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RESEARCH ARTICLE

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The effects of flower supplementation on pollinators and pollination along an urbanisation gradient

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Societal Impact Statement
Enhancing urban greenspaces for pollinator communities by planting flower patches is increasingly common, but their efficacy for different groups of insects (bees, hoverflies and moths) is unclear. Our city-scale experiment demonstrated that the effect of adding flower patches on pollinators is complex, and direct benefits to specific insects are difficult to detect. However, adding flower patches increased pollination services, with an increase in seed set in a model horticultural crop, particularly in more urban areas. Flower patches are likely to benefit pollinator communities and, in turn, humans through pollination services, but further research needs to disentangle the multi-level mechanisms driving variation in pollination and pollinators to improve the ecological and societal benefit provided by this management intervention.

Summary

- The addition of flower patches in human-modified ecosystems is a common practice to mitigate pollinator declines and boost pollination. However, the benefits of these additions for both pollinator communities and pollination services are rarely tested together, especially in urban environments.
- In a city-scale experiment, we added floral resources to urban allotments and monitored the effects on communities of bees, hoverflies and moths, and tested for improved seed set in a model crop (tomato, *Solanum lycopersicum*).
- The addition of flower patches had no detectable effect on allotment pollinator communities but led to a 25.3% increase in tomato seed set, providing evidence that flower patch augmentation can improve urban pollination. Seed set was relatively higher in more urban sites, suggesting an "oasis effect" where pollinating insects are concentrated when greenspace resources are limited. This highlights the precarity of pollination services in highly urban areas.
- Our results suggest that planting flower patches can positively affect pollination services in urban areas; however, the mechanisms remain unclear. Although we did not detect strong effects on pollinator communities when we added flower patches, differences in visitation networks between major pollinator taxa suggest that flower patch addition is likely to benefit some, but not all, insects, and further

research is needed to assess the suitability of current flower seed mixes for non-bee taxa. Overall, adding floral resources to urban systems may play an important role in supporting pollination but highlights the complexity of identifying the specific drivers and taxa underpinning this ecosystem service.

KEYWORDS
'bees', 'experimental flower additions', 'hoverflies', 'moths', 'pollination experiment', 'pollination', 'pollinator conservation', 'urban pollinators'

1 | INTRODUCTION

Pollination by insects is a crucial ecosystem service that is essential for terrestrial ecosystem function (Ollerton et al., 2011) and underpins 33% of global crop production (Potts et al., 2010). There are growing concerns for the resilience of this pollination service due to global insect pollinator declines (Potts et al., 2010; Powney et al., 2019; Wagner et al., 2021). In an effort to halt the declines in the abundance and diversity of key pollinator groups such as bees, there has been a surge in pollinator conservation schemes, driven by policy-led changes (Hall et al., 2017), actions and campaigns of NGOs and community groups, including direct conservation measures and public engagement (e.g. 'No-mow may' [Plant Life, https://www.plantlife.org.uk/] and 'Gardening for Wildlife' [RSPB, https://www.rspb.org.uk/]). These schemes may play an important role in supporting insect communities, making it important to understand their effects on the pollination of both wild plants and crops.

Floral resources (nectar and pollen) are vital for pollinator populations (Frankie & Thorp, 2009; Hicks et al., 2016), and there is strong evidence that floral resource availability affects the abundance and diversity of wild bee populations (Kennedy et al., 2013). Supplementing floral resources has therefore become a focus of pollinator conservation efforts, particularly in human-modified landscapes (Bommarco et al., 2013; Braman & Griffin, 2022). These measures can improve pollination services. For example, in conventional agricultural systems, wildflower planting in field margins and the restoration of hedgerows can offer abundant foraging resources and nesting sites for insect pollinators, and in some cases increase the yield of nearby insect-pollinated crops (e.g., Morandin & Kremen, 2013). The effect of floral additions on pollinators has been well-studied in agricultural contexts where the impact is generally positive (Haaland et al., 2010; but see Delphia et al., 2022). However, despite the rapid expansion of urban areas and a corresponding rise in urban agriculture, fewer studies have been conducted in cities. Consequently, the impact of floral additions at different scales in urban systems remains unclear.

The expansion of cities through the process of urbanisation has been shown to be a key driver of pollinator biodiversity declines (Wagner et al., [2021]). Despite this, there are important opportunities for insect conservation through the provision of floral resources within urban greenspaces. Within cities, there is an emerging willingness of the public to participate in conservation interventions. This engagement has been attributed to overwhelming evidence of the positive relationship between well-being and immersion in nature (Russell et al., 2013), the mental and physical health benefits of gardening (Gulyas et al., 2024) and the popular media coverage of the rapid decline in pollinating insects (e.g., 'Insect Armageddon', The Guardian, 2017). Public awareness of the benefits of insects, including pollinators, has facilitated the establishment of wildflower verges and pocket parks (e.g. the All-Ireland Pollinator Plan, https://pollinators.ie/), with the assumption that these interventions carry benefits for both insect wildlife and human well-being. However, empirical evidence for these benefits is still sparse and is crucial for providing informed management advice and optimising the effects of these interventions on urban wildlife.

Compared to agricultural land, greenspaces within cities can contain a high diversity of plants that are generally beneficial to pollinating insects (Baldock et al., 2015; Clarke & Jenerette, 2015). However, they are often interspersed in a matrix of impervious surfaces and other unsuitable habitat (McKinney, 2008), which limits the availability of these vital resources. Our understanding of how pollinating insects respond to urbanisation is limited due to the few comparative studies that examine the relative responses of both bee and non-bee pollinators (but see Ellis et al., 2025), especially insects that rely on non-floral resources for the completion of their life cycles as larvae, such as hoverflies (Diptera: Syrphidae, Bates et al., 2014; Baldock et al., 2015) and moths (Ellis et al., 2023; Lepidoptera, Ellis & Wilkinson, 2021). As a result, the links between urbanisation, insect community composition and pollination services in cities remain unclear.

The effects of resource availability on pollinator diversity, particularly non-bee pollinators, could have important implications for urban pollination services. Moths complement diurnal pollination networks and account for up to one-third of plant-pollinator interactions in urban plant-pollinator networks (Ellis et al., 2023) and have complex pollen-transport networks in agricultural ecosystems (Alison et al., 2022; MacGregor et al., 2019; Walton et al., 2020). Hoverflies are diurnal pollinators with divergent life-history traits from bees and have been shown to pollinate crops and wild plants, while also contributing to the biocontrol of pest species (Dunn et al., 2020; Jauker et al., 2012; Rader et al., 2020). Due to their non-floral resource requirements, it is likely that the addition of floral resources alone may not have the same benefits shown for bees (Moquet et al., 2018). However, despite their relative vulnerability to urbanisation (Baldock et al., 2015; Ellis et al., 2025; Theodorou et al., 2020), these taxa are rarely assessed when examining the benefits of habitat restoration or floral resource supplementation. Consequently, it remains unclear whether adding flower patches represents an optimal conservation practice that supports all pollinating insects.

Within cities, horticultural spaces such as allotments present unique opportunities to evaluate the benefits of floral resource supplementation along gradients of urbanisation. Allotment sites are large greenspaces with individual plots of land (~250 m^2) rented by individuals or households for growing fruits and vegetables (Dobson et al., 2020) that are dependent on insect pollination. These spaces support urban agriculture and contribute to social capital and mental well-being, extending benefits beyond the plot holders to their broader communities (Dobson et al., 2021; Gulyas et al., 2024). They are excellent spaces for evaluating civic engagement with pollinator conservation (Siegner et al., 2020). The increasing demand for allotments since the COVID-19 pandemic (Gulyas et al., 2024; Lin et al., 2021) underscores the substantial opportunities to enhance their ecological and social value. Moreover, allotments play a key role in fostering food production and promoting healthier diets. For example, it is estimated that UK fruit and vegetable production in allotments can supply more than 50% of the vegetables and 20% of the fruit consumed annually by growers, whose daily fruit and vegetable consumption is 70% higher than the UK national average (Gulyas et al., 2024). Given the crucial role of pollination in maximising many crop yields, the enhancement of pollinator habitats within allotments could further amplify their contribution to food production, thus reinforcing their value as key assets in urban food systems.

