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

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Abstract

Urbanisation 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 present a comprehensive meta-analysis, using 133 studies, on the effects of urbanisation on pollinator diversity and pollination. Our results confirm the widespread negative effects of urbanisation on pollinator diversity, particularly of Lepidoptera. Additionally, pollinator responses were found to be trait-specific, with below ground nesting, solitary, and spring flyers more severely affected from urbanisation. Meanwhile, cities promote a greater diversity of non-native pollinators, which may exacerbate conservation risks to native ones. Surprisingly, despite the negative effects of urbanisation on pollinator diversity, pollination services in cities are enhanced and mediated by the high flower visitation rates of abundant generalists and managed pollinators. We highlight that the richness of local flowering plants could mitigate the negative effects of urbanisation on pollinator diversity. Overall, the results demonstrate the varying magnitudes of multiple moderators on urban pollinators and pollination service provision and could help guide conservation actions for biodiversity and ecosystem function for a sustainable future.

Reviews and Syntheses

The effects ofurbanisation on pollinators and pollination:A meta-analysis

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Statement of authorship

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 final approval for publication.

Data accessibility statement

The datasets we used in our meta-analysis will be archived in Figshare.

Number of words, figures, tables, and references

The number of words in the abstract is 200, and in the main text is 4837.

There are five figures, two tables and 73 references.

Abstract

Urbanisation 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 present a comprehensive meta-analysis, using 133 studies, on the effects of urbanisation on pollinator diversity and pollination. Our results confirm the widespread negative effects of urbanisation on pollinator diversity, particularly of Lepidoptera. Additionally, pollinator responses were found to be trait-specific, with below ground nesting, solitary, and spring flyers more severely affected from urbanisation. Meanwhile, cities promote a greater diversity of non-native pollinators, which may exacerbate conservation risks to native ones. Surprisingly, despite the negative effects of urbanisation on pollinator diversity, pollination services in cities are enhanced and mediated by the high flower visitation rates of abundant generalists and managed pollinators. We highlight that the richness of local flowering plants could mitigate the negative effects of urbanisation on pollinator diversity. Overall, the results demonstrate the varying magnitudes of multiple moderators on urban pollinators and pollination service provision and could help guide conservation actions for biodiversity and ecosystem function for a sustainable future.

Keywords: urban, pollinator diversity, floral resources, functional traits, plant reproductive success

INTRODUCTION

Urbanisation 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 pollution with largely negative influences on wildlife (Grimm *et al.* 2008; McKinney 2008). Urbanisation can affect individual fitness, life-history traits, population dynamics, species interactions, community structure and ecosystem functioning (e.g., Gaston 2010; Buchholz & Egerer 2020; Theodorou 2022). As urban areas continue to expand worldwide (United Nations 2018; Huang*et al.* 2019), 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, the study of pollinators in urban areas is of great interest due to the potential role of cities as refugia for species affected by agricultural intensification and the great premise of urban agriculture for food security (Baldock *et al.* 2015; Baldock 2020; Theodorou *et al.* 2020b; Wenzel *et al.* 2020).

In general, urban development has negative effects on pollinators (Faeth*et al.* 2011; Fenoglio *et al.* 2020; Millard *et al.*2021). Surprisingly, however, recent studies have also shown that urbanisation can have neutral or even positive effects on pollinator biodiversity (Theodorou *et al.* 2020b; Wenzel *et al.* 2020; Millard *et al.* 2021). These varying effects are hypothesised to be due to differences at multiple levels (McKinney 2008; Faeth *et al.* 2011). Firstly, taxonomic group, life-history and functional traits could influence how a pollinator species responds to urbanisation. Previous studies have shown that Hymenoptera insects seem to be more resilient to urbanisation compared to Diptera and Lepidoptera (Baldock*et al.* 2015; Fenoglio *et al.* 2020) and urbanisation seems to benefit large-bodied, social, cavity-nesting, generalist, as well as non-native species (Fitch *et al.* 2019; Buchholz & Egerer 2020). Secondly, the effects of urbanisation on pollinators could vary between climatic 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 high levels of urbanisation in the developed world (Elmqvist *et al.* 2013), the effects of urbanisation on pollinators are expected to be more severe in temperate compared to tropical regions. Thirdly, pollinators respond to the availability of local resources often irrespective of land-use change (Winfree *et al.* 2011; Murray *et al.*2012; Theodorou *et al.* 2020a). In moderately disturbed urban areas with abundant floral resources and continuity of floral resources, it is not surprising to document high pollinator biodiversity (Baldock*et al.* 2015; Theodorou *et al.* 2020b). All the above factors suggest that summarising a global pattern of the effects of urbanisation on pollinators is challenging and multiple moderators should be considered when attempting to do so.

