

ORIGINAL ARTICLE

Pollinators respond positively to urban green space enhancements using wild and ornamental flowers

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Funding information

W. Garfield Weston Foundation; European
Regional Development Fund; Cornwall
Council; University of Exeter

Editor/Associate Editor: Manu Elinor
Saunders

Abstract

1. Pollinator diversity and abundance are under direct threat from human activities. Despite societal dependence on pollinators for crop production, humankind continues to drive pollinator declines through agricultural intensification and urbanisation.
2. Urban environments can provide refuge to some pollinators. There is a need, however, to understand how pollinator communities can be supported in these areas while also considering human needs. Public green spaces provide a promising avenue to target plant–pollinator conservation measures in an urban setting due to their large area, high abundance and low plant–pollinator biodiversity.
3. We used a paired design to compare the plant community, pollinator community and plant–pollinator interactions of (i) public urban green spaces enhanced with wildflower meadows and pollinator-friendly ornamental plantings to (ii) control unenhanced urban green spaces. The planting types within enhanced sites were also separately compared.
4. Our results show that not only was the diversity of the overall pollinator community higher in enhanced than control sites, but also the complexity of some wild Hymenoptera and the abundance of Diptera pollinator groups. The negative impact of urbanisation on some pollinator groups was reduced in enhanced sites compared with control sites. Planting both pollinator-friendly ornamental plants and wildflower meadows significantly increased the visits from Diptera and the diversity in the plant–pollinator community compared with wildflower plantings alone.
5. Our results suggest that enhancing public spaces for pollinators has positive effects on key groups and can help mitigate the impacts of urbanisation. Non-native ornamental plants can also play a role in enhancing green spaces for pollinators while maintaining their recreational functions. This supports a mixed-planting approach for improving public green spaces in urban areas for both people and nature.

KEYWORDS

amenity space, non-native plants, plant–pollinator interactions, restoration, urbanisation, wild pollinator conservation, wildflower meadows

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INTRODUCTION

Pollinating insects provide a fundamental ecosystem service through the facilitation of sexual plant reproduction (Potts et al., 2010). This mutualistic relationship maintains worldwide ecosystem functioning and crop production, and it is estimated that 87.5% of all terrestrial angiosperms and 75% of the 115 most important domestic crops depend on or benefit from biotic pollination (Klein et al., 2007; Ollerton et al., 2011). Anthropogenic pressures on the environment have driven insect population declines which threatens both plant-pollinator diversity and global food production (Blüthgen et al., 2023; Eisenhauer et al., 2019; Ollerton et al., 2011). Wild pollinators provide numerous benefits to wild plant communities, with migrant pollinators exchanging pollen between genetically isolated populations and specialised insects possessing unique morphologies for pollinating specific flowers (Doyle et al., 2020; Orford et al., 2015; Villa-Galaviz et al., 2023). Wild pollinator diversity also enhances pollination efficiency of fruit crop production independent of managed pollinators, providing further impetus to the conservation of insect biodiversity (Garibaldi et al., 2013; Vasiliev & Greenwood, 2020).

In the United Kingdom's highly human-modified environment, agricultural and urban areas dominate the landscape (Seto et al., 2012). Agricultural landscapes have become more intensified, resulting in environments with greatly reduced floral resources and appropriate nesting opportunities for pollinators (Tscharntke et al., 2005). There is mounting evidence that urban areas can provide better floral and nesting resources than intensive agricultural areas for some key pollinators, including bumble bees, due to higher habitat heterogeneity (Baldock et al., 2015; Prendergast et al., 2022; Samuelson et al., 2018). For example, pollinator communities engage in more interactions and visit more specialised flowers in urban areas (Theodorou et al., 2017), which has positive implications for the robustness of plant-pollinator interactions and pollination function (Pimm, 1979; Ponisio et al., 2019). However, this pattern appears to be restricted to specific pollinator groups, as hoverflies, some kinds of wild bees, beetles and wasps continue to respond negatively to urbanisation (Bates et al., 2011; Fortel et al., 2014; Guenat et al., 2019; Theodorou et al., 2020).

Across UK cities, the abundance of key functional pollinator groups is most positively associated with residential gardens and allotments due to their large collective area and high floral abundance of native and non-native plant taxa (Baldock et al., 2019). Public urban green spaces, such as parks and open space areas, appear to support significantly fewer pollinator species and abundance than other urban green spaces (Banaszak-Cibicka & Żmihorski, 2012; Dylewski et al., 2019). Due to their recreational use, these spaces are generally highly managed which contributes to limited floral diversity and availability (Taylor & Hochuli, 2017). In an agricultural matrix, the impact of agri-environment schemes designed to provide environmental benefits, often including resources for pollinators (e.g., Countryside Stewardship in the UK), depend partly on the intensity of surrounding land use (Beyer et al., 2023; Tscharntke et al., 2005). The relationship between land use intensity and the impact of pollinator focused

biodiversity schemes has been relatively rarely studied in an urban setting, with conflicting responses among pollinator groups (Mata et al., 2023; Pérez-Sánchez et al., 2023; Threlfall et al., 2017). Considering their large area, high connectivity and low biodiversity, public green spaces appear to hold promising potential for improving plant-pollinator communities in an urban setting at a national scale (Aronson et al., 2017).

