $p = 0.019$; Figure 3a; Table S4) and a positive, although marginally significant, effect on pollinator abundance ($F = 3.490$; $p = 0.065$; Figure 3b; Table S4). Flowering plant abundance did not affect pollinator abundance and richness (Figure S3; Table S4).

Functional traits

Regarding functional traits, none of the moderators significantly explained the effect size heterogeneity (Table S5). However, pollinator responses were found to be trait-specific (Table S6). Urbanization had a negative effect on the abundance and richness of spring pollinator

TABLE 2 Summary table of meta-analysis with tests of moderators on pollinator abundance, richness and pollination service provision.

Response variables	Moderators	Effect size	Df	Q_m	*p*-value
Abundance	Climatic region	228	1	0.07	0.79
	Pollinator origin	106	1	1.42	0.23
	Taxonomic group (Order)	214	4	5.75	0.22
	Taxonomic group	214	6	6.55	0.36
	Study design	225	2	3.8	0.15
Richness	Climatic region	147	1	0.23	0.63
	Pollinator origin	**20**	**1**	**9.91**	**<0.002**
	Taxonomic group	**128**	**4**	**13.14**	**0.011**
	Study design	140	2	1.33	0.52
Pollination	Climatic region	116	1	0.18	0.67
	Pollinator group	**85**	**7**	**15.59**	**0.016**
	Pollinator origin	47	1	0.19	0.66
	Flower symmetry	92	1	2.05	0.15
	Plant origin	99	1	0.38	0.54
	Reproductive success index	**116**	**4**	**14.9**	**0.005**

Note: Significant moderators are indicated in bold.

