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## RESEARCH ARTICLE

# Effects of flower patch additions and urbanisation on cavity-nesting bees and wasps

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**Abstract**

1. Cavity-nesting bees and wasps provide essential ecosystem services such as pollination and pest control but can be negatively affected by urbanisation. Within urban environments, cavity-nesting hymenopterans use greenspaces to forage for food and nesting resources and may benefit from the addition of flower patches and 'bee hotels' (artificial nests).
2. While the addition of floral resources and artificial nests are common interventions to support urban pollinators, empirical validation of the tools in heterogeneous urban landscapes is still limited. Consequently, we lack empirical evidence to justify their widespread use, which could help optimise conservation interventions for these taxa.
3. To understand how the addition of floral resources influences cavity-nesting hymenopteran communities, we conducted a 2-year, city-wide study in urban greenspaces used for horticulture (allotments) in the United Kingdom. We manipulated floral and nesting resources by adding nectar-rich flower patches and artificial nests and compared nest colonisation by cavity-nesting bees and wasps and their associated parasitoid communities in sites with and without floral additions. Our sites were configured along an urbanisation gradient, allowing us to test whether interventions mitigate the complex effects of surrounding urbanisation.
4. We found no significant difference in artificial nest uptake in sites where floral resources were added, compared to control sites. Cavity-nesting hymenopteran abundance showed a six-fold decrease along our urbanisation gradient, but the negative effect of urbanisation was not mitigated by experimental addition of floral resources or by existing variation in floral resources at an allotment site. While the benefits of floral enrichment could likely be enhanced through an improved understanding of floral nutrition, our results suggest that, as commonly deployed, these interventions may carry fewer benefits for cavity-nesting bee and wasp communities than currently assumed.
5. *Practical implication:* Enhancing floral resources in urban areas is a widely used strategy to support pollinators, particularly bees. However, our results suggest that the benefits of such interventions depend on environmental variation and

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resource requirements among insect groups. Our findings highlight the need for conservation actions that move beyond single-taxon approaches and consider both local resource provision and landscape context.

#### KEYWORDS

bee hotels, cavity-nesting bees, cavity-nesting wasps, flower patch addition, pollinator conservation, trap nests, urban pollinators, urbanisation

## 1 | INTRODUCTION

The conservation of insects is vital to maintain ecosystem function and support the delivery of ecosystem services. Cavity-nesting hymenopterans (bee and wasp species that nest in cavities above ground) are a diverse group of insects that deliver essential ecosystem functions important to ecosystem service delivery in human-dependent systems, particularly pollination and pest control. Cavity-nesting bees provide pollination services to wild and cultivated plants (Brittain et al., 2013; Garibaldi et al., 2013; MacIvor & Packer, 2015; Winfree et al., 2008) and cavity-nesting wasps are effective predators of diverse arthropod pests, including lepidopteran caterpillars and aphids (Bianchi et al., 2006; Careless et al., 2014; Tschamtkke et al., 2005). Adult cavity-nesting wasps, like cavity-nesting bees, also feed on nectar and have been shown to provide an overlooked but effective pollination service (Brock et al., 2021; Mello et al., 2011). Current conservation efforts that enhance the availability of floral resources or provide nesting sites could therefore be important interventions to maintain or enhance both insect communities. However, the effectiveness of these conservation interventions remains poorly understood for cavity-nesting bees, and virtually unknown for cavity-nesting wasps, including both nest-building predatory taxa (e.g. Crabronidae, Sphecidae, Vespidae), and parasitoid and cleptoparasitic taxa (e.g. Chalcidae) that parasitise primary nest builders.

Urban areas pose a complex set of environmental challenges to insect communities. Greenspaces (e.g. parks, allotments, gardens, woodlands) are an integral part of the fabric of urban ecosystems. For example, in the United Kingdom, greenspaces cover up to 50% of a city's land area (Dennis et al., 2018; Edmondson et al., 2020). The complex mosaic of greenspaces, of varying habitat quality, interspersed across the urban landscape can act as refuges for numerous insect taxa, including Hymenoptera communities (Hall et al., 2017). However, greenspaces are not equally dispersed across the urban landscape and, in most cities, the proportion of urban greenspace declines along a gradient towards the city centre. These decreases in habitat availability are associated with declines in many insect communities, including, for example, moths (Ellis, Campbell, & Edmondson, 2025), butterflies (Kuussaari et al., 2014), wild bees (Herrmann et al., 2023) and hoverflies (Ellis, Campbell, & Edmondson, 2025). Multi-taxa studies have demonstrated differing responses among insect groups to urbanisation gradients (Baldock et al., 2015; Ellis et al., 2023; Ellis, Campbell, & Edmondson, 2025;

Herrmann et al., 2023; Theodorou et al., 2020), and these differences may be due to taxon-specific variation in specific greenspace use (Casanelles-Abella et al., 2024; Ellis, Campbell, & Edmondson, 2025; Ellis & Wilkinson, 2021; Rocha & Fellowes, 2018). As overall habitat availability declines in more urbanised areas, the quality of remaining greenspaces, including the diversity and abundance of nesting and foraging resources they provide, becomes increasingly important in mitigating the negative effects of urbanisation.

From an ecological perspective, urban greenspaces have become the focus of both research and pollinator conservation efforts, including initiatives like 'No Mow May', 'Save Our Bees' by the Wildlife Trust and the UK National Pollinator Strategy 2021–2024 (DEFRA, 2022). These schemes generally aim to mitigate the negative effects of urbanisation by increasing the density of resources available to pollinators through the conversion of less diverse greenspaces (e.g. homogeneous amenity grassland) to more diverse flower-rich areas. Originally planned by local authorities and conservation bodies as large-scale conversions, urban wildflower interventions are increasingly targeted at smaller areas (e.g. private gardens), which are better suited for space-limited urban habitats, and more easily implemented and maintained by local communities. Some studies suggest that wild bees, hoverflies and honeybees can benefit from the addition of relatively small (30–200 m<sup>2</sup>) flower patches in cities (Blaauw & Isaacs, 2014a) but some have also reported no detectable responses (Ellis, Edmondson, & Campbell, 2025; Matteson & Langellotto, 2011). These mixed outcomes often depend on the specific insect taxa being studied, the spatial scale of flower additions, and the location, suggesting that complex context-dependencies play significant roles in shaping insect community responses. Urban environments vary significantly in the amount and connectivity of greenspaces, and the benefits of additional floral resources are likely to depend on the quality of the surrounding habitat (Ellis, Campbell, & Edmondson, 2025). Understanding the efficacy of these schemes for different insect communities and in different environments is crucial to ensure that conservation interventions benefit diverse taxa.