Habitats which benefit urban pollinators, such as unmown grassland, tall ruderal herb communities and native shrubs such as brambles, can be perceived to be untidy despite supplying floral resources to pollinators (Hoyle et al., 2017; Mata et al., 2021; Nassauer, 1988). However, the perception that enhancing biodiversity in these public spaces is compatible with maintaining their main recreational functions is growing amongst society (Hoyle et al., 2019; Knapp et al., 2021). Ornamental plantings such as pollinator friendly shrubs and perennials, which may not be native, provide the opportunity to enhance sites for pollinators while also achieving aesthetic value for the people who use these green spaces (Stevenson et al., 2020). Aligned with Li and Nassauer (2020), planting both ornamental and native wildflower patches fit the 'cues to care' concept where acceptance of novel landscape features depends on recognisability, human presence and cultural consistency. Given the cost implications of managing green spaces for biodiversity, it is important to quantify the benefits these changes in management provide, both to the biodiversity and the people.

We investigate the effects of urban green space enhancement on key pollinator groups using both meadow habitats and ornamental plantings along an urbanisation gradient across 10 mid-sized towns (population range: 7342–24,375) in Cornwall, UK. We used sites enhanced as part of the 'Making Space for Nature' project, led by Cornwall Council, the local government authority, which resulted in changes to 60 green spaces between 2017 and 2023, totalling an area of 78 ha. The project aimed at bringing benefits to wildlife and people in public open spaces, with a focus on transforming areas of mown grassland into sites with a variety of plantings such as wildflower meadows, trees and ornamental borders, as well as access improvements, such as paths and benches (Cornwall Council, 2021; Cornwall Council, 2022). We used a paired design to compare the 'enhanced' Making Space for Nature sites to 'control' grass-dominated public open spaces (Archibald et al., 2017; Mata et al., 2023; Mody et al., 2020), to answer the following questions: (i) How do urban sites enhanced for nature differ in visitation frequency, plant-pollinator interactions and diversity of pollinator communities compared to control sites? (ii) How does the impact from the degree of urbanisation on pollinator communities differ between enhanced and control sites? (iii) How do sites with wildflower meadows and pollinator-friendly ornamental plantings differ in visitation frequency, interactions and diversity of their pollinator communities compared to those sites only enhanced with wildflower meadows? We predict sites with enhancements will have increased visitation frequency, interactions and pollinator diversity compared to control sites due to improved floral resource provision (Mata et al., 2023), that at sites with high levels of surrounding urbanisation, there will be no difference between the