In addition to their societal benefits, allotments are among the most species-rich urban green spaces, boasting high plant (Borysiak et al., 2017) and insect (Baldock et al., 2019) diversity. Their wide distribution across urban areas provides an opportunity to simultaneously assess the effects of floral resource additions on pollinator diversity and crop production along an urbanisation gradient. Recent research has shown that pollen-transport networks of Lepidoptera and bees in urban ecosystems are disrupted by the densification of surrounding impervious surfaces and light pollution (Ellis et al., 2023; Herrmann et al., 2023; Macgregor et al., 2015). However, little is known about the consequences for crop production or whether resource supplementation could mitigate urbanisation's negative effects on different insect groups. Supplementing floral resources could increase crop yield through at least two mechanisms: 1) by increasing the number/diversity of visitors (e.g., Garibaldi et al., 2013) and/or 2) by increasing foraging intensity and subsequent pollination efficiency (e.g., Blaauw & Isaacs, 2014). We experimentally tested the benefits that supplemental floral additions have on pollinator community diversity and abundance and crop production in urban allotments and examined the scale dependency of these processes. At two scales expanding from local-flower patch additions to larger landscape-scale urban intensity, we tested whether enhancing floral resources can: (i) influence bee and non-bee pollinator diversity and abundance; (ii) improve pollination services (seed set) and (iii) modulate the impacts landscape-scale urban intensity has on insect communities and pollination efficiency.

2 | METHODS

2.1 | Study system

This study was carried out in 24 allotment sites throughout the growing season in 2020 (March–October) in Leeds, England (53°47′47.33"N, 1°32′52.26"W). The experimental allotment sites were chosen in eight independent groups (experimental blocks) of three sites. To distribute the blocks evenly and capture a broad representation of ecological variation and urbanisation across the city, we strategically selected blocks to radiate outward from the city centre to the administrative boundary (as in Edmondson et al., 2016, Figure 1a).

2.2 | Experimental design

Each experimental block had one treatment site and two controls (control 1, control 2, Figure 1a). The treatment site was assigned a floral treatment (Figure 1). In these sites, flower patches (~100 m^2) were sown with two nectar-rich seed mixes and seven trap nests (bee hotels) were installed (Supplementary Material Figures S1 and S2). The first control site had no experimental flower patches or trap nests

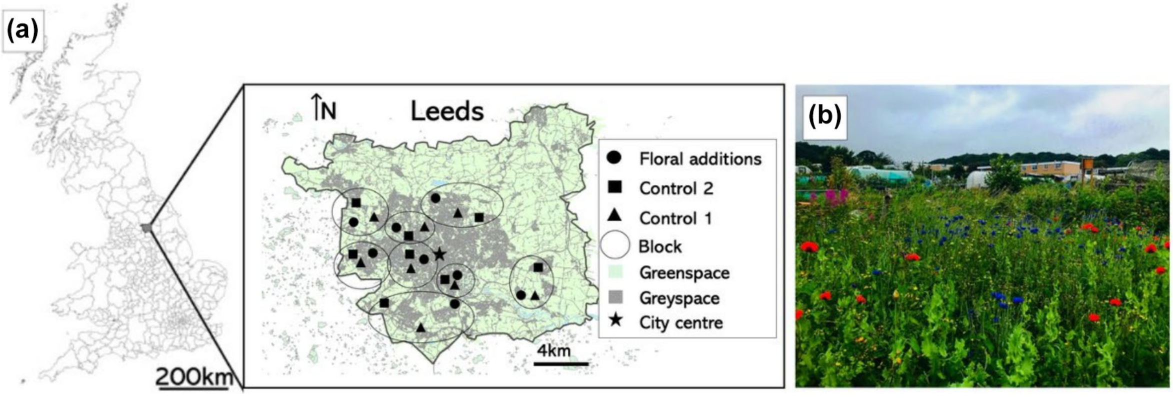

FIGURE 1 (a) Left: City of Leeds' location within the UK. Right: the site locations, treatments and block set-up along an urbanisation gradient from the city centre. (b) An example of a 100 m^2 flower patch added to an allotment site. Photo credit: Emilie Ellis.

added. The second control site had seven trap nests installed around the site (Supplementary Material Figures S1 and S2). The uptake in all trap nests was too low (< 2%) to allow statistical analysis, but we include these sites in our analysis to control for the effect of trap nests in the sites where flower patches were added. It is important to note that low uptake of bee hotels in the first year is not uncommon (MacIvor & Packer, 2015).

2.3 | Flower patch additions

Flower patches were established within 100 m^2 plots, either freely provided (as disused plots) or sublet from larger 250 m^2 allotment plots, with access granted by Leeds City Council and local allotment societies. Site preparation began in March 2020, once daily temperatures exceeded 6°C. Existing vegetation was trimmed to a height of 5–10 cm, followed by the application of glyphosate to suppress regrowth. The soil was then lightly tilled to create a suitable seedbed.

Sowing took place in April 2020, after further clearing of surface remaining vegetation, debris and stones. Seeds were distributed at a uniform rate of 3 $g\,m^{-2}$ using two commercially available nectar-rich mixes from Rigby Taylor©: (1) EuroFlor Native Pollinator™, a mix of native annuals, biennials and perennials, and (2) Banquet™, a mix of high-nectar annual and biennial species selected based on nectar sugar content (after Hicks et al., 2016, see species list in Supplementary Table S1). Due to lower-than-average rainfall in May 2020, plots were manually watered, but no additional maintenance was carried out for the remainder of the growing season, consistent with typical greenspace management practices. Some native wildflowers, such as *Cirsium vulgare*, also emerged naturally from the existing seed bank.

2.4 | Sampling protocols

To account for seasonal variation, insects were sampled on two occasions, first in early summer (20th May–2nd June) before the mass flowering in the flower patches and again in mid to late summer (20th July–17th August) when the flowers were in full bloom. We carried out intensive sampling at each site for each timepoint (Supplementary Material Table S2, Figure S2) and measured the species richness and abundance of three insect groups: hoverflies (Diptera: Syrphidae), bees (Hymenoptera: Anthophila) and nocturnal moths (Lepidoptera). We also measured the flower visitation networks of the bees and hoverflies. Due to the practical difficulty of observing moth-flower interactions (MacGregor et al., 2019), we did not measure moth visitation. Non-syrphid flies, despite being important pollinators (e.g., Tiusanen et al., 2016), were not included due to the limitations of our taxonomic skills.

To ensure that we captured a full representation of the communities at each site, we used a diversity of sampling methods. Passive sampling included pan traps and light traps. We also used active sampling (walking transects and static focal surveys) to gather information on flower species visited by pollinators, all of which are explained in turn below, and more details are included in Supplementary Material Table S2, Figure S2.

2.4.1 | Diurnal pollinators (hoverflies and bees)

Pan traps

To sample diurnal pollinators (bees and hoverflies), we randomly placed six sets of blue, yellow and white pan traps (diameter: 7 cm, height: 6 cm) around each site. Each pan trap was two-thirds filled with unscented soapy water and left for five days at each of the two sampling timepoints.