The availability of nesting sites may also play a key role in determining the value of floral resource supplementation. Consequently, there has been growing interest in providing nesting habitats for cavity-nesting insects through artificial nests, commonly referred to as 'bee hotels' (MacIvor & Packer, 2015). While designed primarily to attract cavity-nesting bees, these interventions also support cavity-nest building wasps (e.g. Crabronidae, Sphecidae, Vespidae),

which are predominantly predators. Nest-building bees and wasps are, in turn, key prey for parasitoid and cleptoparasitic Hymenoptera (e.g. Chalcididae) that act as natural enemies for diverse arthropods. Like floral supplementation, the benefits of artificial nests may be context-dependent and constrained by the availability of other essential resources. In this context, the supplementation of nesting habitat in combination with floral resources could provide more effective support to cavity-nesting insects. However, empirical assessment of these interventions remains extremely limited, and whether they predictably benefit a broader range of taxa remains unknown.

Although cavity-nest building bees and wasps exhibit similar nesting habits and may utilise similar floral resources, there is substantial variation in their life histories which may result in differing responses to urbanisation (Wenzel et al., 2020). Cavity-nesting bees rely on floral resources throughout their life cycle: they provision their young with pollen and feed on nectar and pollen as adults (Frankie & Thorp, 2009). Dense urban areas may have reduced floral resource diversity (Ellis et al., 2023) and impose limits on the foraging range of bees, which may result in population declines for these Hymenoptera (Hernandez et al., 2009). Conversely, urban areas have been shown to increase cavity-nesting opportunities in built structures (Banaszak-Cibicka & Żmihorski, 2012; Hinners et al., 2012), which may compensate for habitat loss for cavity nesters relative to ground-nesting bees (Xie et al., 2022). Compared to bees, predatory and parasitic Hymenoptera may be more sensitive to urbanisation due to the complexity of their resource needs (Dürbaum et al., 2023), the diversity in their reproductive traits (Moretti et al., 2021) and/or their dependency on nest-occupying hosts. Consistent with this hypothesis, parasitoid wasps are more impacted by habitat reductions than their herbivore hosts (Nelson & Forbes, 2014) and cavity-nesting wasps that predate Lepidoptera and spiders have shown a strong negative response to increasing areas of impervious surface (Rocha & Fellowes, 2018). The dependence of parasitoid and cleptoparasitic wasps on cavity-nesting bee and wasp hosts also raises questions about potential trophic interactions that could limit the benefits of added resources. For example, the benefits of plant diversity for nest builders (Nelson & Forbes, 2014) could be offset by the recruitment of predators and parasitoids imposing top-down control of, for example, nest-dwelling bees. Therefore, there is a need to identify conservation interventions that support and enhance both these insect communities by buffering the negative effects of urbanisation.

We assessed the effects of supplementing floral resources on the uptake of artificial nests by cavity-nesting bees and wasps in urban horticultural greenspaces (allotments) along an urbanisation gradient in the city of Leeds, United Kingdom. We hypothesised that artificial nest uptake would be higher in sites with added floral resources due to the increased availability of nectar for both insect communities. We also hypothesised that these benefits would be taxon-specific and would be influenced by the negative effects of urbanisation, particularly the associated reduction of resources at a landscape level (Ellis et al., 2023; Ellis, Campbell, & Edmondson, 2025; Liang et al., 2023; Wenzel et al., 2020). We

experimentally manipulated floral resources by adding patches containing a common, commercially available mix of nectar-rich flower species and compared the species richness and abundance of bees and wasps in artificial nests over two years in sites with and without additional floral resources. We asked four questions: (1) Does the addition of common pollinator-friendly floral mixes enhance the uptake of artificial nests? (2) Does urbanisation affect the uptake of artificial nests by bees and wasps? (3) Are the effects of urbanisation mitigated by the wildflower interventions? (4) Do bees and wasps differ in their responses to floral additions, and/or urbanisation?