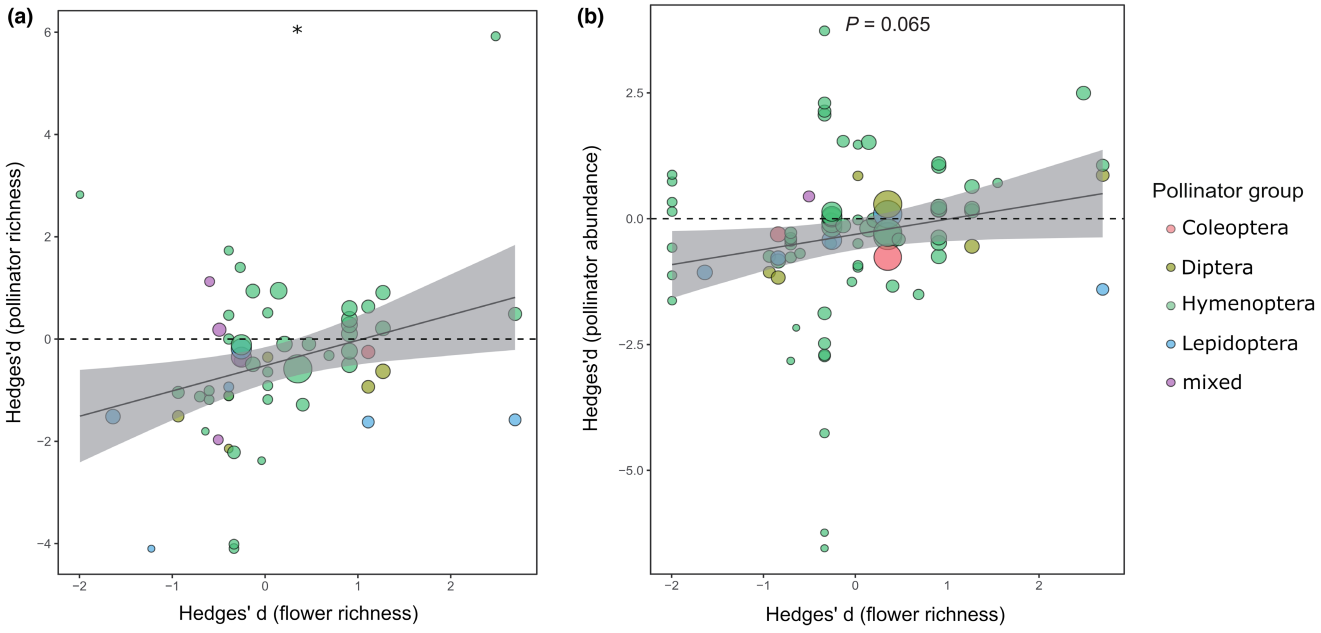

FIGURE 3 Relationships between change in (a) flowering plant richness and pollinator richness and (b) flowering plant richness and pollinator abundance. The solid black lines show the predicted relationship and shaded areas indicate the 95% confidence intervals. Circles represent cases that investigated flowering plant and pollinator diversity simultaneously, circle sizes are weighted by their variances (1/sqrt(vi)), and different colours represent different pollinator taxa ('mixed' means there was more than one pollinator order in that case study). *$p<0.05$.

communities (Figure 4; Table S6). In addition, urbanization had a negative, although marginally significant, effect on the richness of early spring pollinator communities (Figure 4; Table S6). Furthermore, urbanization had negative effects on the abundance of solitary bees and on the abundance and richness of below-ground nesting bees (Figure 4). Urbanization had no significant effects on body size (Figure S4), activity length (Figure S5) and diet specialization (Figure 4; Table S6).

Pollination service provision

Urbanization had no significant overall effects on pollination service provision ($d=0.2$; 95% CI=[−0.10, 0.51]; $p=0.19$). However, the heterogeneity of the effect sizes was large and statistically significant ($Q_t=1543.29$, df=115, $p<0.001$). Specifically, the pollinator groups sampled in the studies that estimated pollination service provision differed significantly in their contribution

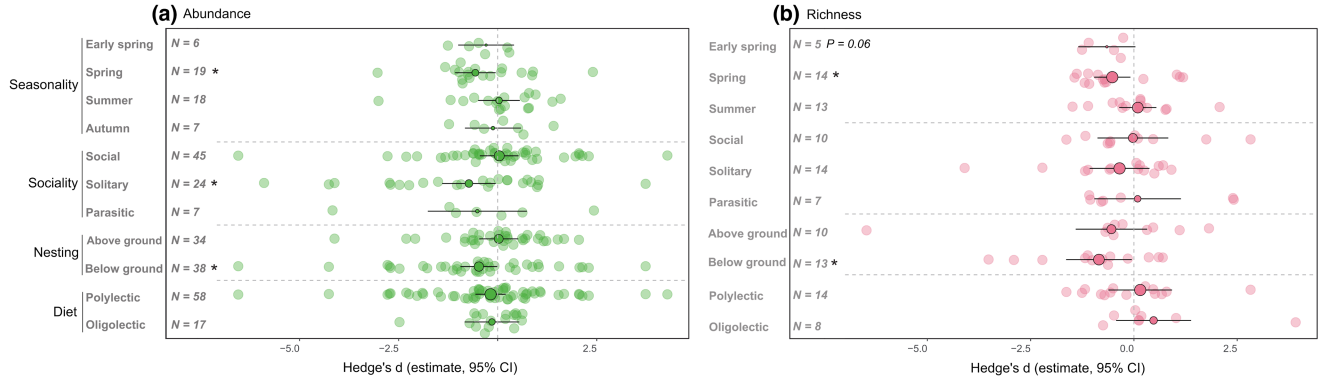

FIGURE 4 Effects of urbanization on seasonality and functional traits of pollinator (a) abundance and (b) richness depending on functional guild. Estimated mean effect sizes and 95% confidence intervals are shown. Sample sizes are shown next to each moderator subgroup. *$p<0.05$.