Although we have a growing understanding of how urbanisation 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 urbanisation 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, urbanisation can affect abiotic and landscape features, the abundance of conspecific flowers and the diversity of flowering plants in an area. These factors may have an impact on pollinators' 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 specialisation may influence its reproductive success in cities. Native plants are generally preferred by pollinators (Chrobock *et al.* 2013) and plants with open radial flowers attract more flower visitors and may be less sensitive to the effects of urbanisation (Ollerton *et al.*2007; Willmer 2011). Recent studies have investigated the effects of urbanisation 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 cities driven by the high abundance of managed and generalist pollinator species (Theodorou *et al.* 2021; Theodorou 2022).

While there are some qualitative reviews on the effects of urbanisation on pollinators and pollination (Baldock 2020; Buchholz & Egerer 2020; Wenzel *et al.*2020; Ayers & Rehan 2021; Maruyama *et al.* 2021; Silva *et al.* 2021), only two meta-analyses investigated the overall effects of urbanisation 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 urbanisation are on taxonomic group and origin (native vs. non-native) of the pollinator species, climatic region of the study and local floral food resource availability. We furthermore assess how urbanisation influences the phenology and seasonality, sociality, nesting behaviour, diet, and body size of pollinator communities. Finally, we investigate the potential effects of urbanisation on pollination service provision.

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 urbanisation on pollinator diversity, 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 urbanisation on pollinator functional traits. To search for studies that investigate the effects of urbanisation 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 in 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 the following two criteria: (1) studies that reported pollinator abundance and/or richness, phenology, nesting behavior, diet specialization, body size, sociality, fruit set, seed set and visitation rates along urbanisation gradients, or comparisons of urbanisation 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 urbanisation gradient studies. A total of 133 publications met our criteria (Appendix S2).

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 (natural, forest, rural, or suburban sites) versus urban (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 urbanisation 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 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 according to 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 supporting material and/or original datasets.

If a publication reported the results of several taxonomic groups or cities separately, each was considered to be 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 higher 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 (Fenoglio *et al.* 2020). For pollination services, in addition to the fruit and seed set, the number, rate and duration of visits were also extracted and used as proxies of plant reproductive success (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 urbanisation differ between pollinator groups, we classified them according to taxonomic affiliation; Aves, mammals, honey bees, bumble bees, other wild bees, Lepidoptera, Diptera, and Coleoptera.

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 databases (references see Appendix S2).

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). Due to data limitations, functional traits were collected mainly for Hymenoptera and Lepidoptera (for details, see Table 1).

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

Effect size calculation andhierarchical meta-analysis

We used Hedges' d , weighted by sample size, as our effect size.r -type and *statistic values* -type data were transformed into Cohen'sd and then into Hedges' d using standard mathematical formulas (Koricheva *et al.* 2013; Borenstein *et al.* 2021; Table S1). Hedges' d was calculated using the R statistical software (R Core Team 2021). In all cases, a negative value of Hedges'd reflects negative effects of urbanisation on pollinator communities. Effect sizes were considered statistically significant if their 95% bias-corrected bootstrap confidence intervals (CI) did not overlap with zero (Koricheva *et al.* 2013; Borenstein *et al.* 2021).