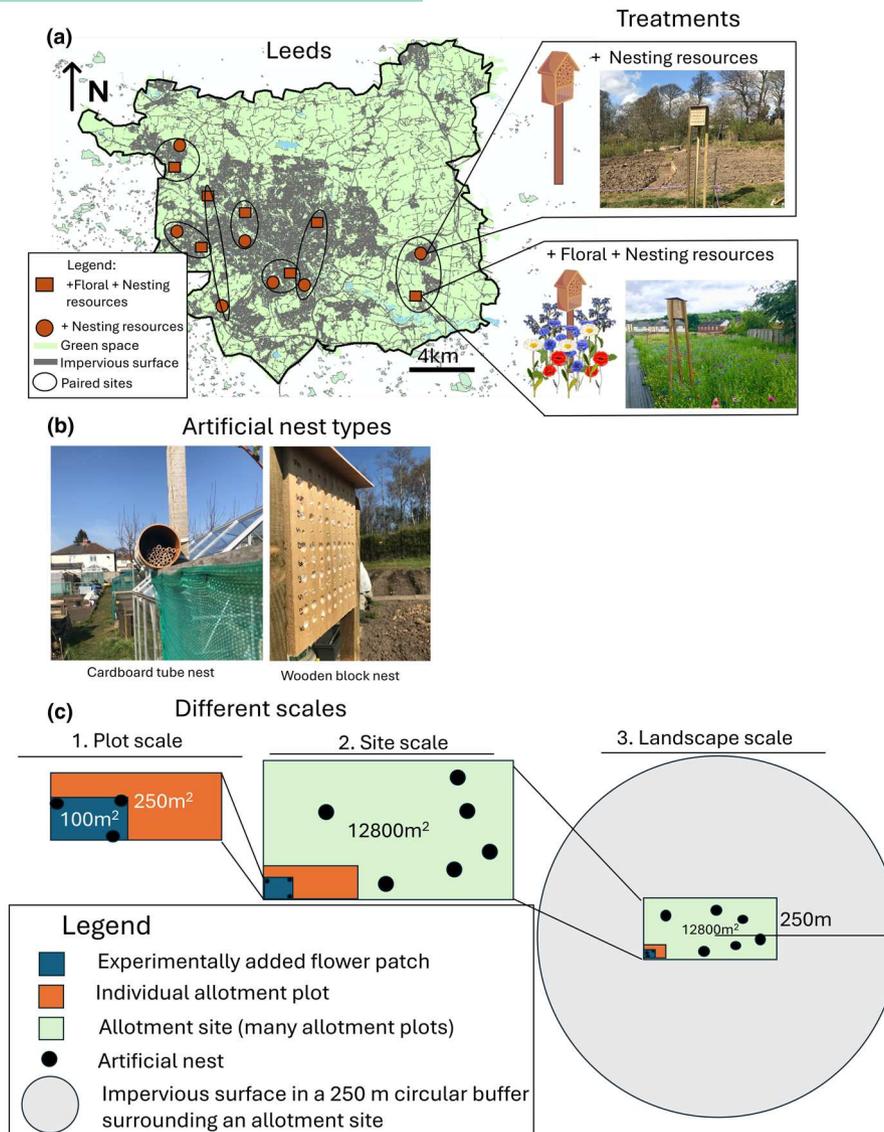
## 2 | MATERIALS AND METHODS

### 2.1 | Study system

This study was conducted in urban allotments. Allotments are urban greenspaces composed of plots of land rented by an individual or household for growing fruits and vegetables (on average, each allotment plot is ~250 m<sup>2</sup> in size; Bloomfield & Draycott, 2024). They have been identified as pollinator and flower hotspots in urban areas (Baldock et al., 2019), containing high insect diversity due to their high floral resources and habitat heterogeneity.

### 2.2 | Experimental design

We designed a city-wide experiment to test whether commonly used floral resource interventions benefit cavity-nesting Hymenoptera. This study was carried out in 16 allotment sites throughout the 2020 and 2021 growing seasons (March–October) in Leeds, England (53°47'47.33" N, 1°32'52.26" W). Leeds is a large city in Northern England with a population of 812,000 and a density of 1472/km<sup>2</sup> (<https://observatory.leeds.gov.uk/>). The sites were selected in eight pairs, with each pair consisting of two geographically close sites (or similar in their distance from the city centre if this was not possible). One pair was dropped from the analysis due to a failure of the artificial nests in 2021; thus, the final number was seven pairs (14 sites). Within each pair, allotment sites were separated by 1.54–8.87 km (mean ± SD = 3.90 ± 2.57 km; Figure S2), ensuring independence at the spatial scales considered. These pairs were positioned along an urbanisation gradient extending out from the city centre (Figure 1a). Within each pair, there was one site assigned nesting provisioning treatment where artificial nests were added to supplement nesting resources. The second site was assigned a nesting and a floral provisioning treatment. Here, ~100 m<sup>2</sup> flower patches were sown with nectar-rich seed mixes in March of each year as well as the addition of artificial nests (Figure 1; Figure S1). These patches are larger than common urban pollinator intervention experiments (e.g. Simao et al. (2018) (10 m<sup>2</sup>), Dietzel et al. (2023) (8 m<sup>2</sup>) and Griffiths-Lee et al. (2020) (1 m<sup>2</sup>) but similar to Blackmore and Goulson (2014)). In 2020, this experimental setup was also used to test the effects of flower patch additions on crop pollination (see Ellis, Edmondson,



**FIGURE 1** (a) A map of Leeds with allotment sites used in this experiment, showing the configuration of the paired site set-up along an urbanisation gradient towards the city centre (increasing area of impervious surfaces). Each site received a treatment (+floral + nesting or +floral), which is depicted by the shape of each site location. The right side shows the different treatments of our site pairs where floral and nesting resources were added, and the other sites that had only nesting resources installed (controls). (b) Artificial nest type 1: Cardboard tube nest, made of 8 mm cardboard tubing. Artificial nest type 2: Wooden block nests were made by drilling 5, 8, 10 and 12 mm holes in wooden blocks. (c) The three spatial scales at which patterns were analysed: (1) Plot scale, focusing on the flower patch within an allotment plot; (2) Site scale, encompassing the entire allotment area; and (3) Landscape scale, including the surrounding area within a 250 m radius of the allotment site.

& Campbell, 2025), with additional sites lacking artificial nests (excluded here due to the focus on cavity-nesting insects).

### 2.3 | Flower patch additions

Flower patches were established within designated 100m<sup>2</sup> areas (Figure S1), provided freely or rented as sub-plots of larger 250m<sup>2</sup> plots, sourced from Leeds City Council or local allotment societies for the duration of the study. Site preparation began in March 2020 when the daily temperature was above 6°C to prepare the ground

for sowing. Vegetation was initially cut down to a height of 5–10 cm; a glyphosate application was used to remove existing plants, and the soil was turned over to create suitable planting conditions.

Seedbed preparation and sowing were done in April 2020. Persistent weeds were removed and the surface debris and stones were raked off the topsoil. Seeds were sown at a constant density of 3g/m<sup>2</sup>. We used two nectar-rich seed mixes both provided by Rigby Taylor© (species list Table S1): (1) EuroFlor Native Pollinator™: composed of a native mix of annual, biennial and perennial flowers, (2) Banquet™ seed mix: composed of annual and biennial flowers chosen for their high nectar sugar content (after Hicks et al., 2016).

Plots were watered in May 2020 due to lower-than-average rainfall, but similar to comparable greenspace interventions, there was no further maintenance of the patches throughout the season. There was some regeneration of flowering species from the existing seed-bed (e.g. *Cirsium vulgare*). The flower patches were left with dead biomass over winter. In March 2021, the plots were cut back to 5 cm, gently raked, re-sown with additional seed mix. In order to facilitate biennial and perennial flower growth, we did not turn over the soil in Year 2.

## 2.4 | Artificial nests

As artificial nest design can influence bee uptake (Maclvor & Packer, 2015), we deployed two complementary nest types. We constructed artificial nests from PVC pipe filled with cardboard tubes ([www.masonbees.co.uk](http://www.masonbees.co.uk), diameter 8 mm; length 13 cm;  $n=25$  per PVC pipe; Figure 1b), henceforth referred to as cardboard nests. We also constructed wood nests from unprocessed pine wood (25×20×20 cm) which were drilled with 90 holes of different diameters (equal numbers of 5, 8, 10, 12 mm holes) and 13 cm in length (henceforth referred to as wooden nests; Figure 1b). Each hole was lined with parchment paper before being put in the field so that the larvae could be extracted in winter.