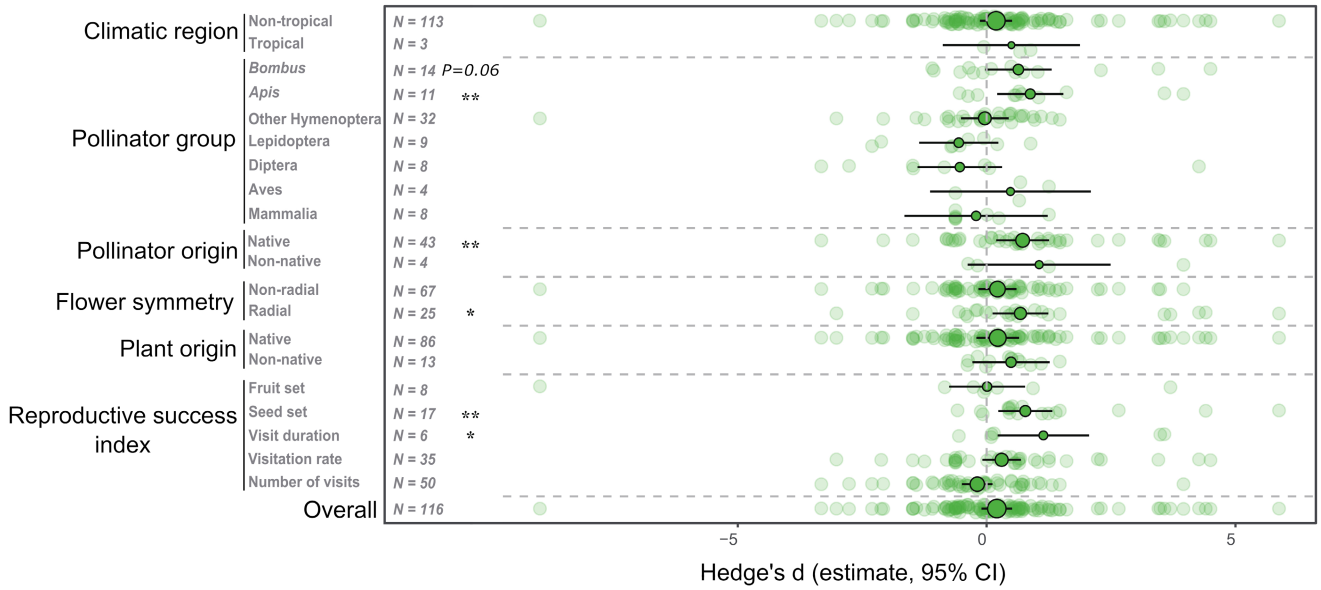

FIGURE 5 Effects of urbanization on overall pollination services ($N=116$) depending on climatic region, pollinator group, pollinator origin, flower symmetry, plant species origin and reproductive success index. Estimated mean effect sizes and 95% confidence intervals are shown. Sample sizes are shown next to each moderator subgroup. *$p<0.05$, **$p<0.01$.

to plant reproductive success (Figure 5; Table 2). *Apis* (honey bees) significantly and *Bombus* (bumble bees) marginally significantly boosted plant reproductive success in non-tropical cities (Figure 5). The five reproductive success indices significantly explained the effects of urbanization on pollination (Table 2), with significant positive responses to urbanization in studies that estimated seed set and visitation duration and no effects of urbanization in studies that measured fruit set, visitation rate and number of visits (Figure 5). In addition, flowering plants with radial flowers and flowering plants that are visited by native pollinators had significantly higher reproductive success in cities (Table 2; Figure 5). The climatic region (non-tropical vs. tropical) and the origin of plant species (native vs. non-native) did not explain the effects of urbanization on pollination (Figure 5; Table 2; Table S7). Lastly, pollinator richness and abundance were not significantly related to pollination service provision (Figure S6; Table S8).

Publication bias

The funnel plots were symmetric for body size and pollination service provision (Figure S7; Table S9). Although the funnel plots of pollinator abundance and activity length were asymmetric (Figure S7), the regression estimates using the Trim and Fill method did not change. Pollinator richness changed from significant to marginally significant ($p=0.054$); however, the fail-safe number ($N=12{,}053$) is much higher than the one required ($N=745$), indicating that publication bias can be safely ignored (Table S9). We

interpreted asymmetry in funnel plots carefully given the small sample sizes, for example for activity length or the lack of bidirectional outcomes for the effects of urbanization on some variables, for example pollinator richness, which have been found to decrease across a lot of study systems, and thus will inevitably lead to a biased plot.

DISCUSSION

In this study, we reviewed the literature and performed a meta-analysis on the effects of urbanization on pollinators and pollination. Our meta-analysis revealed an overall negative effect of urbanization on pollinator abundance and richness. The effect's magnitude depended on the pollinator's taxonomic group, origin and functional traits. Furthermore, flowering plant richness had a positive effect on pollinator richness revealing the importance of local floral food resource availability for pollinators. Pollination services measured as seed set are enhanced in urban areas which is most likely due to the high abundance of generalist and managed pollinator species in non-tropical cities. Publication bias inferred through funnel plots may indicate the small sample size for some underrepresented taxonomic groups and regions that need further research. Below, we expand on these results and discuss their implications for pollinator conservation in cities.