Transects and focal surveys

To record site-level insect visitation networks, on warm calm days (between 9 am and 5 pm), one 20-minute transect with a sweep net was carried out through the central path of each allotment site at each timepoint, and all insect-plant visitation (any event of an insect landing on a flower) was recorded. To test if the visitation patterns of insects were different in our manipulated flower patch addition sites compared to control sites, at each timepoint three 10-minute focal surveys were carried out on 0.5 × 0.5 m flower patches in both control sites and in the treatment sites. In the control sites, the focal surveys were conducted in three random flower patches around the allotment. In our treatment sites, at the first timepoint (before our experimental flower patches were flowering), these focal surveys were conducted in random flowering patches around the allotment (as in the controls). In our second timepoint, when the patches were in full bloom, the three focal surveys were all carried out in different areas of the experimental flower patch.

For both transect and focal surveys, all pollinators (bees and hoverflies) and the plants they visited were recorded to the lowest taxonomic rank and aggregated by site at each timepoint. Insects were identified on the wing where possible, and when field identification was not possible, they were collected to be identified in the lab. Bees were grouped into life history categories of social and solitary following Bees, Wasps & Ants Recording Society (BWARS) comprehensive life-history information (https://www.bwars.com/).

2.4.2 | Nocturnal pollinators (moths)

Nocturnal moths were sampled in each site during each sampling timepoint on calm, warm nights using a 12-V portable Heath Trap (NHBS product code SK22) equipped with a 15 W actinic bulb.

To ensure the sites within the blocks were closely related, we carried out each sampling method in each block's specific site within three days of each other at each timepoint. The order in which blocks were sampled in the first timepoint was randomised, and this randomisation was repeated at the second timepoint, as was the order of the three sites visited within the block, to minimise any temporal biases.

2.5 | Quantifying crop pollination

To quantify differences in pollination services across our treatment vs control, we used (*Solanum lycopersicum*, Montello-F1 bush variety) as phytometers at each site. Though tomato is predominantly pollinated by bumblebees (*Bombus* spp.), there is evidence that they also benefit from non-buzz pollinating visitors (Cooley & Vallejo-Marín, 2021). Tomatoes are commercially grown as annual plants with a global annual value of USD $10.8B (Cooley & Vallejo-Marín, 2021) and are also one of the most frequently grown fruits on allotments (Edmondson, Cunningham, et al., 2020). These attributes make them an excellent model system to quantify the ecosystem service of pollination in our study system.

Seeds of tomatoes were germinated and grown for one month in a controlled environment chamber before placement at our study sites. To ensure standard soil conditions for each tomato plant, they were planted in individual growbags (Tomorite Grow Bag). Six tomato plants (growbags), with two trusses of open inflorescences, were placed in each site during the mass flowering of the experimental flower patch additions. Four growbags were randomly placed around the site, and two were placed next to flower patches in our treatment sites. Standardised watering of all plants was carried out throughout the growing season. On each plant, one truss was bagged throughout the experiment with fine net (1 mm gauze) to prevent insect visitation and assess incidental site variation in self-pollination. To balance sample sizes between treatments and controls, we randomly selected three tomato plants from each control site for analysis, resulting in 48 plants in total for both treatment and control groups. After fruit set, three tomatoes were harvested from both the open and bagged trusses on each plant. All seeds were counted and used as a measure of pollination.

2.6 | Local tomato patch habitat mapping

To measure whether the addition of flower patches increased the habitat quality surrounding tomato plants, and whether this influenced seed set, we conducted visual surveys of the 4 m^2 area surrounding each tomato plant (see examples in Supplementary Material Figure S3), recording all habitat types and plant species present in July 2020. These habitat maps were then digitised using ImageJ (Schneider et al., 2012).

From these maps, we extracted two key variables: the local tomato patch species richness of flowering plants and the habitat heterogeneity using the Shannon diversity index (H) with vegetation/land use cover used as an abundance proxy (via the *vegan* package in R). As expected, flower species richness and habitat heterogeneity were strongly correlated (Adj. $R^2 = 0.65$, $p < 0.00001$; Supplementary Figure S4). Therefore, we used local tomato patch habitat heterogeneity (henceforth simply referred to as habitat heterogeneity) as the explanatory variable in subsequent analyses of seed set (see section: Model Fitting and Inference).

2.7 | Landscape urbanisation

Landscape-scale urbanisation was estimated for each site. We quantified the proportion of impervious space in a 250 m circular buffer surrounding each allotment using 'Manmade' land cover data from OS Mastermap in a geographic information system (ArcGIS version 10.7.1). We found that the area of impervious surfaces and distance from the city centre were negatively correlated ($R^2 = 0.37$, $p = 0.0017$, Supplementary Material Figure S5A), and across all sites, we captured a range of 18.4–81.7% gradient of impervious surface. There was some variation in impervious surface within each block despite being clustered spatially (Supplementary Material Figure S5).

2.8 | DATA ANALYSIS

All analysis was done in R version 12 (R Core Team, 2022).

2.8.1 | Sampling efficiency

We used the iNEXT package (Hsieh et al., 2016) to compute pollinator diversity estimates and explore our sampling efficiency. We used diversity estimates to ensure our treatment and control sites did not have uneven sample saturation/completeness. Specifically, we used sample-size-based sampling curves (i.e., a plot of the diversity estimates as a function of sample size). We first estimated treatment-specific species richness (across taxonomic groups and time points) to compare our sample efficiency across treatment sites and our two control sites. We then generated Shannon diversity estimates (a Hill number, which is the exponential of Shannon entropy) by using the observed sample of abundance to compute the estimate and associated 95% confidence intervals. We calculated estimated Shannon diversity values for each pollinator group at each site at each time point and used them as a pollinator community measure (response variable) in the analysis below.

2.8.2 | Modelling fitting and inference

Our analytical framework was designed to disentangle the multiple, scale-dependent drivers of pollination and seed set (Figure 2). The data encompassed multiple spatial and temporal resolutions, introducing complexities in model structure, particularly due to repeated measures and nested sampling. For instance, pollinator data were collected at two separate time points, seed set was measured per plant, per growbag and per site, while habitat features were characterised at the growbag (plant) level. Fitting all variables in a single model resulted in a rank-deficient (i.e., overfitted) model due to multicollinearity and insufficient degrees of freedom. To address this, we employed a hypothesis-driven, modular approach by grouping models into two thematic scales: **site-level** and **within-site**. This allowed us to explore broad treatment and landscape effects independently from finer-scale local drivers of pollinator and pollination variation.

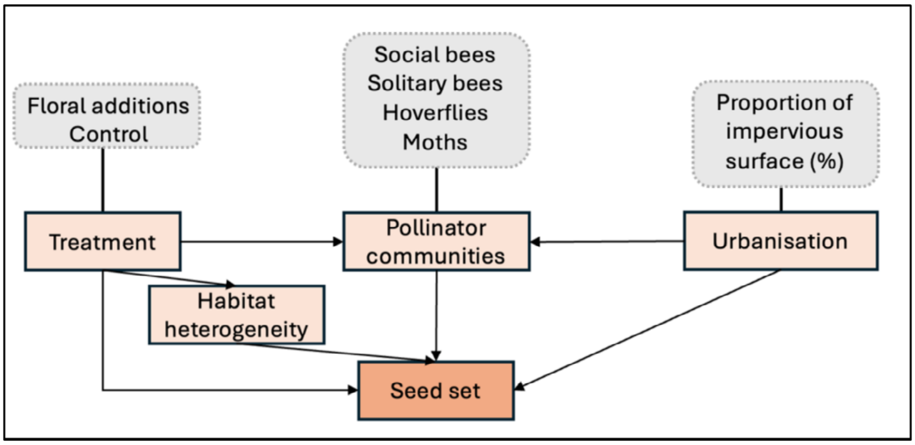

FIGURE 2 Visual representation of how our variables may be directly or indirectly linked to seed set (dark orange box). Orange boxes indicate different variables, and the arrows indicate the relationship tested between variables. Grey boxes show the levels of factorial variables, or the details of continuous variables.