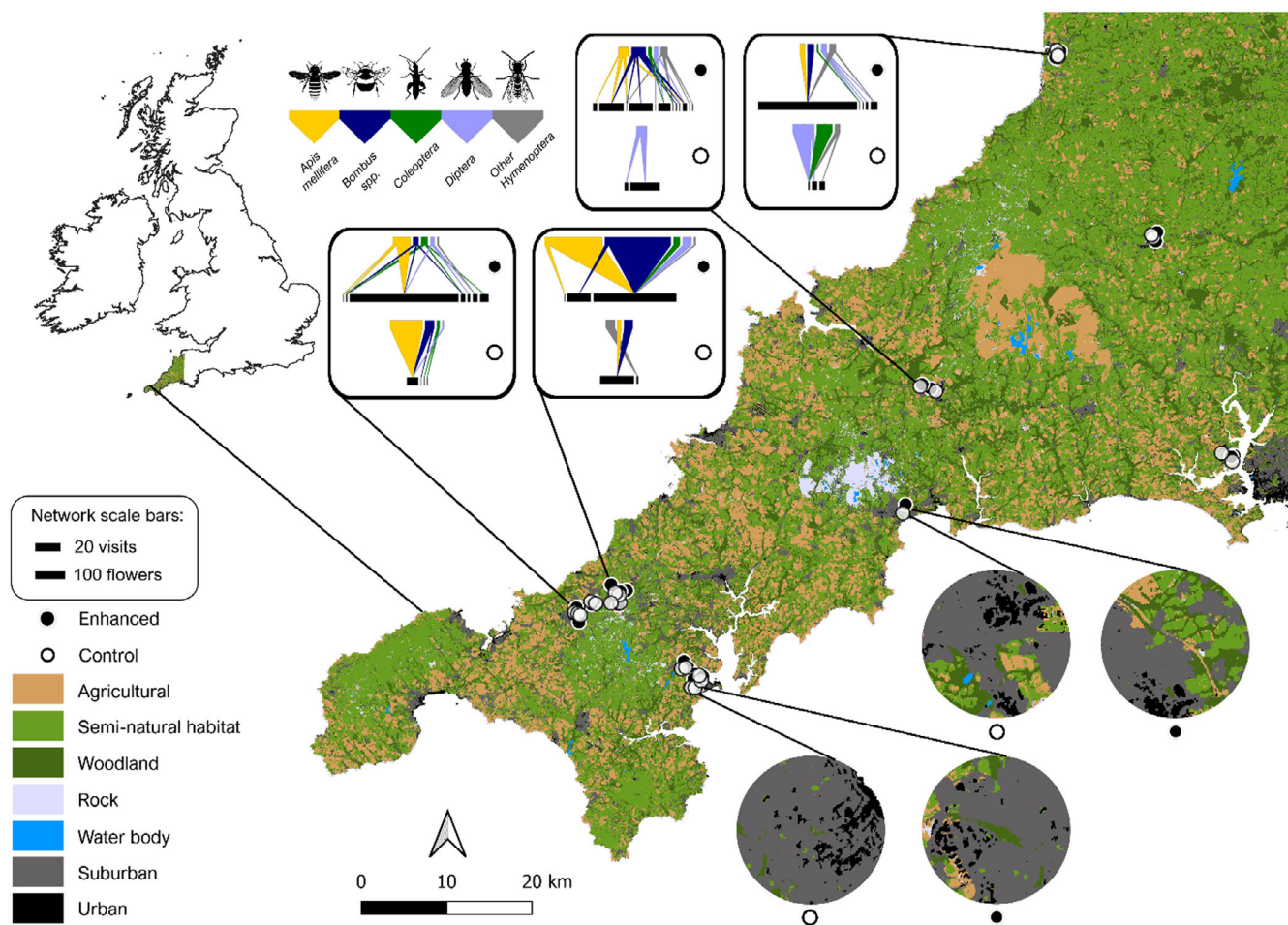


FIGURE 1 Landscape characteristics, survey site locations and typical plant–pollinator visitation web comparisons across Cornwall, UK. Plant–pollinator visitation webs depict bipartite interactions (links) between pollinators (upper bar) and flowering plant taxa (lower bar). Upper bar widths are proportional to the visitation frequency (visits) for each taxonomic group. Lower bar widths are proportional to the floral abundance of each plant taxa. The width of the links is proportional to the visitation frequency between pollinators and plants. All webs are drawn to the same scale. Landscape composition around sites varied in urbanisation as shown in the enlarged circles taken from a 750 m radius of four sites. For clarity, only a subset of sites (chosen at random) are displayed.

pollinator communities of enhanced and control sites due to the limiting impacts of urbanisation (Wenzel et al., 2020) and that having both pollinator-friendly ornamental flowers and wildflower meadows will increase pollinator visitation frequency and diversity, even during peak flowering of native plants (Zaninotto et al., 2023).

MATERIALS AND METHODS

Study sites

Fifty paired urban public greenspace sites were selected in Cornwall, UK (Figure 1, 50.262951, –5.050700), consisting of a Making Space for Nature (enhanced) site paired with a nearby unenhanced (control) site within 1.3 km and of similar size. Park design and retrofitting of enhanced sites consisted of pollinator-friendly ornamental plant beds and wildflower seeded areas which were variable in size between sites. New planting beds and meadows were created on previously highly mown amenity grass. The enhanced sites were implemented in

two phases with consistent seed mixture, age and management within each phase (Table S1). Phase 1 habitat interventions were planted in 2018 and 2019 (14 sites), and phase 2 were planted in 2021 (11 sites). Control sites were defined as any urban public greenspace which had received no habitat management to enhance its biodiversity and were typically characterised by extensive species-poor grassland (frequently mowed) with trees along the perimeter. Control sites were selected under the following criteria: (i) 0.3–1.3 km from the paired enhanced site to account for foraging distances of target species and ensure some degree of independence of pollinator communities (Zurbuchen et al., 2010), (ii) within the same town to account for environmental variation and local management and (iii) similar site area to account for the species-area relationship (Connor & McCoy, 1979).

Survey methods

Floral and pollinating insect surveys were conducted from 7 June 2022 to 7 July 2022. All sites were surveyed once due to project time

constraints. A high number of sites per treatment combined with enhanced and control pairs sampled within the shortest possible time frame of each other on the same day was done to minimise possible confounding temporal and climatic effects. A 100×2 m linear transect divided into 10 m sections was set up on each site aiming to include a representative sample of the vegetation types present at that site, or for sites smaller than 100 m long, two parallel transects were set up 20 m apart to create a total length of 100 m.

Floral surveys were conducted along transects in 1 m^2 quadrats placed randomly in each section ($10 \times 1 \text{ m}^2$ quadrats \times site). The total number of floral units per species in each quadrat was recorded. Native wildflower species were identified using Rose and O'Reilly (2006) and horticultural plants identified using iNaturalist (2022), Pl@ntNet (2022) and Seek (2022), confirmed by experts in these applications. One floral unit was defined as a head (e.g., *Trifolium repens* Linnaeus (Fabales: Fabaceae)), an umbel (e.g., *Heracleum sphondylium* L. (Apiales: Apiaceae)) or a capitulum (e.g., *Centaurea nigra* L. (Asterales: Asteraceae)) (outlined by Carvell et al., 2006 and Tarrant et al., 2013). Only open and fresh flowers were included in floral counts. It was acknowledged that counting floral units under these broad size and flower number terms likely gives an overestimation of floral resource provision at sites with predominantly small flowers while underrepresenting those sites with larger resource-rich flowers.

Using published data on the daily nectar production of flowering plant species, we estimated the amount of nectar sugar (in milligrams) produced per square metre per day at each site based on our floral surveys (Baude et al., 2016; Hicks et al., 2016). Most plant species from the floral surveys had available data (64/94) either measured or modelled, and weighted averages were taken when values were present from both data sources (Timberlake et al., 2019). When species specific values were unavailable, nectar values were taken as the mean value of the genus (10/94), family (15/94) or when neither were available, the mean floral unit nectar value from that site was given (5/94) (Table S2).