Pollinator responses to urbanization

Urbanization results in a drastic modification of habitats with negative effects on biodiversity (McKinney, 2008). The negative effects of urbanization on both pollinator abundance and richness, reported in our study, are in line with previous meta-analyses (Fenoglio et al., 2020; Millard et al., 2021). The strong negative effects we observed in studies that used a gradient of urbanization (i.e. impervious surfaces) or compared semi-natural to urban ecosystems, suggest that urban densification and impervious surfaces, which cause habitat loss and fragmentation are the primary drivers for the observed reduction of pollinator diversity in cities (González-Varo et al., 2013; Vanbergen & Initiative, 2013). The lack of an effect of urbanization in studies that contrasted urban versus rural ecosystems could be due to the study design and the choice of landscapes, land uses and habitats to compare. The urban ecosystem contains several land uses and habitats that differ in their value for pollinators (Baldock et al. 2019). Similarly, rural ecosystems can be comprised of conventional/intensively managed or organic, extensively managed farmland landscapes, which also differ in their effects on pollinators (Millard et al., 2021). Alternatively, it might be that urban and rural areas offer similar ecological opportunities for some pollinator groups (Theodorou, Radzeviciute, et al., 2020). While pollinator richness in cities was lower compared with semi-natural areas, pollinator abundance did not differ between the two ecosystems, which suggests that some species are abundant in urban areas. Moderate levels of urbanization could increase habitat heterogeneity and the availability of floral and nesting resources for some pollinators (intermediate disturbance hypothesis) and thus drive comparable pollinator abundances in urban green spaces and natural areas (Baldock et al., 2015; Theodorou, Radzeviciute, et al., 2020; Wenzel et al., 2020). Urban conservation actions should prioritize the creation and connectivity of green infrastructure with suitable and diverse floral and nesting resources to allow the occurrence of species with different ecological needs and promote pollinator species richness in cities (Fischer et al., 2016; Persson et al., 2020).

In addition to the overall negative effects on pollinator diversity, our results revealed that pollinator taxonomic groups differ in their sensitivity to urbanization. Lepidoptera was the taxonomic group found to be most affected by urban development and should be prioritized for conservation in cities. Many butterflies and moths require specific host plants for larval development and nectar consumption as adults and appear to be very sensitive to urban environmental stressors such as heat-island effects, air and light pollution (Callaghan et al., 2021; Fenoglio et al., 2020; Ramírez-Restrepo & MacGregor-Fors, 2017). Due to their sensitivity to human disturbances, our results further highlight the suitability of Lepidoptera as a bioindicator taxon to quantify responses to urbanization. Aves were not affected by urbanization, which suggests that bird species with certain biological traits (e.g. habitat generalism and tree-nesting) could survive in cities that have plenty of bird-pollinated plants and sugar feeders (Coetzee et al., 2018; Davis et al., 2015). Nonetheless, there is a clear bias in the literature towards studying Hymenoptera and Lepidoptera and the lack of data on other important pollinator groups (e.g. Aves and Diptera; Ollerton, 2017) precludes conclusions and highlights the need for future studies.

The climatic region of the study was not an important moderator of the effects of urbanization on pollinators. Urban development is a global phenomenon that leads to the convergence of urban environments (Santangelo et al., 2022). This global convergence of city environments could be the main driver of the observed declines in pollinator species richness, irrespective of the climatic region of the study. However, urbanization significantly affected the abundance of pollinators only in non-tropical regions. The lack of an effect of urbanization on tropical pollinator abundance could be due to the relatively small number of studies conducted in the tropics. Alternatively, it might reflect the overall high levels of urbanization and thus higher impacts on pollinators in non-tropical temperate regions (Elmqvist et al., 2013;

Faeth et al., 2011). Expanding current biased knowledge from temperate cities to include cities in tropical Asia and Africa will be of great importance, as these countries will experience most of the predicted global urban expansion in the coming decades (Huang et al., 2019).