We fitted linear mixed-effects models using the lme4::lmer function (Bates et al., 2015). Random effects structures were tailored to the resolution and replication of each response variable (see below). Where singular fits or convergence issues arose (notably in *Model 6*), models were simplified to fixed-effects structures (stats:lm, R Core Team, 2022) with equivalent random variables retained as fixed effects.

1) At the site level: We modelled log-transformed mean seed set per site as a function of treatment (flower patch vs. control sites), percent of impervious surface within a 250 m circular buffer of each site, and mean habitat heterogeneity (Shannon diversity index (H) of the habitat surrounding each growbag averaged per site). All two-way interactions were initially included, and Block was treated as a random effect to account for spatial clustering. Model weights were defined as the inverse of the squared standard error of site-level mean seed set estimates ($weight = {}^{1}/_{(\text{standard error}^2)}$):

$$\begin{aligned}\log(\text{mean seeds}) \sim\ & \text{Treatment} + \text{Proportion of impervious surface} \\ & + \text{Mean H} + [\text{two} - \text{way interactions}] \\ & + (1|\text{Block}), \text{weights} \\ & = \mathit{weight}\end{aligned} \quad (\text{Model 1})$$

To test whether pollinator diversity or abundance explained variation in seed set, we modelled log-transformed mean seed set against the log-transformed richness (Model 2) or abundance (Model 3) of moths, hoverflies, social bees and solitary bees, with Block again included as a random effect:

$$\begin{aligned}\log(\text{mean seeds}) \sim\ & \log(\text{moths} + 1) + \log(\text{social bees} + 1) \\ & + \log(\text{solitary bees} + 1) + \log(\text{hoverflies} + 1) \\ & + (1|\text{Block}), \text{weights} \\ & = \mathit{weight}\end{aligned} \quad (\text{Model 2 \& 3})$$

We next modelled how urbanisation and treatment across two different sampling timepoints influenced three different pollinator community metrics: species richness (Model 4), total abundance (Model 5) and estimated insect Shannon diversity (Model 6). All diversity metrics were log-transformed and modelled as a function of treatment, proportion of impervious surface, pollinator group (4-level factor: moths, hoverflies, social bees, solitary bees), time (early and late summer) and their two-way interactions. A random intercept for Block was included (except in Model 6).

$$\begin{aligned}\log(\text{diversity metric}) \sim\ & \text{Treatment} + \text{Proportion of impervious surface} \\ & + \text{Pollinator group} + \text{Time} \\ & + [\text{two way interactions}] + (1|\text{Block})\end{aligned} \quad (\text{Model 4, 5 \& 6})$$

For Model 6 (estimated insect Shannon diversity), we had to fit a linear model (stats:lm, R Core Team, 2022) with 'Block' as a main effect due to singularity in the mixed model approach. We also fitted this model with weights of the confidence intervals surrounding the estimated diversity measure: ${}^{1}/_{(\text{Upper confidence }95\% - \text{Lower confidence }95\%)}$.

In all cases, initial models were fitted to include all two-way interactions. Rather than arbitrarily removing variables, we used an information-theoretic model selection approach via the MuMIn::dredge() function (Bartón, 2025). This generated all possible subsets of the global model and ranked them based on AICc (corrected Akaike Information Criterion), enabling an unbiased selection of the most parsimonious models. We then selected the best model returned.

2) Within site level: This set of models explores how the addition of flower patches influences the within site local habitat heterogeneity measure (i.e. the habitat heterogeneity surrounding each tomato's growbag at each site):

$$\text{Local habitat heterogeneity} \sim \text{Treatment} + (1|\text{Block}:\text{Site}) \quad (\text{Model 7})$$

Then we tested whether habitat heterogeneity variation influences the seed set of the tomatoes it surrounds:

$$\log(\text{seed set}) \sim \text{Local habitat heterogeneity} + (1|\text{Block}:\text{Site}) \quad (\text{Model 8})$$

Where *log (seed set)*, the response variable, is the average seed set per plant (mean seeds of three fruits sampled on each tomato plant). *Block:Site* denotes a nested random effect structure to account for growbags sampled within the same site and block.

All models were checked for assumptions of linearity, homoscedasticity and normality using the 'performance' package (Lüdecke et al., 2021). Residual plots were visually inspected. Although initial models were fit on raw values, model assumptions were best met when both seed set and pollinator metrics were log-transformed (sometimes adding 1 to avoid undefined values at zero). The statistical significance of model terms was assessed using Type II Wald chi-square tests (analysis of deviance, car::Anova, Fox & Weisberg, 2019).

Our preliminary analysis revealed no significant differences between the two types of control sites (those with and without bee hotels; see Supplementary Material Table S3 and Figure S6). This finding justified our decision to combine these groups into a single control level for all subsequent analyses, ensuring a more streamlined and statistically robust comparison with our treatment sites.

2.8.3 | Network construction and analysis

We constructed diurnal networks based on field observations to compare the network structure metrics of hoverflies, solitary and social bees using (bipartite::networklevel, Dormann et al., 2009). Using the data from sweep net insect-plant observations (both line-transect and focal surveys), we constructed networks for 24 sites and calculated the following network metrics: total number of plants foraged on, linkage density and host range of insect species. These metrics were used to assess how their visitation patterns were influenced by our flower patch addition treatment and the surrounding urbanisation, following the model structure of *Model 4* outlined above.

3 | RESULTS

3.1 | Hoverfly, bee and moth communities in urban allotments

In total, 5,354 insects, belonging to 188 species, were collected and observed across the two sampling periods (Table 1). Sample coverage of pollinator communities was similar across treatments; overall, we sampled 50% of communities in control sites and 53% in treatment sites (Supplementary Material Figure S7, Table S4). The honeybee (*Apis mellifera)* accounted for 30% of the total insect community (n = 1,618), and bumblebees (*Bombus* spp.) made up 35% (n = 1,856). Moths were the most species-rich, with 108 species recorded (997 individuals) (Table 1; Supplementary Tables S5–S7 for full species lists). During the transects and focal collections, we recorded a total of 4,611 insect-plant interactions. In total, 171 plant species were visited (Supplementary Material Table S8), and the most visited plants were *Rubus* sp. (n = 472 visits), *Origanum vulgare* (n = 368 visits), *Centaurea cyanus* (n = 302), *Jacobaea vulgaris* (n = 253) and *Borago officinalis* (n = 249).

3.2 | The effect of flower patch additions on pollination and pollinators

Tomato seed set was 25.3% higher in sites where flower patches were present compared to control sites ($\chi^2 = 5.70$, $p = 0.017$, Figure 3a). However, there was no significant difference between pollinator abundance, species richness or estimated Shannon diversity in sites with flower patch additions compared to the control (Figure 3b–d, Supplementary Material Tables S9-S12).