Pollinating insect surveys were conducted along the same transect as the floral survey on warm, sunny days, with little wind (<5 Beaufort) (O'Connor et al., 2019) between 10:25 AM and 6:50 PM. Surveying commenced between 11:00 AM and 5:00 PM for most sites (41/50; 20 enhanced, 21 control); however, logistical difficulties dictated early or late commencement at some sites, of which the pairs were surveyed in quick succession to minimise any effect of time of day. The weather was appropriate for surveying at all times. Each transect was walked either by two surveyors each observing 1 m to the left or right of the transect or by one surveyor observing 1 m to the left of the transect line then repeating the transect and observing 1 m to the right, resulting in equal areas surveyed. Surveyors walked at a slow pace and recorded a plant–pollinator visit whenever an insect visitor touched the sexual organs of a receptive flower (Tarrant et al., 2013). Pollinating insects were targeted and either identified in the field, collected and determined to morphospecies level by expert entomologists or uploaded to the 'iNaturalist' community for identification and validation by other entomologists. Two cryptic species of bumble bee workers, *Bombus lucorum*

L. (Hymenoptera: Apidae) and *B. terrestris* L., were not captured due to their vast abundance and similarity and were identified as 'white/buff tailed bumble bees' in the field.

Site characteristics

Within-site vegetation types were identified as the following categories: wildflower meadow (planted wildflower habitats consisting of mainly native species, with a small proportion of non-native species added), amenity grassland (frequently mown grass), woodland (areas where tree cover is over 50%), scrub (dominated by native shrub species such as bramble *Rubus fruticosus* L. (Rosales: Rosaceae), black-thorn *Prunus spinosa* L. or hawthorn *Crataegus monogyna* L.), ornamental planting (mix of planted ornamental shrubs and herbs containing a mix of native and non-native species), herbal planting (ornamental perennials, consisting of a mix of native and non-native species but predominantly non-native or garden cultivars), semi-improved grassland (grassland dominated by coarse and fine grasses and managed less frequently) and rough grassland (semi-improved grassland and scrub interspersed) (broadly following JNCC, 2010). Ornamental plantings were selected to be 'wildlife friendly', including many plants with value for pollinators and some native species (Table S1). The percentage cover of these vegetation types within each 10×2 m section of the transect was estimated, and the total area covered by each vegetation type per transect was calculated. Across enhanced sites, ornamental plantings covered a total of 134 m^2 , whereas wildflower vegetation covered 1838 m^2 . Post-surveying, plant taxa from the floral surveys were allocated to the respective vegetation type categories; however, crossover in plant taxa between vegetation types provided too much ambiguity to compare at this resolution. Therefore, vegetation types were classified as wildflowers (native species) or ornamental planting (non-native species) (following Stace, 2001) allowing allocation of floral unit counts to each (Table S2).

Landscape characteristics

For each site, we measured surrounding landcover data at multiple spatial scales using QGIS (v 3.30.3, QGIS Development Team). Landcover data were downloaded from the UKCEH Land Cover Map for 2021 at $10 \text{ m} \times 10 \text{ m}$ spatial resolution (Marston et al., 2022). Buffer zones around each site were established at radii of 250, 500, 750 and 1000 m, representing the common dispersal and foraging distances of pollinator groups analysed in this study (Bates et al., 2011). We acknowledge that although some foraging trips in bees, for example, can greatly exceed these distances (Beekman & Ratnieks, 2000; Kendall et al., 2022), most foraging trips are far shorter (Osborne et al., 1999). 'Urban' was the landcover class used to calculate urban percentages within buffer zones because it is the environment which provides least value for pollinators (defined as dense urban, such as town and city centres, where there is little, if any, vegetation,

including areas such as dock sides, car parks and industrial estates; Marston et al., 2022). Surrounding urban cover of study sites ranged from 0% to 36% with a mean of 7% across all sites over the four radii (250, 500, 750, 1000 m; Table S3).

Data analysis

To quantify differences in the structure of plant–pollinator communities between enhanced and unenhanced urban green space sites, three variables were used: visitation frequency, number of interactions and Shannon diversity. Visitation frequency is the total number of flower visits, which can be calculated for each taxonomic group or for the community and is correlated with pollination efficiency (Vázquez et al., 2005). One visit was recorded when a pollinator touched the reproductive part of a flower. The number of interactions is the total number of unique interactions between individual plant taxa and a pollinator taxon in a community, which describes structural complexity (Bascompte et al., 2003). Shannon diversity index incorporates the number of species in a community and their abundances (evenness) to produce a measure of diversity and has been widely used when comparing ecological communities due to its pragmatic interpretation (Fründ et al., 2010; Tew et al., 2021).

All data analyses were performed in R software version 4.3.1 (R Core Team, 2023), using generalised linear mixed effects models (GLMM) for all species combined and for each taxonomic group: *Bombus* species, *Apis mellifera* L., Diptera, Coleoptera and other Hymenoptera. Other flower visiting groups (Hemiptera, Lepidoptera and Orthoptera) were not analysed as single models and were removed from models that included taxonomic group as a variable due to a low visitation frequency. Further sub-division into functional groups was attempted but provided too little data to perform our planned analysis and were thus kept as taxonomic groups. GLMMs were performed using the *glmer* and *glmmTMB* functions from the *lme4* and *glmmTMB* packages. Fixed effects for all GLMMs were tested for correlation using the *cor.test* function from the *stats* package (R Core Team, 2023). Shannon diversity could not be modelled separately for taxonomic groups due to small sample sizes and the nature of the modelling approach.