Pollinators of native or non-native origin responded differently to urbanization. Non-native pollinator species richness increased, and native pollinator species richness decreased with urbanization. Our results suggest that cities might be hotspots of non-native pollinator species (Fitch et al., 2019; Normandin et al., 2017). This phenomenon could be driven by species that are introduced into cities through human activities, for example international commerce and urban beekeeping (Egerer & Kowarik, 2020). Following an introduction, a species' diet breadth, nesting behaviour and thermal tolerance might further facilitate its establishment in cities. Generalist species with strong preferences for exotic flowering plants, cavity nesters, as well as species with thermal tolerance that matches the urban conditions, are usually good urban invaders (Goulson, 2003; Hamblin et al., 2017). However, it is worth noticing that non-native pollinators may exacerbate conservation risks to native wild species by competition for floral resources, nesting sites or transmission of parasites and pathogens (Fitch et al., 2019).

Pollinator trait shifts

Species responses to urbanization are trait-specific (Buchholz & Egerer, 2020; Wenzel et al., 2020), and the implementation of ecological trait approaches for urban biodiversity conservation provides a mechanistic understanding of the relationship between biodiversity and urban environmental constrains. Urban landscapes can act as environmental filters for pollinator species depending on their ecological traits, facilitating or hindering their colonization and survival in cities (Buchholz & Egerer, 2020). In our meta-analysis, we found that the pollinator traits mainly affected by urbanization are those of Hymenoptera species that are related to nesting behaviour and sociality. Regarding nesting behaviour, our analysis confirmed the hypothesis that below-ground nesting bees are negatively affected by urbanization (Geslin et al., 2016; Neame et al., 2013). The increase in impervious surfaces with urban development and the intensive management of urban green land uses result in a reduction in the availability of suitable habitat (i.e. bare soil) for ground nesting bees (e.g. Andrenidae, Halictidae, Colletidae; Potts et al., 2005; Pereira et al., 2021). Sociality is also hypothesized to be an important trait related to urban environmental filters (Wenzel et al., 2020). In our meta-analysis, we found that the abundance of solitary bees was negatively affected by urbanization. The lack of ecological and behavioural flexibility, as well as their relatively small population sizes compared to social bees, might be the main drivers of solitary bee abundance declines with urbanization (Banaszak-Cibicka & Zmihorski, 2012; Chapman & Bourke, 2001).

Although the pollinator activity length was not affected by urbanization, we found seasonal variation in the effects of urbanization on pollinator communities. Urbanization had strong negative effects on the abundance and richness of spring pollinator communities. As suggested by previous studies, this might be driven by the scarcity of early spring and spring-blooming shrubs and trees in cities and thus the overall lack of early spring and spring food resources for pollinators (Matteson et al., 2008; Twerd et al., 2021). Solitary bee species that are ground-nesters and spring flyers (e.g. Andrenidae) are at increased risk due to urbanization, and conservation efforts should be primarily directed towards increasing spring floral resource availability as well as nesting opportunities for those pollinators in cities (Banaszak-Cibicka & Zmihorski, 2012).

Pollinators differ in their life-history traits; however, they all depend on floral food resources for their survival (Willmer, 2011). Floral resources are a limiting factor for the populations of all pollinators (Willmer, 2011). Furthermore, there is a strong relationship between flowering plant species richness and pollinator richness in a community (Ollerton, 2017). Our meta-regression analyses revealed this intrinsic link between flowering plant richness and pollinator diversity. This relationship is of great conservation importance as it reinforces current pollinator initiatives (e.g. Royal Horticultural Society 2021, 'Plants for Pollinators' initiative) that argue for flower plantings to promote pollinator diversity.

Pollination services

In our meta-analysis, pollination services, estimated as seed set or flower visit duration, increased with urbanization in non-tropical regions. Pollination could be influenced by pollinator visit quantity and 'quality' as well as by the structure of the local flowering plant community that could influence visitation rates (Bruckman & Campbell, 2014). The increase in flower visit duration as well as seed set in cities point to the importance of the 'quality' of the pollinator in terms of the number of compatible pollen grains deposited on stigmas (Ne'eman et al., 2010). The increase in flower visit duration in cities suggests a lack of a dilution effect and pollination efficiency due to the potentially high supply of floral resources in urban green land uses. Plants with radial flower morphology particularly benefited from urbanization, because they typically have shallow, exposed nectaries, making both nectar and pollen easily available to flower visitors (Willmer, 2011). Plants with these floral traits are thought of as generalists (Ollerton et al., 2007) and are visited by many wild pollinator taxa including

generalist and managed bee species that could be abundant in cities.