Within our experimentally added flower patches, 47 species of plants were recorded (this was less than expected due to a drought in the spring). *Centaurea cyanus* (n = 203), *Borago officinalis* (n = 100), *Limnathes douglasii* (n = 56), *Symphytum officinale* (n = 51), and naturally regenerating *Cirsium vulgare* (n = 48), *Jacobaea vulgaris* (n = 30) and *Sonchus oleraceus* (n = 28) were the most visited flowers in the patches. At the site level, there was no significant difference in average habitat heterogeneity surrounding each tomato plant between treatment and control sites ($F_{[1,63]} = 0.7557$, $p = 0.39$; Figure 4a; Supplementary Material Table S13), but growbags directly adjacent to flower patches had higher habitat heterogeneity compared to other growbags within the same site (Figure 4a). However, we found no significant relationship between habitat heterogeneity and tomato seed set ($\chi^2 = 0.017$, $p = 0.89$; Figure 4b; Supplementary Material Table S9).

Variation in seed set was associated with taxon-specific pollinator community metrics, particularly in bees. Solitary bee species richness had a significant positive effect on seed set ($\chi^2 = 8.96$, $p = 0.0028$; Figure 4c; Supplementary Material Table S14) and social bee species richness had a marginally non-significant positive effect on seed set ($\chi^2 = 3.02$, $p = 0.082$; Figure 4c, Supplementary Material Table S14). The abundance of social bees also had positive effects on seed set ($\chi^2 = 4.76$, $p = 0.029$; Figure 4d; Supplementary

TABLE 1 Summary of the insect species richness and abundance of bees (social and solitary), hoverflies and moths collected in urban allotment sites in Leeds during the growing season 2020.

	Abundance		Species richness	
	Early summer	Late summer	Early summer	Late summer
Solitary bees	1,482	1992	27	22
Social bees	251	155	10	7
Hoverflies	73	404	17	30
Moths	524	473	83	58
Total	**2,330**	**3,024**	**137**	**117**

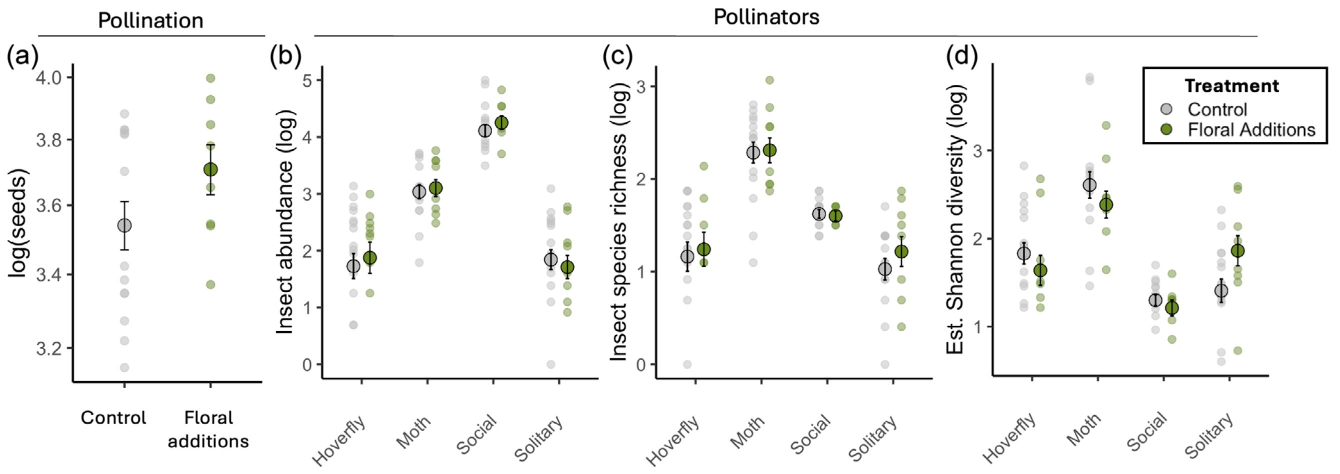

FIGURE 3 (a) Log-transformed average seed set per allotment site compared across treatment (flower patch addition) (green) and control (grey) sites. (b–d) Site-level pollinator metrics averaged across two timepoints, comparing the effect of adding flower patches on the: (b) abundance, (c) species richness and (d) estimated Shannon diversity of hoverflies, moths and bees (social and solitary). In all panels, transparent points represent individual site values and outlined points show treatment-level means ± standard error.

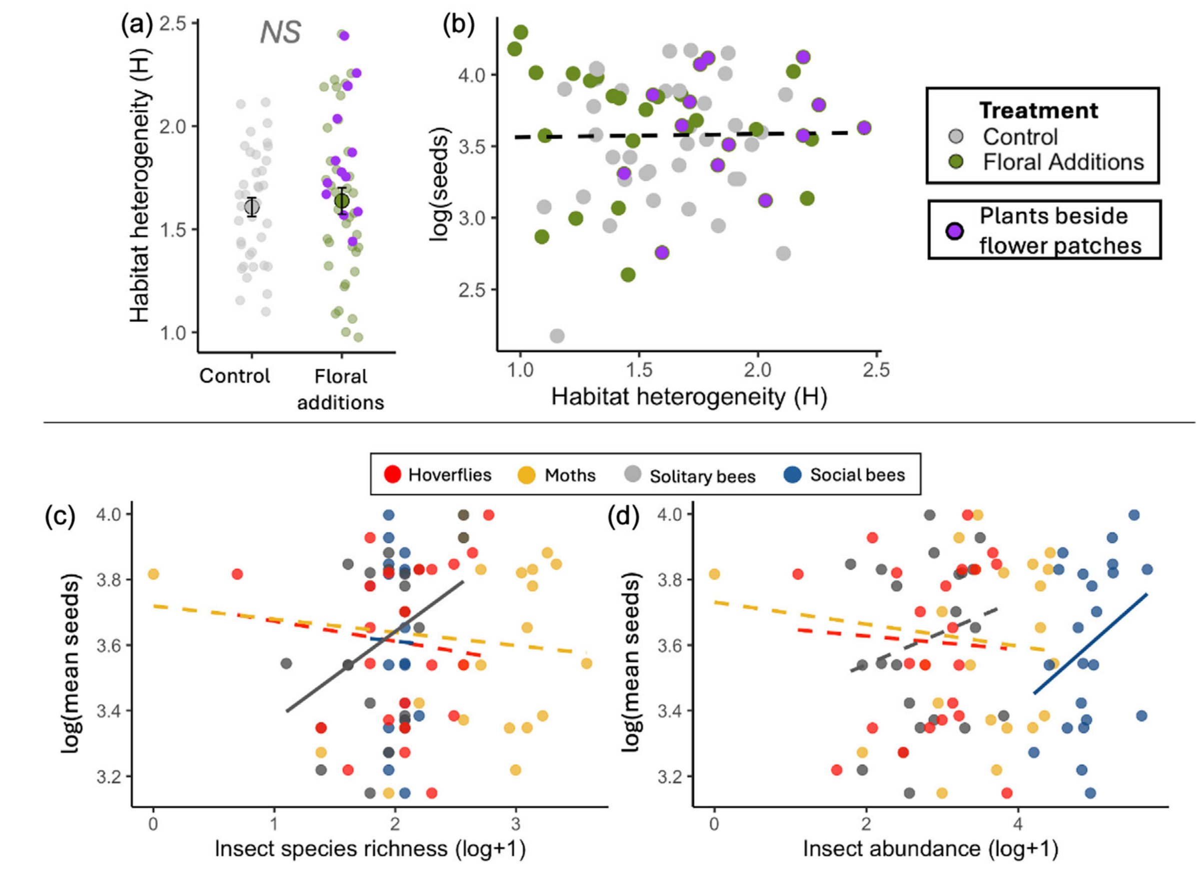

FIGURE 4 Relationships between local habitat heterogeneity, pollinator communities and tomato seed set. (a) Habitat heterogeneity values surrounding individual tomato plants in the flower patch addition (green) and control (grey) sites. Purple points highlight tomato plants located directly adjacent to the experimentally added flower patches. Outlined points indicate treatment means ± standard error. (b) Relationship between local habitat heterogeneity and seed set per plant (mean of three fruit), with point colours matching panel A. (c–d) Relationships between mean seed set per site (log-transformed) and pollinator community metrics: (c) total species richness (log + 1), (d) total abundance (log + 1), coloured by pollinator group: hoverflies (red), social bees (blue), solitary bees (grey) and moths (yellow). Solid lines indicate significant effects ($p < 0.05$) from linear mixed-effects models; dashed lines indicate non-significant trends.