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 urbanisation on pollinator abundance and richness, flower abundance and richness, functional traits, and pollination separately. Second, we incorporated moderators, including the climatic region of the study, the origin of the species, the taxonomic group of pollinators, and the symmetry of the flowers. To assess the levels of the 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 the moderators on the effects of urbanisation 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 (Viechtbauer 2010; R Core Team 2021).

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. 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 publications and 837 observations reporting the effects of urbanisation on pollinator abundance (228), richness (147), phenology and functional traits (381), floral resources (58) and plant reproductive success (116; Appendix S2). The geographical distribution of the studies was clearly uneven (Fig. 1). More than three-quarters of the studies were carried out in two continents (Europe 39.8% and North America 36.8%), and the remaining studies were carried out in Asia (12%), South America (6%), Oceania (3%) and Africa (2.4%). Furthermore, 85.7% of the studies were conducted in non-tropical regions and only 14.3% were conducted in tropical regions. Most studies focused on bees and butterflies and a small number of studies involved moths, beetles, flies, and vertebrate pollinators such as mammals, bats, and hummingbirds (Appendix S2).

Pollinator abundance and richness

Overall, urbanisation 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]; $P < 0.001$; Fig. 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, $P < 0.001$). The taxonomic identity of the pollinator was not an important moderator of the effects of urbanisation on pollinator abundance (Table 2). Although this moderator was not significant, urbanisation had a significant negative effect on the abundance of Lepidoptera (Fig. 2a). The taxonomic identity of the pollinator was an important moderator of the effects of urbanisation on pollinator richness (Table 2). The richness of Diptera, Hymenoptera, and Lepidoptera was negatively influenced by urbanisation (Fig. 2b). When the Hymenoptera were divided into bumble bees, honey bees and other wild bees, the results were qualitatively similar. We did not detect an effect of urbanisation on bumble bee, honey bee or other wild bee abundance (Fig. S1).

The climatic region (tropical vs. non-tropical) did not explain the heterogeneity of the effects of urbanisation on pollinator diversity (Table 2). However, pollinators studied in non-tropical regions were more severely influenced by urbanisation than in the tropics (Fig. 2a). The origin of the pollinator was not an important moderator of the effects of urbanisation on pollinator abundance (Table 2), however, it was an important moderator of the effects of urbanisation on pollinator richness (Table 2). Urbanisation had a negative effect on native pollinator species richness and a positive effect on non-native pollinator species richness (Fig. 2b).

Flowering plant richness had a positive effect on pollinator richness (F = 5.838, P = 0.019; Fig. 3a, Table S2) and a positive effect, although not statistically significant, on pollinator abundance (F = 3.490, P = 0.065; Fig. 3b, Table S2). Flowering plant abundance did not affect pollinator biodiversity (Fig. S2, Table S2). Furthermore, urbanisation was not found to influence the richness and abundance of flowering plant species (Fig. S3, Table S3).

Functional traits

Regarding functional traits, urbanisation had a negative, although not statistically significant effect on body size (d = -0.16; 95% CI = [-1.46, 1.13]; p = 0.81, Fig. S4) and a positive, although not statistically significant effect on activity length (d = 1.34; 95% CI = [-0.6, 3.28]; p = 0.18, Fig. S5). Nonetheless, urbanisation had a strong negative effect on the abundance and richness of spring pollinator communities (Figs 4a & 4b).

Furthermore, urbanisation had a negative effect on the abundance of solitary bees and on the abundance and richness of below ground nesting bees (Figs 4a & 4b).