Each year, artificial nests were added in March and collected in October (to prevent mould and bacterial colonisation and empty tubes were cleaned in 2020 for placement in 2021). Nests were positioned 1.2–1.5 m off the ground using wooden stakes or the nests were attached to existing fences or trees, positioned south-facing in full sun.

In 2020, six cardboard nests and one wooden nest were placed at each of the 16 sites, for a total of 96. Due to an increase in technical assistance after the COVID-19 lockdown, in 2021, an additional two wooden nests were added to each site (total wooden nests  $n=3$  per site). However, in 2021, two sites (one pair) were excluded from the experiment due to the failure of artificial nest installation. In flower addition sites, a total of three artificial nests were placed at the experimentally added flower patch, and the remaining artificial nests were placed randomly around the site. In the control sites, all nests were placed randomly around the site (Figure 1c; Figure S1).

All colonised tubes from 2020 and 2021 were overwintered at 4°C and then incubated at 21°C starting in early March until all of the insects had emerged. Bees were identified to species level using Falk (2018). Wasps were identified to the lowest taxonomic level possible using the Bees, Wasps and Ants Recording Society's (BWARS) database (<https://bwars.com/>), resulting in family, genus and morphospecies identification. Wasps were subsequently classified as either cavity-nesting predators or as parasitoid/cleptoparasites of cavity-nesting hosts based on published life-history information in the BWARS database. We quantified three measures of nest uptake for both bees and wasps: (1) the total number of bees and wasps emerged (abundance), (2) the total number of species of bees and wasps (species richness), (3) functional diversity, based on feeding and life-history strategies: pollen-feeding bees; cavity-nest building

predatory wasps; and parasitoid or cleptoparasitic wasps that exploit the nests of cavity-nesting bees and wasps (based on information from the BWARS database).

## 2.5 | Habitat and landscape mapping

At each allotment site, a series of site-level and landscape-scale variables were estimated. We mapped the area of flowering plants (i.e. area of managed flower beds, wild flowering areas, flowering fruit and vegetable crops on each plot) in each site using visual surveys. These maps were then digitised in ImageJ (Schneider et al., 2012) and the area (m<sup>2</sup>) of flowers was extracted. The area of flowering plants was used as a proxy for floral resources at a site level. While this approach does not allow us to assess the beneficial effects of individual plant species due to nutritional differences in nectar and/or pollen, it does capture overall flowering plant availability and may be relevant to community-level studies of insects with diverse feeding preferences and nutritional requirements. For each allotment site, we quantified the level of urbanisation as the area of impervious surface surrounding the allotment sites, which was extracted from UK Ordnance Survey MasterMap© (<https://digimap.edina.ac.uk/>). Impervious surface included all land-types described as 'man-made', including buildings and roads. Circular buffers surrounding each allotment site, with the centre of the circle being the centre of the site, were drawn with a radius of 250 m (Figure 1c). The area of impervious surfaces (m<sup>2</sup>) was then exported and used for subsequent analysis. The 250 m buffer was selected to characterise local urbanisation because recent work conducted in the same city demonstrated that impervious surface measured at this scale was a strong and consistent predictor of insect abundance and species richness compared to larger buffer sizes (500 and 1000 m), although urbanisation effects were detectable across all spatial scales (Ellis, Campbell, & Edmondson, 2025). This scale effectively captures biologically relevant local urbanisation in fragmented urban landscapes (see Figure S2 for the distribution of impervious surface and distance from the city centre across sites and pairs).

All fieldwork was granted approval by the University of Sheffield ethics committee (application number O33331).

## 2.6 | Data analysis

All analysis was done in R version 4.1.2 (R Core Team, 2022).

We employed a two-level analytical workflow to account for processes operating at multiple spatial scales: (1) Since planting flowers in this context represents an individual action, our analysis began at the plot level (i.e. the 100 m<sup>2</sup> flower patch within its 250 m<sup>2</sup> allotment plot). (2) Given that colonisation of cavity-nesting bees and wasps is influenced by the broader environment surrounding each plot, we extended our analysis to the site-level (Figure 1c). First, we assessed whether our flower patch addition treatment increased floral resources compared to control sites, where no flowers

were added. At the plot level, for treatment sites, floral resource availability was calculated as the area of flowers within the 250m<sup>2</sup> plot containing the flower patches. In control sites, floral resource availability was determined as the average area of flowering plants across three 250m<sup>2</sup> plots where corresponding artificial nests were installed. To evaluate these differences, we fit simple linear models:

$$\log(\text{area of flowers}) \sim \text{Treatment}$$

Since allotment plots are embedded within larger allotment sites composed of multiple plots (see illustration; Figure 1c; Figure S1), we next examined whether our flower patch additions increased site-level floral resource availability. Using the same modelling approach as described above, we calculated the total floral area and floral density (area of flowers/area of site) for each site and compared it across treatments.

We then analysed how bee and wasp abundance, species richness and functional diversity were affected by the addition of floral resources, and the interaction of these terms using generalised linear mixed models (GLMMs). GLMMs were constructed using MCMCglmm::MCMCglmm (Hadfield, 2009) as the data was over-dispersed, zero-inflated and Poisson distribution assumptions were the best match. Credible intervals (CI) are derived from the posterior distribution of a parameter, which is sampled using the MCMC algorithm. We report the CIs as 'CI-95% [X, Y]', where X is the lower CI and Y is the upper CI. *p*-values were generated from the posteriors with standard parameter-expanded priors in MCMCglmm (pMCMC) and are defined as the probability that the estimate is negative or positive (whichever probability is smallest; Hadfield, 2009).