Material Table S15). In contrast, there was no evidence of a relationship between seed set and variation in moth or hoverfly communities (Supplementary Material Table S14, S15).

3.3 | The effect of urbanisation on pollinators and pollination

We found that the proportion of impervious surfaces surrounding allotment sites had a positive effect on aspects of pollination services and pollinator communities. Sites with a higher percentage of surrounding impervious surfaces exhibited increased seed set ($\chi^2 = 10.44$, $p = 0.001$; Figure 5a), with no significant interaction between urbanisation and treatment.

Pollinator responses to urbanisation were taxon-specific (Figure 5b–d). Specifically, taxon-specific species richness and Shannon diversity exhibited significant interactions with impervious surface (species richness x impervious surface: $\chi^2 = 10.50$, $p = 0.015$; Estimated Shannon diversity x impervious surface: $F_{[1,3]} = 4.70$, $p = 0.004$). This was driven by a positive response of solitary bees to increasing impervious surfaces (Figure 5B and D; post-hoc test: $p < 0.05$; Supplementary Material Tables S10 and S12). Impervious surface had no detectable effect on overall insect abundance (Figure 5c).

3.4 | Visitation patterns of pollinators

Solitary bees, social bees and hoverflies visited distinct floral communities (Figure 6). Only 25% of the 171 plant species recorded were visited by both bees (social, solitary) and hoverflies. The addition of hoverfly-plant interactions increased the number of plant species visited by 14%, with 23 plant species exclusively visited by hoverflies. When bees were separated based on sociality, we also found distinct

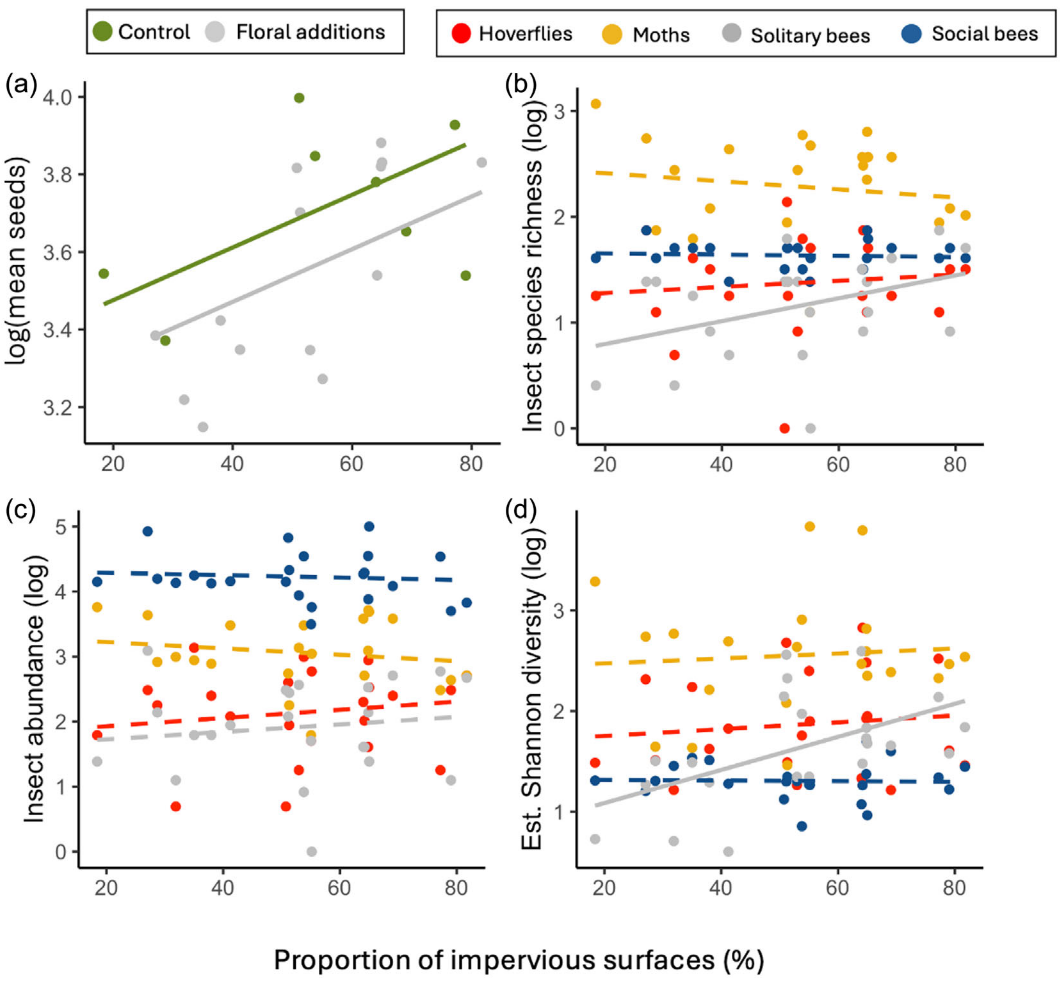

FIGURE 5 Effect of increasing impervious surface cover on pollination and pollinator communities. (a) Mean seed set per site, comparing treatment sites with added flower patches (green) and control sites (grey) along an increasing gradient of area of impervious surfaces (%). Parallel solid lines indicate significant main effects of treatment and urbanisation from a linear mixed-effects model. (b–d) Responses of pollinator communities to impervious surface cover: (b) species richness, (c) abundance and (d) estimated Shannon diversity. Colours indicate pollinator taxa: blue = social bees, grey = solitary bees, red = hoverflies, yellow = moths. Solid lines show significant taxon-specific effects of urbanisation ($p < 0.05$; post hoc test from urbanisation × taxon interaction), while dashed lines indicate non-significant relationships ($p > 0.05$).