To check that the enhancement treatment was not confounded with size or extent of urbanisation, we compared site area and degree of urbanisation between treatments using GLMMs with ‘pair’ as a random effect. There were no significant differences in site area ($z = 0.59$, $p = 0.56$), urbanisation at 250 m ($z = -0.19$, $p = 0.85$), 500 m, ($z = 1.43$, $p = 0.15$), 750 m ($z = 0.56$, $p = 0.57$) or 1000 m ($z = 0.36$, $p = 0.72$) between treatments (Table S3). To understand if phase 1 and phase 2 sites needed to be treated separately in models, they were tested for differences in pollinator visitation frequency, number of interactions, Shannon pollinator diversity, floral abundance and nectar production using GLMMs. There were no significant differences in visitation frequency ($z = -0.81$, $p = 0.42$), number of interactions ($z = -0.29$, $p = 0.77$), Shannon pollinator diversity ($z = 0.22$, $p = 0.83$), floral abundance ($z = -0.29$, $p = 0.93$) or nectar production ($z = -0.65$, $p = 0.51$) between phase 1 and phase 2 sites

and were consequently grouped as ‘enhanced’ for all further analyses (Table S3).

To test the effects of treatment and urbanisation on visitation frequency, number of interactions and Shannon pollinator diversity, we fitted GLMMs with Poisson error distribution (log link) for count data and Gaussian error (log link) for continuous non-integers (Bates et al., 2015; Brooks et al., 2017). The ‘visitation frequency’, ‘number of interactions’ and ‘Shannon pollinator diversity’ of each taxonomic group was fitted as the response variable, ‘treatment’ (enhanced or control) and ‘urban percentage’ and their interaction as fixed effects, and ‘town’ and ‘pair’ as random effects. To account for the strong correlation between insect visitation and floral abundance, and number of interactions and floral species richness, floral abundance in visitation models and floral species richness in number of interactions models, were included as an offset term to standardise against these sources of sampling bias. We ran a multi-model inference process using the ‘MuMin’ package in R to select the most appropriate spatial scale where urban cover predicted visitation frequency, number of interactions and Shannon pollinator diversity for all pollinators and visitation frequency and number of interactions of each taxonomic group (Bartoń, 2023). This approach allowed simultaneous model comparisons and determination of the best fitting models (Table S4). We selected the best models using corrected Akaike Information Criteria (AICc) or conducted model averaging to obtain parameter estimates if multiple models were within delta two AICc values of the best fitting model (Burnham & Anderson, 2002; Grueber et al., 2011).

To assess the importance of native and non-native vegetation types (wildflowers and ornamental plantings) for the taxonomic groups, we ran GLMMs including only enhanced sites ($n = 25$) and grouped the sites into two categories based on the presence or absence of non-native ornamental plantings at that site. ‘Visitation frequency’, ‘number of interactions’ and ‘Shannon pollinator diversity’ were fitted as the response variables. We included ‘nectar production per site’, ‘taxonomic group’ and ‘vegetation type’ and their interactions as fixed effects. Offsets were used on the same response variables as in the models previously mentioned. ‘Site’ was fitted as a random effect because only enhanced sites had the full range of vegetation types, and therefore, the unenhanced control pairs were not included. Final models were selected by stepwise dropping non-significant interaction terms with *drop1* and comparing the fit of the simplified model with the original model using AICc with the *bbmle* package (Bolker & R Core Team, 2022).

To investigate differences in the nectar production and the diversity of nectar sources we calculated nectar production per site and the Shannon diversity index of the floral contributors using the *vegan* package (Oksanen et al., 2022), following Baude et al. (2016) and Tew et al. (2021). Nectar production and diversity were analysed using GLMMs with gamma (log link) and gaussian (log link) family types respectively to compare between treatments and between enhancement vegetation types. Models comparing treatment included ‘treatment’ as a fixed effect and ‘town’ and ‘pair’ as nested random effects and vegetation models included ‘vegetation type’ as a fixed effect and ‘town’ as a random effect.

Model diagnostics were inspected using the *DHARMA* package (Hartig, 2022). When overdispersion was detected for any of the

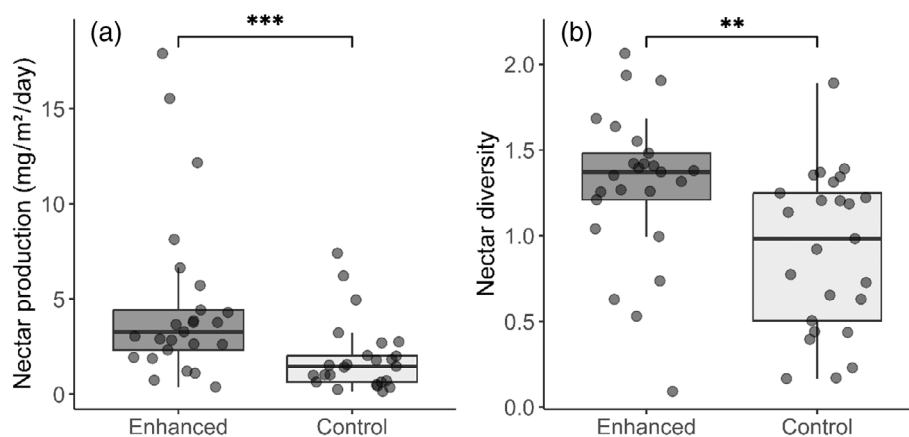


FIGURE 2 Nectar comparisons (a) nectar sugar production $\text{mg}/\text{m}^2/\text{day}$ and (b) floral nectar Shannon diversity index between enhanced versus control sites. Comparisons are modelled using generalised linear mixed effects models (GLMMs). Boxplots depict the median, 25th and 75th percentiles. Significant differences between treatments are indicated by $**p < 0.01$, $***p < 0.001$.

Poisson GLMMs, we refitted the model with a negative binomial distribution (Hilbe, 2011). R^2 values were calculated using the *r.squaredGLMM* function from the *MuMin* package. The bipartite package was used to create the visitation webs in Figure 1 (Dormann et al., 2008). The *ggpredict* and *ggplot* functions from the *ggplot2* package were used to produce Figures 2–4 (Wickham, 2016).