At the plot level, we focused on a subset of three artificial nests installed directly adjacent to the flower patch additions in treatment sites (and three corresponding nests in control sites). At the site level, we expanded the analysis to include data from all artificial nests (see Figure 1c). Due to many individual artificial nests having zero uptake, insect data were aggregated by taxa (wasp or bee), nest type (wooden or cardboard) and year at each site, resulting in eight observations for each site. The model incorporated key variables, including year (2020 and 2021), nest type (cardboard or wooden) and insect taxa (bees or wasps), as outlined below. The functional group analysis was the only exception where there were 16 observations per site (four functional groups in two nest types, across two years). All models adhered to the same structure, with site pair as a random effect:

$$\begin{aligned} \text{trap nest uptake measure} &\sim \text{Insect taxa} + \text{Treatment} \\ &+ [\text{Insect taxa} \times \text{Treatment}] + \text{Year} + \text{Nest type} + (1 | \text{Pair}) \end{aligned}$$

Finally, we evaluated the influence urban density (area of impervious surface in the 250m buffer surrounding each site; Figure 1c) has on the patterns of artificial nest uptake in allotment sites and whether floral additions, or existing area of flowers (site-level area of flowers) mitigated any urbanisation effects. Our models have the following structure:

$$\begin{aligned} \text{trap nest uptake measure} &\sim \text{Insect taxa} + \text{Treatment} \\ &+ \text{Area of impervious surface} + \text{Area of flowers (site scale)} \\ &+ [\text{two-way interactions}] + \text{Year} + \text{Nest type} + (1 | \text{Pair}) \end{aligned}$$

Due to the skewed species distributions, we also separately analysed how the four most abundant species/morphospecies (Chalcididae wasps, *Megachile ligniseca*, *Osmia leaiana* and *Hylaeus hyalinatus*, collectively accounting for 74% of the total abundance) varied by urbanisation and our treatment:

$$\text{Species abundance}_i \sim \text{Area of impervious surface} \times \text{Treatment} + (1 | \text{Pair})$$

where *i* denotes each species. In all analyses with multiple terms and interactions, any non-significant interactions were removed from the final model. Non-significant main effects are included in the final models and reported statistics.

Finally, because sites were in relatively close proximity to each other, we tested for spatial autocorrelation prior to modelling. For each year (2020 and 2021) and nest type (wooden and cardboard), we calculated global Moran's *I* (ape::Moran.I; Paradis & Schliep, 2019) for bee and wasp abundance and species richness using an inverse-distance spatial weights matrix derived from site coordinates. All tests were non-significant, indicating no detectable spatial autocorrelation and confirming that additional spatial structure did not need to be accounted for in the models (Table S2).

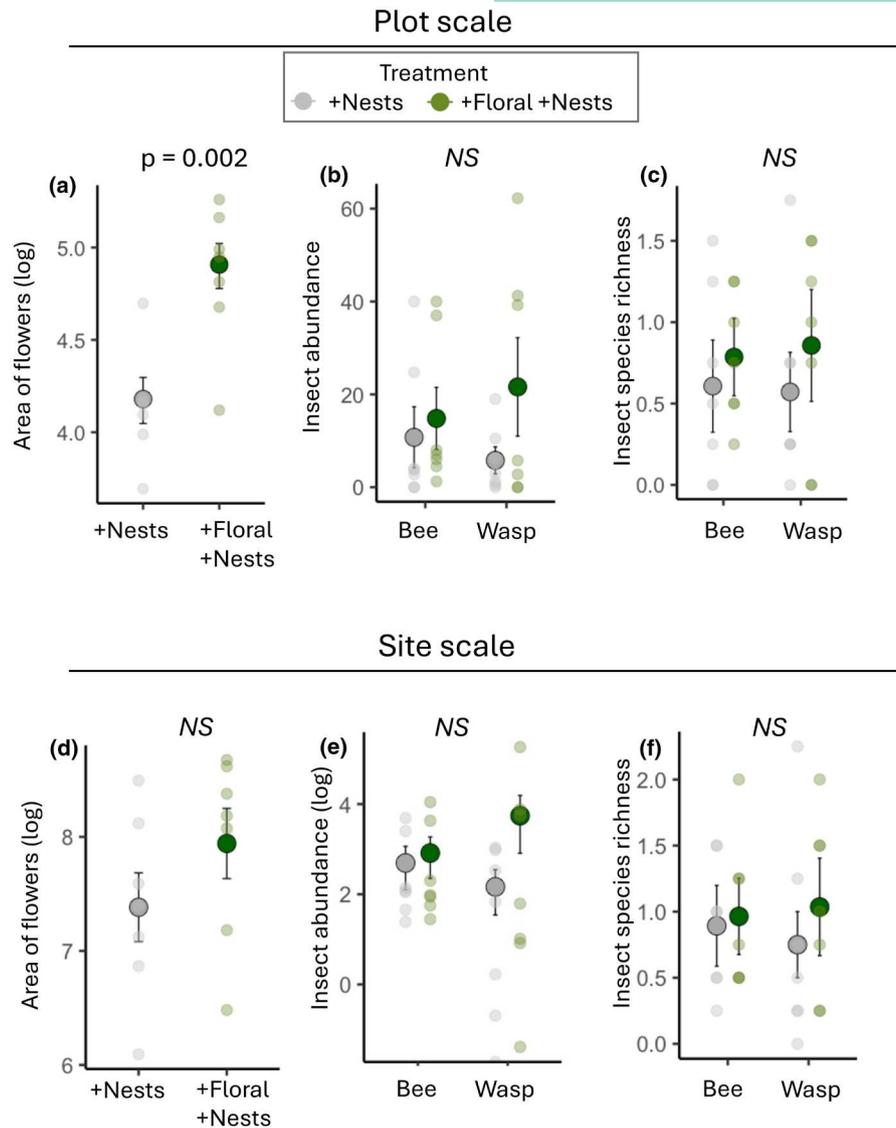
### 3 | RESULTS

The addition of flower patches increased the area of flowering plants by up to 20% in our treatment plots, compared to control plots ( $F_{(1,12)} = 14.59$ ,  $p = 0.0024$ ; Figure 2a). However, at a site level, there was large variation of floral area among sites, and we found no increase in overall floral area when our additional 100m<sup>2</sup> were added compared to control ( $F_{(1,12)} = 1.68$ ,  $p = 0.22$ ; Figure 2d).

Across the two years, a total of 2527 insects emerged from the artificial nests (Table 1). Twenty-five species or species groups colonised the nests, including eight bee species and 17 wasp taxa (Table 1; Table S3). Bees accounted for 39% ( $n = 979$ ) of all individuals, while cavity-nesting predatory wasps represented 20% of the community ( $n = 327$ ). The most abundant host species were the leaf-cutter bee *M. ligniseca* ( $n = 296$ ), followed by the mason bee *O. leaiana* ( $n = 211$ ) and the yellow-faced bees *H. hyalinatus* ( $n = 199$ ) and *Hylaeus communis* ( $n = 130$ ). The most frequently used cavity size was 8mm ( $n = 1191$  individuals), followed by 5mm ( $n = 376$ ), 10mm ( $n = 140$ ) and 12mm ( $n = 13$ ).