The positive effect of urbanization on pollination in non-tropical regions was driven by generalists and managed bee species (*Bombus* and *Apis*). *Bombus* and *Apis* bees are abundant in urban areas and among the most important pollinators in both natural and agricultural ecosystems (Bennett & Lovell, 2019; Garibaldi et al., 2013; Hung et al., 2018; Kleijn et al., 2015). The increase in *Apis* visitation rates in non-tropical cities is probably due to urban beekeeping. Urban beekeeping is currently booming with both benefits and negative implications (Ropars et al., 2019; Sponsler & Bratman, 2021). Urban beekeeping might help with the pollination of urban agricultural crops and wild flowering plants and provide locally produced honey; however, it might also lead to resource competition with wild pollinators and to increased transmission of diseases between managed *Apis* bees and non-*Apis* wild pollinators (Proesmans et al., 2021; Ropars et al., 2019; Sponsler & Bratman, 2021).

Although, based on our results, it appears that urban generalists and managed pollinators provide better pollination services to flowering plants in non-tropical cities, the importance of a diverse pollinator community, should not be neglected in enhancing plant reproduction (Garibaldi et al., 2013). We thus argue that city authorities should regulate the intensity of urban beekeeping and future studies should further investigate the effects of non-native and/or managed pollinators on wild native pollinators and pollination in cities.

Future directions

In addition to discussing the results of our meta-analysis, we have highlighted some research gaps and below we provide three directions for future studies. Firstly, the current studies are geographically and taxonomically biased and empirical research is urgently needed from understudied regions especially in the tropics and developing countries (Maruyama et al., 2021), as well as from underrepresented pollinator groups (i.e. Aves, Mammalia and Diptera and Coleoptera of Insecta). Secondly, functional ecological studies of pollinators in cities are needed to investigate which traits influence their sensitivity to urbanization and may help predict how such pollinator responses affect pollination service provision (Buchholz & Egerer, 2020; Cohen et al., 2022). Examples of understudied traits of relevance to urban living include phenology, heat tolerance and mobility (Hamblin et al., 2017; Luder et al., 2018). Lastly, it is important to disentangle the role of various biotic drivers (e.g. competition between native and non-native species, managed and wild species, predation and parasitism), as well as abiotic factors (e.g. environmental stressors, landscape composition, urban green land-use type, size and connectivity, management practices) on pollinator assemblages in cities (Theodorou, 2022; Wenzel et al., 2020). This will allow us to better manage urban ecosystems to maximize the conservation of pollinators and pollination for food security, wild flower diversity, ecosystem stability and human welfare.

Conclusions

In summary, our meta-analysis showed that urbanization had overall negative effects on pollinator abundance and richness. We further highlighted that pollinator ecological traits as well as local floral resource richness could mediate the responses of pollinators to urbanization. Regarding pollination services, our results point towards the importance of generalist and managed bees for plant reproduction in urban areas. As cities are expanding worldwide (Huang et al., 2019; United Nations, 2018), more research in cities is needed to disentangle the underlying mechanisms of pollinator responses to urbanization and guide proper conservation actions to improve the quality of urban environments for pollinators, not only for the intrinsic values of preserving local biodiversity and ecosystem services but also for improving human physical and mental health by connecting city dwellers to nature (Dearborn & Kark, 2010; Mansur et al., 2022).

AUTHOR CONTRIBUTIONS

HL and CFY designed the study. HL and YDH collected and undertook data analysis. HL, PT and CFY drafted the manuscript and participated in data interpretation. All authors gave their final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

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DATA AVAILABILITY STATEMENT

The datasets we used in our meta-analysis are available from Dryad (https://doi.org/10.5061/dryad.dv41ns23r).

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SUPPORTING INFORMATION

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

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