Pollination service provision

Urbanisation had an overall positive effect, although not statistically significant, on pollination service provision (d = 0.20; 95% CI = [-0.10, 0.51]; p = 0.19). The heterogeneity of the effect sizes was large and statistically significant (Q_t = 1543.29, df = 115, P < 0.001). The pollinator groups sampled in the studies that estimated pollination service provision differed significantly in their contribution to plant reproductive success (Fig. 5, Table 2). Honey bees significantly boosted plant reproductive success (Fig. 5). Flowering plants with radial flowers had an increased reproductive success with increasing urbanisation (Table 2, Fig. 5). The origin of plant species (native vs. non-native) did not explain the effects of urbanisation on pollination services (Table 2). Urbanisation had a positive effect, although not statistically significant, on the pollination of both native and non-native plants (Fig. 5). The five reproductive success indexes significantly explain the effects of urbanisation on pollination (Table 2), with positive responses in studies that estimated seed set and visitation duration; positive but not statistically significant responses for studies that measured fruit set and visitation rate and negative responses, although not statistically significant, for studies that evaluated the number of flower visits (Fig. 5). In addition, the richness and abundance of pollinators were not significantly related to pollination service provision (Fig. S6, Table S4)

Publication bias

The funnel plots were symmetric for body size and pollination service provision (Fig. S7, Table S5). Although the funnel plots of pollinator abundance and activity length were asymmetric (Fig. S7), the regression estimates using the Trim and Fill method did not change. Pollinator richness changed from significant to not significant; 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 S5). We interpreted asymmetry in funnel plots carefully given the small sample sizes e.g., for activity length, or the lack of bidirectional outcomes for the effects of urbanisation on some variables, e.g., pollinator richness, which have been found to decrease across a lot of study systems, and thus will inevitably lead to a biased plot.

DISCUSSION

Pollination is an important ecosystem function for both natural and anthropogenic habitats yet, the effects of urbanisation on pollinators and pollination are poorly known. In this study, we reviewed the literature and performed a meta-analysis on the effects of urbanisation on pollinators and pollination. Our meta-analysis revealed an overall negative effect of urbanisation on pollinator abundance and richness. The magnitude of the effect was dependent on the taxonomic group of the pollinator, its origin and functional traits. Furthermore, flowering plant richness had a positive effect on pollinator richness revealing the importance of local habitat resource availability for pollinators. Our meta-analysis also revealed that pollination services are enhanced in urban areas most likely due to the high abundance of generalist and managed pollinator species. Below, we expand on these results and discuss their implications for pollinator conservation in cities.

Urbanisation results in a drastic modification of habitats with negative effects on biodiversity (McKinney 2008). The negative effects of urbanisation 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 increase in impervious surfaces, habitat loss, fragmentation, and degradation as well as environmental pollution are the primary hypothesised drivers for the observed reduction of pollinator biodiversity in cities (González-Varo *et al.* 2013; Vanbergen & Initiative 2013). In addition to the overall negative effects on pollinator biodiversity, our results revealed that pollinator taxonomic groups differ in their sensitivity to urbanisation. Lepidoptera was the taxonomic group that was found to be most affected by urban development. Many butterflies and months require specific host plants for larval development and nectar consumption as adults and they appear to be very sensitive to urban environmental stressors such as heat island effects, air and light pollution (Ramírez-Restrepo & MacGregor-Fors 2017; Fenoglio *et al.* 2020; Callaghan *et al.* 2021). Due to their sensitivity to human disturbances, our results further highlight the suitability of Lepidoptera as a bioindicator taxon to quantify responses to urbanisation. Our results further demonstrate that Lepidoptera is the taxonomic group most at risk from urbanisation and should be prioritised for conservation in cities.

The climatic region of the study was not an important moderator of the effects of urbanisation on pollinators. As has been shown in a previous study (Fenoglio *et al.* 2020), urbanisation had a negative effect on pollinator richness in both tropical and non-tropical cities. Urban development is a global phenomenon that leads to convergence of urban environments (Santangelo *et al.* 2022). This global convergence of city environments could be the main driver of the observed declines of pollinator species richness irrespective of the climatic region of the study. Nonetheless, urbanisation significantly affected the abundance of pollinators only in non-tropical regions. This lack of an effect could be due to the relatively small number of studies conducted in the tropics. Alternatively, it might reflect the high levels of urbanisation and thus higher impact on pollinators in non-tropical temperate regions (Faeth *et al.* 2011; Elmqvist *et al.* 2013).