Natural enemies of cavity-nesting hosts, including parasitoid and cleptoparasitic wasps, accounted for a substantial proportion of artificial nest occupants (Table 1). Gregarious parasitic chalcid wasps were the most abundant group, with 1164 individuals, representing 46% of all insects recorded. These taxa exploit the nests of cavity-nesting bees and wasps rather than constructing nests themselves, highlighting the importance of trophic interactions in shaping artificial-nest communities.

Uptake was low in the first year (2020) with only 15 of the 112 artificial nests (13%) being used but increased to 41 of the 126 artificial nests (32%) in 2021 (Table 1). Both bees and wasps showed the same preference for wooden artificial nests compared to cardboard



**FIGURE 2** Plot-level (a–c) and site-level (d–f) responses across treatment (+Floral + Nests) and control (+Nests) allotment sites. (a) Area of flowering plants within the 250 m<sup>2</sup> allotment plot. (b) Total abundance of bees and wasps colonising artificial nests at the plot level (summed across artificial nests). (c) Species richness of bees and wasps colonising artificial nests at the plot level. (d) Total area of flowering plants at the site level. (e) Total abundance of bees and wasps colonising artificial nests at the site level (summed across all artificial nests within each site). (f) Species richness of bees and wasps at the site level. Darker points show treatment means ( $\pm$ SE), and lighter points represent site-specific observations. Colours indicate treatment: Grey denotes control sites (artificial nests only) and green denotes sites with floral resource supplementation (artificial nests + floral patches).

nests for both species richness (effect size =  $-1.38$ , CI-95% [ $-1.98$ ,  $-0.80$ ],  $p < 0.0001$ ) and abundance (effect size =  $-2.44$ , CI-95% [ $-4.29$ ,  $-0.64$ ],  $p = 0.009$ ).

The mean uptake of artificial nests of bees and wasps did not differ between taxa and all interactions between taxa and treatment were also non-significant ( $p > 0.05$ ; Tables S4 and S5 for full model outputs); thus, we report the average effects for both bees and wasps. There were no significant increases in nest uptake between treatments (floral additions vs control) at that plot scale (species richness: effect size =  $0.41$ , CI-95% [ $-0.13$ ,  $0.95$ ],  $p = 0.13$ ; abundance: effect size =  $1.46$ , CI-95% [ $-0.66$ ,  $3.55$ ],  $p = 0.15$ ) nor the site scale (species richness: effect size =  $0.09$ , CI-95% [ $-0.44$ ,  $0.57$ ],  $p = 0.74$ ; abundance: effect size =  $0.09$ , CI-95% [ $-1.89$ ,  $2.11$ ],

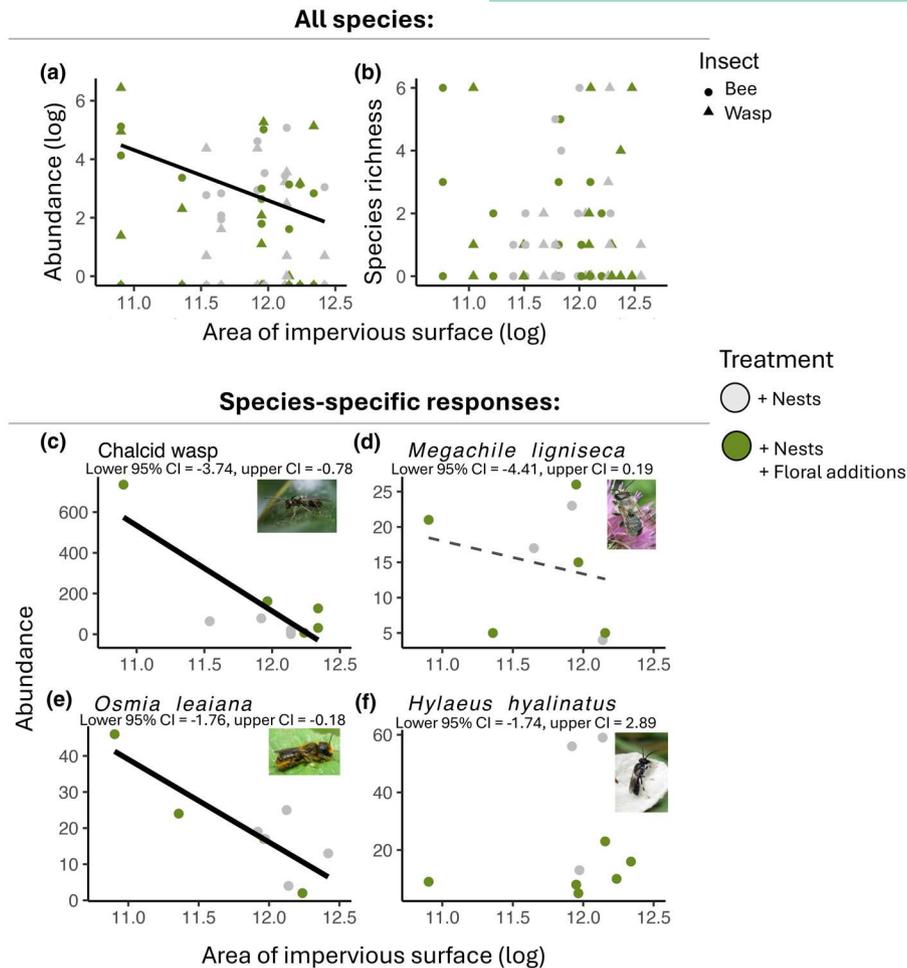
$p = 0.93$ ). Despite the fact we detected no statistically significant treatment effects, there was a trend of increased uptake in response to floral addition in abundance and richness in both bees and wasps, evidenced by the constantly positive effect sizes (see Figure 2). When individual functional groups were analysed, there was also no significant effect on the additional flower resources (Table S5).