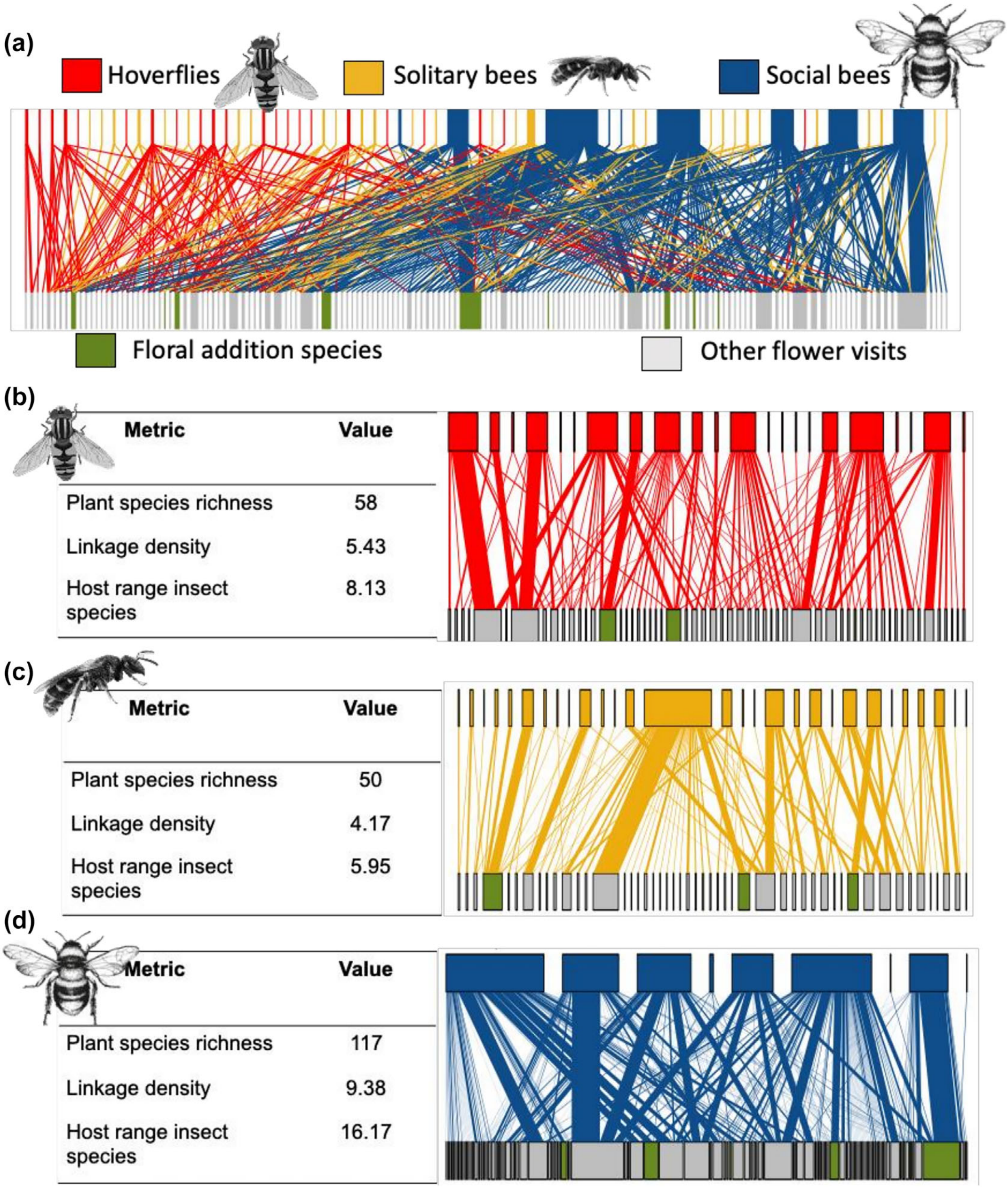

FIGURE 6 Bipartite networks showing the insect-plant visitations of diurnal pollinating insects including bees (social and solitary) and hoverflies in 24 allotment sites in Leeds, UK in the summer of 2020. (a) Shows all taxa in one network and illustrates the difference of visitation frequency across insect groups, the top nodes represent insect species (coloured by insect group) and lower nodes represent the plant species visited (coloured by plant species presence in the flower patches added to allotments) and size of node indicates number of occurrences (either insect abundance (top) or number of plant visits (bottom)). (b) the hoverfly visitation network with network metrics for the illustrated network, as (c) shows this for solitary bees and (d) for social bees.

plant communities visited by social (Apidae) and solitary (non-Apidae) species with only a 33% overlap (Figure 6). Social bees dominated the plant visitation observations, visiting more plant species, having higher individual host ranges and linkage density compared to solitary bees and hoverflies (Figure 6).

There was no change in pollinator-plant network structure (number of plants visited, linkage density and host range of insect) in sites with flower patches added compared to sites without additions (Supplementary Material Table S16).

4 | DISCUSSION

Our study demonstrates that incorporating flower patches into urban landscapes can enhance pollination services, as evidenced by up to a 25% increase in seed set of our model crop. Notably, we also found a positive relationship between urbanisation and pollination success, which is a result that challenges the conventional perception of urban areas as being at risk for poor pollination services. However, the lack of clear links between pollination and pollinators highlights the

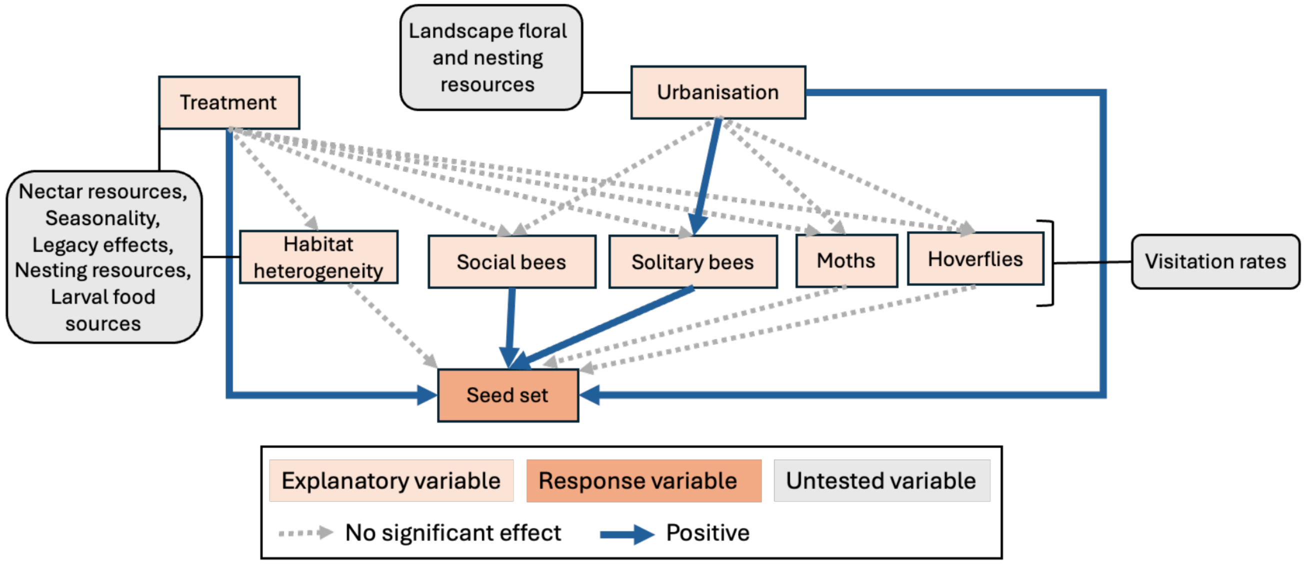

FIGURE 7 Summary of measured and potential drivers of seed set. Light orange boxes represent variables measured in this study, and the dark orange box indicates the response variable: seed set. Grey boxes denote additional variables not measured here but proposed for future investigation. Blue arrows show significant relationships identified in our analysis, while dashed grey arrows represent non-significant pathways.

difficulty of predicting the outcomes of urban pollinator conservation interventions (Figure 7).

While we observed clear benefits to seed set, these improvements were not directly associated with changes in local pollinator community metrics. Specifically, we found no significant changes in pollinator abundance or diversity following the addition of flower patches, nor did we detect significant impacts of local habitat quality on pollination success. Furthermore, local habitat heterogeneity did not appear to increase after flower patch augmentation when examined at a site level (Figure 4a). These patterns suggest that the enhanced seed set cannot be solely attributed to measurable shifts in pollinator community composition or habitat quality.