RESULTS

We recorded 385 interactions between 75 plant taxa and 103 pollinator taxa across all sites, contributing to 1482 flower visits (Table S5). From these visits, 1420 (96%) were performed by the following taxonomic pollinator groups: 518 (35%) by *Bombus* species, 352 (24%) by Diptera, 235 (16%) by *A. mellifera*, 221 (15%) by Coleoptera and 94 (6%) by other Hymenoptera species (comprised of 27 Halictidae, 23 Andrenidae, 9 Colletidae and 35 individuals from 8 other families). The remaining 62 (4%) of the recorded visits included visits by Hemiptera, Lepidoptera and Orthoptera.

We counted over 12,280 floral units during the flower counts across both treatments (Table S2). Across floral and pollinator surveys 98 flowering plant taxa were recorded at enhanced sites while there were 47 at control sites, of which 51 and 19, respectively, were found exclusively in that treatment. Shannon floral diversity and floral abundance was higher at enhanced than control sites (Model results, respectively: $z = 4.81$, $p < 0.001$; $z = 2.12$, $p < 0.05$; Table S3). Enhanced sites produced 2.5 times more nectar sugar on average per day than control sites ($4.5 \text{ mg}/\text{m}^2/\text{day}$ vs. 1.8), and nectar diversity was also significantly higher at enhanced sites than control sites (Model results respectively: $z = 3.9$, $p < 0.001$; $z = 3.01$, $p < 0.01$; Figure 2a,b). The most common flowering plant species, the white clover *T. repens*, was similarly abundant at both enhanced and control sites and accounted for 42% (5737) of all recorded floral units and 23% (342) of all pollinator visits across both treatments ($z = -0.10$, $p = 0.92$; Table S3). The common daisy *Bellis perennis* L. was more abundant at control sites and accounted for 19% (1022) of floral units

and 7% (23) of all pollinator visits at control sites, compared with 2% (177) of floral units and 1% (13) visits at enhanced sites ($z = -2.96$, $p < 0.01$; Table S3).

Plant–pollinator interactions

Shannon pollinator diversity was significantly higher at enhanced sites for all pollinators combined ($z = 2.9$, $p < 0.01$; Table S4). *Bombus* species and Diptera benefitted greatly from greenspace enhancement. Their visitation frequencies were on average 104% (*Bombus* spp.) and 123% (Diptera) higher than in the control sites; however, after accounting for floral abundance only Diptera maintained a statistically significant difference ($z = 1.97$, $p < 0.05$; Table S4). The number of interactions for other Hymenoptera was higher at enhanced than control sites ($z = 2.51$, $p < 0.05$; Table S4).

Urbanisation

Overall community

The final averaged models indicated significant interactions between urbanisation at the 250, 500 and 750 m spatial scales and treatment for visitation frequency of all pollinators combined, with negative effects at control sites but not enhanced sites (750 m: $z = 2.66$, $p < 0.01$; Figure 3a). There was a significant interaction between urbanisation at 1000 m and treatment for the number of interactions of all pollinators, with negative effects at control sites but not enhanced sites ($z = 2.16$, $p < 0.05$; Figure 3b).

Taxonomic groups

We found a decrease in visitation frequency for *Bombus* species and other Hymenoptera species with urbanisation at the 250 and 750 m

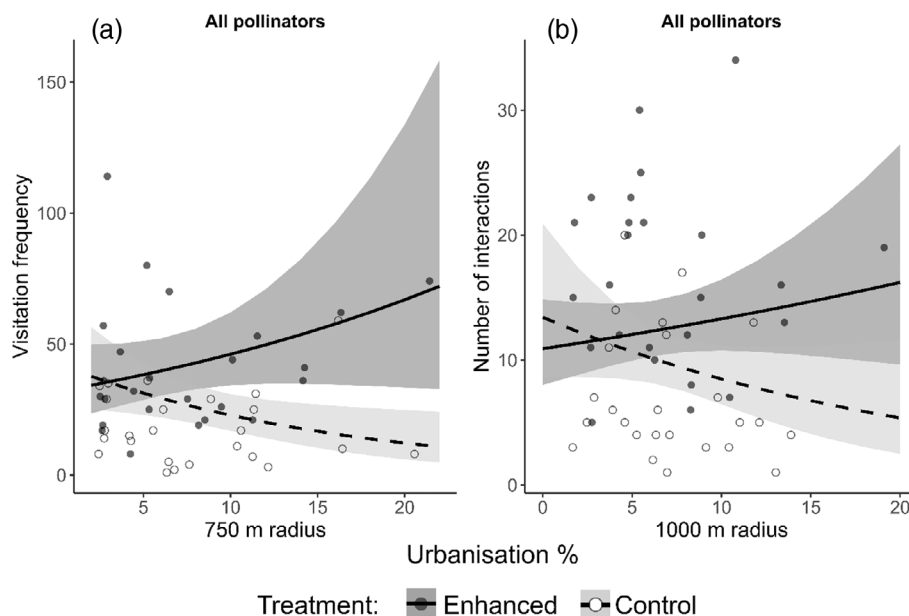


FIGURE 3 Mean predicted visitation frequency and number of interactions across the urbanisation gradient and between treatments ($\pm 95\%$ confidence interval), with raw data overlaid for (a) all pollinators at 750 m urbanisation radius, and (b) all pollinators at 1000 m scale. Predictions are derived from the highest ranked models from model averaged sets including treatment and urbanisation predictors (Table S4).

scale, respectively, at control sites but not at enhanced sites ($z = 2.15$, $p < 0.05$; $z = 2.08$, $p < 0.05$; Figure S1a,b). There was a significant interaction between urbanisation at 500, 750 and 1000 m for Coleoptera visitation frequency with positive effects detected at enhanced sites and negative effects at control sites (1000 m: $z = 2.09$, $p < 0.05$; Figure S1c).