Species responses to urbanisation are trait-specific (Buchholz and 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 colonisation and survival in cities (Buchholz & Egerer 2020). In our meta-analysis, we found that the pollinator traits mainly affected by urbanisation are those related to nesting behaviour and sociality. In regard to nesting behaviour, our analysis confirmed the hypothesis that below ground nesting bees are negatively affected by urbanisation (Neame*et al.* 2013; Geslin *et al.* 2016). 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 hypothesised to be an important trait related to urban environmental filters (Wenzel *et al.*2020). In our meta-analysis, we found the abundance of solitary bees to be negatively affected by urbanisation. 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 urbanisation (Chapman & Bourke 2001; Banaszak-Cibicka & Zmihorski 2012). Although the pollinator activity length was not affected by urbanisation, we found seasonal variation in the effects of urbanisation on pollinator communities. Urbanisation 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 spring-blooming shrubs and trees and the overall lack of spring-foraging resources for pollinators in cities (Matteson *et al.* 2008; Banaszak-Cibicka & Zmihorski 2012). Solitary bee species that are ground-nesters and spring flyers (e.g., Andrenidae) are at increased risk due to urbanisation, and conservation efforts should be primarily directed towards increasing spring floral resource availability as well as nesting opportunities for those pollinators in cities.

Pollinators of native or non-native origin also responded differently to urbanisation. Non-native pollinator species richness increased, and native pollinator species richness decreased with urbanisation. Our results suggest that cities might be hotspots of non-native pollinator species (Normandin *et al.* 2017; Fitch *et al.* 2019). This phenomenon could be driven by species that are introduced into cities through human activities, for example, 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, nest sites, or transmission of parasites and pathogens (Fitch *et al.*2019).

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. 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 trivial, although rarely explored intrinsic link between flowering plant richness and pollinator diversity. This relationship is of great conservation importance as it reinforces current pollinator initiatives that argue for flower plantings to promote pollinator diversity.

In our meta-analysis, pollination services, estimated either as seed set or flower visit duration, increased with urbanisation. 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 urbanisation. Plants with radial flowers and a central cluster of anthers typically have shallow, exposed nectaries, making both nectar and pollen easily available to flower visitors (Willmer 2011). Plants with these floral traits are typically 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 urbanisation on pollination was driven by generalists (bumble bees) and managed bee species (honey bees). Honey bees and bumble bees are generalist pollinators and the most important pollinators in both natural and agricultural ecosystems (Garibaldi*et al.* 2013; Kleijn *et al.* 2015; Hung *et al.* 2018). The increase in honey bee visitation rates in 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 honey bees and non-*Apis* bees (Ropars *et al.* 2019; Proesmans*et al.* 2021; Sponsler & Bratman 2021). We argue that city authorities should regulate the intensity of urban beekeeping and future studies should further investigate the benefits and negative aspects of urban beekeeping for wild pollinators and pollination in cities. Nonetheless, based on our results, it appears that urban generalists and managed pollinators provide adequate pollination services to flowering plants.

In conclusion, our results provide evidence that urbanisation has negative effects on pollinator communities however these are not necessarily translated into negative effects on pollination service provision. While we acknowledge the small sample size for some of our moderators, our meta-analysis further highlighted that Lepidoptera are the pollinator group most affected by urbanisation, and that pollinator ecological traits as well as local floral resource richness could mediate the responses of pollinators to urbanisation. Regarding pollination services, our results point towards the importance of generalist bees as well as the managed honey bee for plant reproduction in cities. Overall, more research in cities is needed to guide conservation actions and policies for pollinators and pollination for food security and wild flower reproduction.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