The disconnect between pollination success and pollinator community responses may have several possible explanations (Figure 7). First, unmeasured behavioural or ecological mechanisms such as changes in foraging behaviour, increased foraging efficiency, floral resource quality and quantity, or visitation by highly mobile taxa may underlie the observed pollination benefits, even without detectable changes in pollinator abundance or diversity. Second, our phytometer plants might better capture pollinator activity than traditional insect collection methods, potentially reflecting visitation patterns that standard surveys miss. Third, landscape-scale factors, including baseline floral availability, nesting habitat and other urban features, could mediate the effectiveness of floral enhancements in ways that remain poorly understood. Taken together, these results emphasise the complexity of urban pollinator interactions and caution against drawing simple mechanistic links between floral interventions and pollination services. They also highlight the need for future research to explore behavioural aspects of pollinator activity, detailed floral and nesting resource measures and alternative sampling methods to more fully understand how urban pollinator conservation efforts shape pollination dynamics.

To date, the supplementation of floral resources has been shown to enhance crop pollination, in both agricultural (Albrecht et al., 2020) and urban (Griffiths-Lee et al., 2020) settings. However, in both agricultural and urban contexts, habitat amendments can have complex, variable effects on pollination and on different pollinator populations, with many studies detecting no positive effects on pollinator communities (Griffiths-Lee et al., 2022; Wood et al., 2015). Of our two hypothesised mechanisms (either increasing pollinator abundance/diversity or enhancing foraging activity), our results suggest that flower additions boost foraging intensity and pollination efficiency rather than increasing insect species richness or abundance (as observed in Matteson & Langellotto, 2011). This discrepancy may arise from the attraction and redistribution of local pollinators, which then spill over to the experimental tomato plants (Harris et al., 2023). However, our data was unable to pinpoint these specific mechanisms. For example, although we observed higher local habitat heterogeneity and floral diversity near flower patches, this was not directly reflected in the seed set of the tomato plants adjacent to those patches (in contrast to Griffiths-Lee et al., 2020). Local habitat quality did not explain variation in seed set, suggesting that other factors were at play. We did observe a positive relationship between the abundance of social bees and the diversity of solitary bees with seed set, which was an expected result given that tomatoes are primarily visited by these groups (Cooley & Vallejo-Marín, 2021). Increased density of effective pollinators, rather than shifts in community diversity, may underlie the observed boost in seed set; however, a measure of visitation rates would be needed to truly quantify this (Figure 7). Finally, while our insect sampling was relatively intense (>5,000 insects sampled), phytometers have the advantage of integrating the cumulative pollination services across the flowering period and may thus provide a more powerful measure of differences in pollinator activity. To disentangle these processes and link pollinator communities to seed set, again, we suggest that future studies should measure actual visitation rates (e.g. by using camera traps (Alison et al., 2022).

Overall, the improvement in pollination efficiency carries significant implications for urban agriculture, where many allotment crops rely on effective pollination to produce higher yields and quality produce (Edmondson, Childs, et al., 2020). Thus, our results show that for urban growers, the addition of flower patches can enhance pollination and, therefore, food security. However, there is a need for future research to assess if these patterns are consistent for the diversity of important insect-pollinated fruit and vegetable crops.

4.1 | Urbanisation has complex direct and indirect effects on pollinators and pollination

Disentangling the drivers of plant-pollinator interactions as well as their pollination services is a difficult task, especially in intensely modified urban areas where there are both social and environmental factors to consider when assessing complex ecological interactions (Figure 7, Theodorou et al., 2020; McDougall et al., 2022). The counterintuitive increase in pollination in areas of greater urban intensity (Figure 5a) is potentially driven by an ecological process known as the oasis effect (as observed in Theodorou et al., 2020). Specifically, flower-rich sites (i.e. allotments) located within an inhospitable landscape (highly urban) may attract and retain insects from greater distances than sites in more floristically rich landscapes (less urban), leading to a concentration of foraging in more urban areas, which then enhances the pollination services provided. The strength of the oasis effect is likely to also depend on variation in a range of habitat quality measures, including host plant diversity and nesting sites, that are known to differ within and among greenspace types (Baldock et al., 2019); therefore, we predict that if the remaining greenspaces surrounding highly urban allotments are of high habitat quality for pollinators (e.g. gardens and allotments), the oasis effect would be weaker as foraging becomes more dispersed. Future research needs to explicitly test this by incorporating the diversity of greenspace habitat types in their analysis, to understand the nuances and variability of the oasis effect.

The oasis effect may play a key role in driving variation in ecosystem service delivery in urban environments. Specifically, the presence and frequency of oasis habitats may be particularly relevant for species with more limited foraging ranges, such as solitary bees. Consistent with this hypothesis, we found positive effects of increasing impervious surface cover on solitary bee diversity in our sites. Moreover, one of the most notable effects in our study was the positive relationship between solitary bee diversity and seed set (Figure 7). Thus, the benefits of the oasis effect may depend on how isolated "oases" are relative to the foraging distance of the effective pollinators. Other ecological factors, such as nesting requirements, are likely to influence this effect: solitary bees include both cavity- and ground-nesting species, which often respond differently to urbanisation (Wenzel et al., 2020), with ground-nesting bees more limited by sealed surfaces and reduced bare soil availability.

4.2 | There are distinct floral preferences for different pollinating taxa

Different taxonomic groups exhibit variation in the nectar and pollen rewards they seek (Tew et al., 2021; Matteson & Langellotto, 2011). Notably, most insect visitation was occurring on 'weedy' plants rather than those included in our sown flower patch mix (de Vere et al., 2017). This preference for distinct species that did not occur in our flower patches may explain the lack of a detectable effect on pollinator community diversity. We also found distinct flower communities visited by social bees, solitary bees and hoverflies, with only a quarter of the plant species visited by all three insect groups. Our network analysis suggests that solitary bees, hoverflies and social bees may provide complementary pollination roles for some plant species while acting as primary visitors for others. These relationships are likely shaped not only by the abundance and diversity of floral resources, but also their quality, including nectar sugar content, pollen protein and lipid content and floral accessibility (Tew et al., 2021) as well as seasonal availability (Sponsler et al., 2023). Early-flowering flower patches, for instance, could provide critical resources during periods of low floral availability in urban landscapes, supporting both early-emerging pollinators and their subsequent ecosystem services (Tew et al., 2022; Timberlake et al., 2024). Future work should therefore prioritise not just the quantity and quality of floral resources, but also their phenology and timing to ensure they align with the activity periods of diverse pollinator groups.

Consistent with previous research showing that social bees are among the most generalist pollinators (Kleijn et al., 2015; Ollerton, 2017), we found that they had the highest linkage density and diversity of flower visits. However, our results also underscore the importance of broadening conservation efforts to support a wider diversity of insect pollinators beyond the charismatic social bees (Ollerton, 2017). Urban allotments may offer a unique opportunity to engage the public in pollinator conservation, as many plot holders are already interested in nature (Dobson et al., 2021) and are likely to engage as citizen scientists with researchers to address applied questions around improvement in urban habitat management.

5 | CONCLUSION

Our study highlights the complex and often counterintuitive interactions that shape urban pollinator communities and the ecosystem services they provide. While the addition of flower patches did not directly enhance pollinating insect group abundance or diversity, they nevertheless increased pollination services, with important implications for urban food production. These findings add to a growing body of evidence indicating that effective pollinator conservation must consider the diverse resource and habitat requirements of different insect groups across their life cycles. Understanding these nuanced foraging and habitat needs, alongside the broader landscape context, will be essential for designing urban green spaces that support both biodiversity and ecosystem services.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

Data Availability Statement

All code was run using existing packages, which are cited in the manuscript. Please follow this link to access the datasets and code: DOI:10.5281/zenodo.17182071.

STATEMENT OF AUTHORSHIP

EEE, SAC and JLE conceived and developed the idea. EEE and SAC set up the field experiment. EEE carried out field and lab work. EEE analysed the data. EEE wrote the first draft of the manuscript, and all authors contributed substantially to subsequent revisions.

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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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