Apis mellifera responded to urbanisation independent of treatment with negative effects detected at both the 500 m and 750 m spatial scales for visitation frequency (750 m: $z = 2.50$, $p < 0.05$; Figure S1d) and 500 m for number of interactions ($z = 2.24$, $p < 0.05$; Figure S1g). Urbanisation at 750 m had a negative effect on the number of interactions of other Hymenoptera ($z = 10.99$, $p < 0.001$; Figure S1e). There was also a significant interaction between urbanisation at 250, 500 and 750 m and treatment for the number of interactions in Coleoptera, with negative effects at control sites but not enhanced sites (750 m: $z = 2.45$, $p < 0.05$; Figure S1f).

Differences between enhancement vegetation types

At wildflower patches and ornamental plantings from enhanced sites, 73 native and 32 non-native flowering plant taxa were recorded, with 246 and 51 distinct interactions recorded between insect pollinators and native and non-native species, respectively. Ornamental flowers were visited by 36 pollinator taxa, consisting of *A. mellifera*, 6 *Bombus*, 16 Diptera, 2 Coleoptera, 7 other Hymenoptera, 2 Hemiptera and 2 Lepidoptera species, whereas wildflowers were visited by 93 species, consisting of *A. mellifera*, 7 *Bombus*, 47 Diptera, 8 Coleoptera, 21 other Hymenoptera, 5 Hemiptera, 3 Lepidoptera and 1 Orthoptera species. Models including the interaction between pollinator group and

vegetation type did not improve the model fit for number of interactions ($AIC_{\text{reduced}} = 453.62$; $AIC_{\text{full}} = 461.88$) or Shannon diversity ($AIC_{\text{reduced}} = 98.58$; $AIC_{\text{full}} = 102.90$) and so were not included in the final models. The visitation frequency of Diptera was significantly higher at sites with wildflower and ornamental planting types ($z = 3.24$, $p < 0.01$; Figure 4a). All other taxonomic pollinator groups responded similarly to enhancement vegetation types in terms of visitation frequency, number of interactions and Shannon diversity (Table S6). Generally, however, the Shannon diversity across pollinator groups at sites with ornamental plantings was significantly higher than at sites without ornamental plantings ($z = 2.07$, $p < 0.05$; Table S6). We also found significantly higher nectar production and Shannon nectar diversity at sites with ornamental plantings compared to those without (Model results, respectively: $z = 2.22$, $p < 0.05$; $z = 3.34$, $p < 0.001$; Figure 4b,c).

DISCUSSION

Here, we demonstrated how enhanced green spaces in urban areas can have positive impacts on plant–pollinator communities compared to ‘standard’ green spaces with low biodiversity value. As floral abundance, nectar production, Shannon flower diversity and nectar flower diversity were lower at control sites, it is likely that the higher Shannon diversity of the pollinator community at enhanced sites was driven by an amalgamation of these properties. Amenity grassland is typically species-poor, which may be a response to frequent mowing (Pauleit & Breuste, 2011). Control sites were mainly composed of amenity grass and possessed very high numbers of common daisy, which were rarely visited by pollinators in our study, possibly because

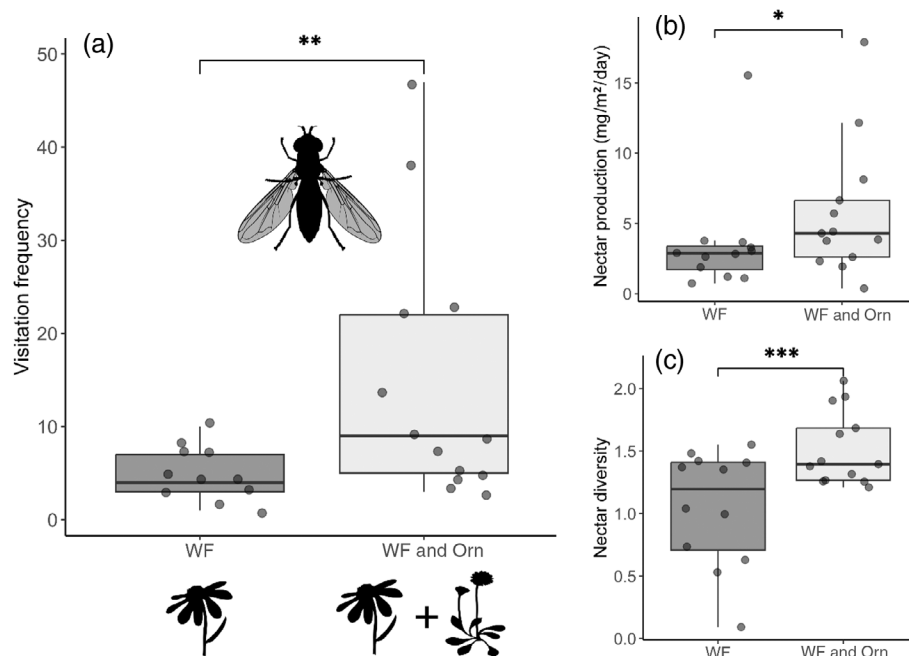


FIGURE 4 Boxplots depicting wildflower (native) versus wildflower and ornamental plantings (native and non-native) comparisons for (a) Diptera visitation frequency, (b) nectar sugar production mg/m²/day and (c) Floral nectar Shannon diversity index. Comparisons are modelled using generalised linear mixed effects models (GLMMs). Boxplots depict the median, 25th and 75th percentiles. Significant differences between treatments indicated by * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Orn, ornamental plantings; WF, wildflowers.