Increasing urbanisation had non-interactive negative effects on the overall abundance of both bees and wasps (Figure 3a; effect size =  $-2.9$ , CI-95% [ $-5.82$ ,  $-0.05$ ],  $p = 0.034$ ); this effect was not mediated by floral addition treatment (no significant interaction: urbanisation  $\times$  treatment). There was no significant negative effect of urbanisation on species richness of bees and wasps (Figure 3b;

Identification	Trophic position	Nest type	Year 2020	Year 2021
Host species (nest-building taxa)				
<i>Eumeninae</i> spp.	Predator	Wooden	14	4
		Cardboard	17	6
<i>Passaloecus</i> spp.	Predator	Wooden	3	102
		Cardboard	0	0
<i>Trypoxylon</i> sp.	Predator	Wooden	0	1
		Cardboard	0	0
<i>Hylaeus communis</i>	Pollen feeding	Wooden	0	130
		Cardboard	0	0
<i>Hylaeus hyalinatus</i>	Pollen feeding	Wooden	0	199
		Cardboard	0	0
<i>Megachile centuncularis</i>	Pollen feeding	Wooden	0	20
		Cardboard	0	0
<i>Megachile ligniseca</i>	Pollen feeding	Wooden	0	238
		Cardboard	0	58
<i>Osmia bicornis</i>	Pollen feeding	Wooden	5	59
		Cardboard	37	15
<i>Osmia leaiana</i>	Pollen feeding	Wooden	0	96
		Cardboard	19	52
Natural enemies of cavity-nesting hosts				
<i>Chalcidae</i> sp.	Parasite	Wooden	0	599
		Cardboard	0	627
<i>Chrysis ignita</i>	Parasite	Wooden	0	14
		Cardboard	1	0
<i>Ichneumonidae</i> spp.	Parasite	Wooden	0	26
		Cardboard	0	0
<i>Sapyga</i> spp.	Cleptoparasitic	Wooden	0	12
		Cardboard	0	0
<i>Coelioxys inermis</i>	Cleptoparasitic	Wooden	0	2
		Cardboard	0	0

**TABLE 1** Summary table showing bee and wasp abundance, identified to the lowest taxonomic grouping (sp. denotes one species in the group and spp. denotes more than one species in the group) and assigned trophic position across artificial nest types (cardboard tubes and wooden blocks) and years (2020 and 2021).

Note: Host species include cavity-nesting bees and predatory wasps, while natural enemies comprise parasitoid and cleptoparasitic taxa that exploit the nests of cavity-nesting hosts.



**FIGURE 3** The effect of increasing urbanisation on (a) abundance and (b) species richness of bees (circles) and wasps (triangles) in our treatment sites (+nests and nests+floral additions). The effect of increasing urbanisation on the abundance of (c) Chalcid wasp, (d) *Megachile ligniseca*, (e) *Osmia leaiana* and (f) *Hylaeus hyalinatus*. Solid lines illustrate the significant overall effect of urbanisation (no interaction); dashed lines show some evidence of an urbanisation effect ( $p=0.08$ ; Table S6) and no line shows a non-significant effect of urbanisation ( $p>0.08$ ). Photo credit: Steven Falk.

effect size =  $-0.61$ , CI-95% [ $-1.51$ ,  $0.24$ ],  $p=0.13$ ) or when analysed at the functional group level (Table S5).

There was some evidence of species-specific variation in the response to urbanisation. Specifically, the abundance of mason bees (*O. leaiana*) and chalcid wasps declined with increasing urbanisation, with no treatment effect (Figure 3c,e; Table S6). There was also weaker (non-significant) evidence that the leafcutter bee (*M. ligniseca*) abundance was negatively influenced by urbanisation (Figure 3d; Table S6). Yellow-faced bees (*H. hyalinatus*) showed no response to increasing urbanisation (Figure 3f; Table S6).

## 4 | DISCUSSION

Pollinator conservation management strategies often focus on improving the provision of floral resources through habitat enhancement (Potts et al., 2005; Spivak et al., 2011), and commonly used approaches include the addition of flower patches or supplemental nesting habitat. However, the efficacy of these interventions is rarely

assessed while accounting for complex landscape heterogeneity associated with urbanisation, or for less charismatic taxa. Our city-wide manipulation experiment augmented both nesting and floral resources for a diverse community of cavity-nesting Hymenoptera to evaluate whether common pollinator interventions also provide benefits to cavity-nesters and mitigate the negative impacts of urbanisation. Contrary to prevailing assumptions, there were few consistent benefits of flower interventions over the 2 years of our study, although there was a trend of increased uptake overall. These results contrast with some prior findings for bees (Blaauw & Isaacs, 2014a, 2014b), but align with others (Matteson & Langellotto, 2011), highlighting growing uncertainty about the efficacy of these interventions. To the best of our knowledge, this is the first experimental test of whether these interventions affect cavity-nesters in urban systems. Even with the addition of floral resources, there remained an overall negative effect of surrounding impervious surface area on both wasp and bee colonisation of artificial nests. Our results suggest that 'pollinator-friendly' floral interventions may not carry the assumed benefits for cavity-nesting Hymenoptera.

Three non-exclusive mechanisms may explain the lack of significant effects from flower patch additions on cavity-nesting Hymenoptera. First, there may be limitations in the utility of this management intervention for these taxa and their niches (Potts et al., 2005; Turo & Gardiner, 2019). For example, DNA metabarcoding has demonstrated that pollen from trees is an important resource for cavity-nesting bees (Dürbaum et al., 2023; Fernandes et al., 2022; Maclvor et al., 2014), and therefore, the species in our flower seed mixes may not provide the resources that are actually limiting cavity-nesting bees in urban settings. For cavity-nesting wasps, abundant prey species are necessary to sustain their communities, particularly larval hosts (Tschardt et al., 2005). In addition, wasps may act as a top-down constraint on bee abundance in nest-limited sites typical of urban greenspaces, reducing the benefits of floral additions. We found that compared to bees, the effect size for the impact of floral treatment, wasp abundance had a larger (non-significant) increase (Figure 3b,e) indicating that trophic interactions may have played a role in the lack of effect on overall insect abundance. This result suggests that future work should aim to elucidate how urbanisation interacts with resource type and trophic position to drive cavity-nesting community composition.

Second, prior research has shown that the tangible benefits of experimentally adding floral resources are highly context dependent, varying by taxa, the scale of the addition (Blaauw & Isaacs, 2014b; Matteson & Langellotto, 2011; Simao et al., 2018) and the specific local environment (Wolfen et al., 2023). In our study, our addition of floral resources increased plot level resources by ~20%, yet we found no significant benefits for the uptake of artificial nests, suggesting that local-scale floral patches may not have the diversity of resources needed to affect the establishment of cavity-nesting insect communities. However, at a site level, the high variation of floral resources meant that we were unable to detect a significant difference between treatment and control sites in floral area. Allotments have some of the highest floral diversity in urban areas (Baldock et al., 2019), and resource saturation may have played a role in the lack of strong effects (as shown in Matteson & Langellotto, 2011). However, our results suggest that wildflower and nest interventions may not predictably increase resource levels for cavity nesters in highly heterogeneous urban landscapes. Consequently, when assessing the potential benefits and costs of interventions, explicit consideration of local habitat quality around the intervention is recommended in order to optimise investment in biodiversity enhancement.