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Figures and tables

Figure 1-5

Table 1-2

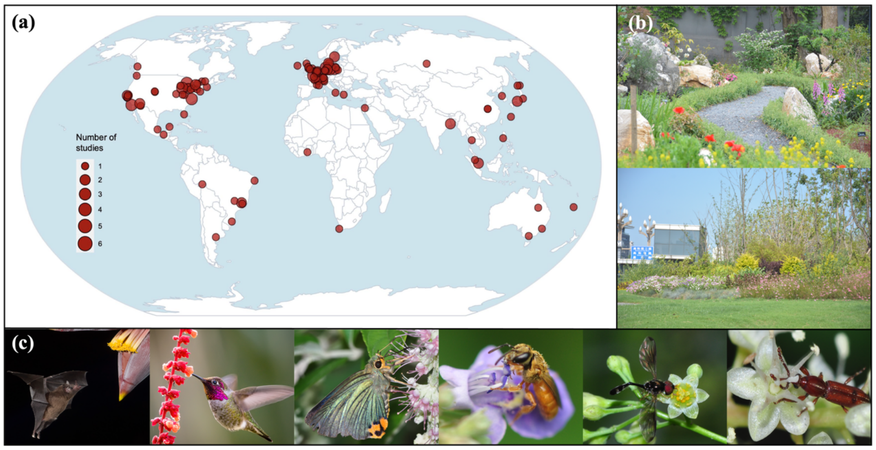

Figure 1 . (a) Distribution of studies included in the meta-analyses (N=133). Circle sizes are proportional to the number of studies. (b) Green space in cities, such as parks and road verges can support diverse pollinators. (c) Photos of representative pollinator taxa included in our database, left to right: mammals (e.g., nectar-feeding bat), Aves (*Calypte anna*), Lepidoptera (*Chaospes hemixantha*), Hymenoptera (*Halictus varentzowi*), Diptera (*Allobaccha apicalis*), and Coleoptera (Brentidae sp.). The first two photos were adapted from Flickr under Creative Commons license CC BY 2.0., taken by Doug Greenberg and Becky Matsubara, respectively. The other four photos were by Dr. Xiao-Fang Jin.

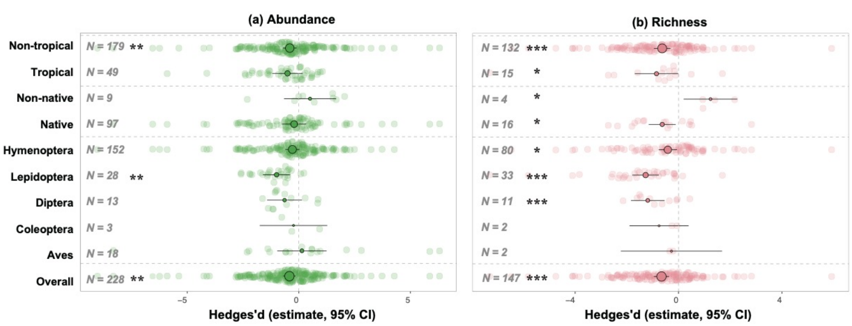

Figure 2 . Effects of urbanisation on (a) pollinator abundance and (b) richness. Estimated mean effect sizes, 95% confidence intervals and sample size numbers of three moderators (climate region, pollinator origin, taxonomic group) for explaining diversity are shown. *p < 0.05, **p < 0.01, ***p < 0.001.

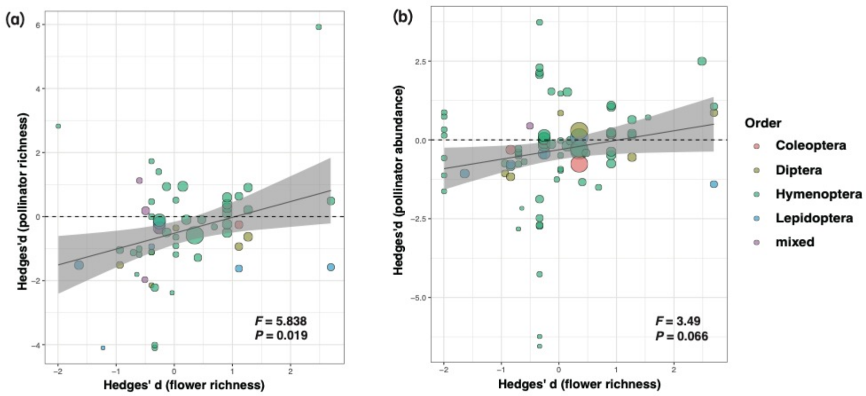

Figure 3 . Relationships between change in (a) flowering plant richness and pollinator richness and (b) flowering plant richness and pollinator abundance. The solid black line shows the predicted relationship and shaded areas indicate the 95% confidence intervals. Circles represent cases that investigated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