Third, the temporal scale of our study may have influenced our findings. The response of insect populations to floral additions often involves natural time lags, where current population sizes reflect past resource availability (Roulston & Goodell, 2011). Blaauw and Isaacs (2014b) demonstrated that the benefits of flower strips in supporting wild pollinators and enhancing pollination services emerged only after 3 years. Thus, while our cultivated flower patches may have appeared insufficient, longer-term studies might reveal delayed yet significant impacts on cavity-nesting insects within urban settings. Overall, our results highlight the need for future experimental

approaches to take into account the large spatial and temporal variation in resources when assessing cavity-nesting insects.

Landscape characteristics had a strong impact on these insect communities. Sites with higher areas of impervious surfaces surrounding them had lower uptake of nests compared to sites with lower areas of impervious surfaces, and the addition of floral resources did not mitigate these declines (Figure 3). Cavity-nesting bees and wasps require divergent resources, but contrary to our predictions, they did not differ in their sensitivity to urbanisation in our study (as shown in Rocha & Fellowes, 2018). Thus, while the mechanism driving the decline of these two distinct groups might differ, the effect on nest recruitment was the same (aligning with Holzschuh et al. (2010) and Xie et al. (2022)). The reduction in cavity-nesting bees in response to increasing urbanisation is contrary to the common hypothesis that cavity-nesting bees can persist in highly urbanised areas due to the nesting opportunities associated with human-made surfaces (Banaszak-Cibicka & Żmihorski, 2012; Cane, 2005; Hinnert et al., 2012) and suggests that the specific combination of limiting resources, including floral resources (Dürbaum et al., 2023; Ellis et al., 2023) may vary among species. Our results also differ from Dürbaum et al. (2023), who found that cavity-nesting wasps were more strongly negatively affected by urbanisation than cavity-nesting bees. For wasps, habitat quality (Pereira-Peixoto et al., 2016), amount (Casanelles-Abella et al., 2024) and connectivity are the best predictors of their colonisation of artificial nests (Bianchi et al., 2006; Holzschuh et al., 2009). Therefore, the associated decreases of habitat connectivity and increased fragmentation with increasing urbanisation (Liu et al., 2016) are likely driving the declines observed in wasps. Finally, the similar effects of urbanisation on cavity-nesting bees and wasps may stem from the close ecological link between host bees and their parasitic wasps (Pereira-Peixoto et al., 2016). The survival of parasitic wasps depends on the presence of the bee species they parasitise, and thus any negative impact on the bee host due to urbanisation should affect their parasites as well (Casanelles-Abella et al., 2024; Pereira-Peixoto et al., 2016; Rocha & Fellowes, 2018).

Our study highlights the importance of identifying the diversity of resources that cavity-nesting communities rely on in order to disentangle the direct and indirect drivers of their declines due to urbanisation. Considering the ecosystem services provided by cavity-nesting bees and wasps in urban systems (Brock et al., 2021; Fernandes et al., 2022), our report of a six-fold decline in abundance as urbanisation increases may pose a threat to the functioning of our city ecosystems. While localised conservation efforts have shown promise in mitigating landscape pressures in agricultural ecosystems (Banks-Leite et al., 2020), our research underscores the limitations of small-scale interventions in addressing the complexities of urban systems. The lack of knowledge surrounding urban cavity-nesting wasps exacerbates the issue, as their declines likely have far-reaching and poorly understood ecological consequences. Advancing our understanding of these pollinator groups is especially important in an urban horticultural context as these areas directly depend on pollinators and predators for optimal crop production.

## 5 | CONCLUSIONS

Our study highlights the complexities involved in effectively implementing urban insect conservation efforts. While adding floral resources is a common strategy, our results indicate that these interventions may not reliably support cavity-nesting bee and wasp communities or mitigate the adverse effects of urbanisation. Our findings also highlight the challenges posed to cavity-nesting Hymenoptera by urban environments. The significant decline in the abundance of bees and wasps that we observed could have important implications for urban ecosystems, underscoring the need for further research to develop more effective conservation strategies tailored to urban landscapes. Finally, given the substantial inconsistency in the efficacy of pollinator conservation measures among studies, particularly in urban pollinator research, we argue it is crucial to assess variability in surrounding habitat quality when designing or implementing pollinator interventions to ensure these provide their intended benefits to insects across urban contexts.

### AUTHOR CONTRIBUTIONS

Emilie E. Ellis, Stuart A. Campbell and Jill L. Edmondson conceived and developed the idea. Emilie E. Ellis and Stuart A. Campbell set up the field experiment. Emilie E. Ellis carried out field and laboratory work. Emilie E. Ellis analysed the data. Emilie E. Ellis wrote the first draft of the manuscript, and all authors contributed substantially to subsequent revisions.

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### CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

### PEER REVIEW

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### DATA AVAILABILITY STATEMENT

All data and R code to reproduce the analysis are deposited in Zenodo doi:[10.5281/zenodo.18257766](https://doi.org/10.5281/zenodo.18257766).

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## SUPPORTING INFORMATION

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

**Table S1.** Species list of seed mix of EuroFlor and Rigby Taylor Native pollinator and Banquet seed mix (for a more complete list directly contact authors).

**Table S2.** Results of Moran's *I* tests assessing spatial autocorrelation among allotment sites for insect abundance and species richness.

**Table S3.** List of cavity nesting bees and wasps, their species or morphotypes, feeding behaviours that colonised artificial nests during 2020 and 2021 in 16 allotment sites in Leeds.

**Table S4.** Plot-level analysis.

**Table S5.** Site-level analysis.

**Table S6.** Summary from generalised linear mixed effect models (MCMCglmm) for the analysis of the effect urbanisation (area of impervious surface surrounding an allotment at a 250m buffer) on the four individual species of bees and wasps found to uptake artificial nests during 2 years (aggregated).

**Figure S1.** Example of the experimental set-up at an allotment site.

**Figure S2.** Site characteristics and spatial configuration of allotment study sites in Leeds, United Kingdom.

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