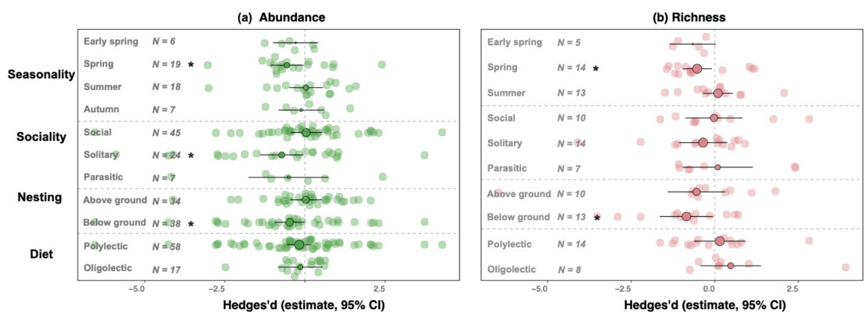

Figure 4 . Effects of urbanisation on seasonality and functional traits of pollinator (a) abundance and (b) richness. Estimated mean effect sizes, 95% confidence intervals and sample size numbers are shown. *p < 0.05, **p < 0.01, ***p < 0.001.

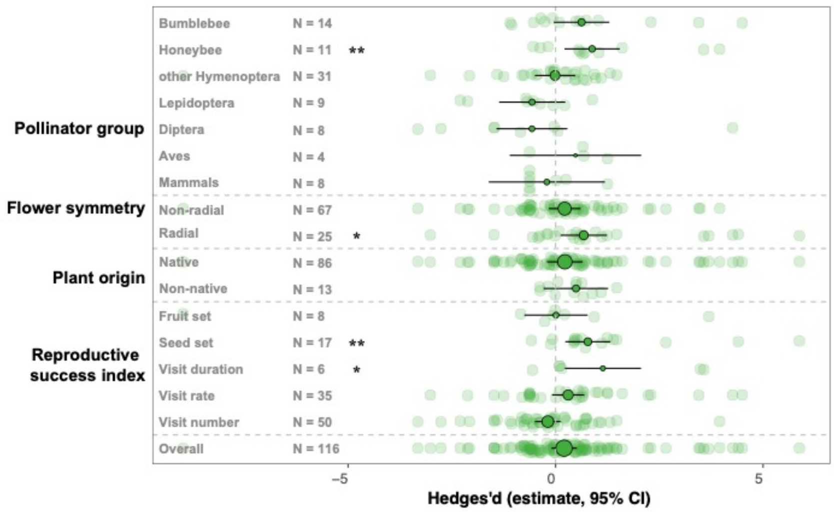

Figure 5. Effects of urbanisation on overall pollination services (N=116) depending on four moderators; flower symmetry, reproductive success index, plant species origin, and pollinator group. Estimated mean effect sizes, 95% confidence intervals and sample size are shown. *p < 0.05, **p < 0.01, ***p < 0.001.

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	-

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

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	Climate 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
Richness	Climatic region	147	1	0.23	0.63

Response variables	Moderators	Effect size	df	Q_m	p-value
	Pollinator origin	**20**	**1**	**9.91**	**<0.0016**
	Taxonomic group	**128**	**4**	**13.14**	**0.0106**
Pollination	Flower symmetry	92	1	2.05	0.15
	Reproductive success index	**116**	**4**	**14.90**	**0.0049**
	Plant origin	99	1	0.38	0.54
	Flower visitor group	**85**	**7**	**15.36**	**0.0371**

Note: Significant moderators are indicated in bold.

SUPPORTING INFORMATION

Figure S1-7

Table S1-5

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