of its low nectar and pollen reward (Hicks et al., 2016). White clover is another species that tends to be strongly associated with amenity grassland and frequent mowing (Larson et al., 2014), but in our study, flowers of white clover were similarly abundant at both treatments and accounted for a large proportion of total flower visits. Time since enhancement seemed to play no role in explaining the observed patterns, which suggests that pollinators respond quickly to the enhancement measures. Similar rapid changes in pollinator foraging behaviour have been observed in other restoration studies, both here in the United Kingdom (Forup & Memmott, 2005) and elsewhere (Kaiser-Bunbury et al., 2017). Diptera and other Hymenoptera (incorporating wasps and solitary bees but excluding *Bombus* and *Apis*) responded particularly positively to the enhancements as their visitation frequency and interactions respectively increased significantly. These groups of wild pollinators are declining in the United Kingdom (Powney et al., 2019), so their positive responses to these restoration measures provide encouraging results for wild pollinator conservation.

Our study provides a snapshot in time of the plants and pollinators, during peak pollinator and flowering season, and so our results are representative only of the communities at this time. This means that effects seen in the important spring and late summer seasons cannot be assessed, and further investigation into these seasons would be beneficial. Enhanced sites possessed more non-native plants than controls, which typically have longer flowering periods than amenity associated plant taxa (Zaninotto et al., 2023), meaning that our design may have underestimated the impact of this vegetation type. We also acknowledge that there is a range in taxonomic resolution at the plant and the pollinator level which would

affect our measures of number of interactions and Shannon diversity (Tables S2 and S4). However, as this was done indiscriminately, we believe that it would not introduce a systematic bias, allowing numbers to be comparable across sites.

Urbanisation and enhancements on taxonomic groups

The degree to which urbanisation impacted pollinators differed between treatments, with *Bombus* species, Coleoptera and other Hymenoptera particularly affected by the landscape context at control sites. The three groups showed a significant interaction between the response to urbanisation and treatment, which indicates that their visitation frequencies suffer particularly from species-poor vegetation of amenity grasslands at control sites in highly urbanised areas. Additionally, the significant interaction between the response to urbanisation and treatment with the number of interactions from Coleoptera further demonstrates the suppressed ecological complexity at highly urbanised control sites. Similarly, when all pollinators are analysed together, the visitation frequency and number of interactions dropped sharply with degree of urbanisation at control sites but not at enhanced sites (Figure 3a,b). These findings suggest that enhanced sites mitigate the negative effects of urbanisation on pollinators, specifically for *Bombus* spp, Coleoptera and other Hymenoptera.

Urbanisation, irrespective of treatment, negatively affected the visitation frequency and the number of interactions of the domestic honey bee *A. mellifera*; a pattern which could be attributed to hive locations being selectively positioned away from urban centres. This

highlights the potential for enhanced urban green spaces to provide wild pollinators refuge from the prevalent generalist *A. mellifera* which can outcompete wild bees (Iwasaki & Hogendoorn, 2022; Weaver et al., 2022). In fact, this explanation may contribute to the relative success of some wild bees within urban areas as observed at enhanced sites. The only group of pollinators that appeared to be little affected by urbanisation were Diptera, which may be partly due to the dominance of hoverflies in this group, which are highly mobile. However, Diptera have previously been shown to be more sensitive to urbanisation (Bates et al., 2011; Geslin et al., 2013). Urbanisation at low levels generates habitat diversity and thereby positively affects pollinator diversity, compared to urban densification, which has negative effects, which could explain why Diptera did not show a response to urbanisation in our study (Wenzel et al., 2020).

Differences between enhancement vegetation types

Our findings suggest that non-native ornamental plantings in addition to native wildflower enhancements have some impact on the pollinator community in terms of Shannon diversity while also attracting more visits from Diptera. Higher Shannon diversity indicates that the sites with wildflower and ornamental plantings attract a broader array of pollinator species in a more even abundance than those with only wildflower plantings. This is complemented by the finding that nectar production and diversity was also higher in sites with ornamental plantings, suggesting that non-native plants provide an important variety of nectar sources at these sites and are being included in the diets of pollinators (Fründ et al., 2010). The pattern of indiscriminate flower visitation by the majority of pollinators has been previously observed in other studies (Garbuzov & Ratnieks, 2014; Martins et al., 2017). However, Dipteran visitors appear to benefit from the addition of ornamental plantings which, despite being possibly attributed to the high diversity of species and morphology in this group, still indicates the attractiveness of non-native flowers to an important group of pollinators (Doyle et al., 2020; Orford et al., 2015). To maximise the conservation of insect diversity, it is important to account for specialised pollinator species that are often dependent on specific native plant species for development, feeding and breeding. Thus, we must emphasise that native plants should be supplemented rather than replaced with non-natives in planting schemes (Chrobock et al., 2013; Hanley et al., 2014).

The flowering period of most native plants is between May and August, but this period varies for non-native plants, which can be more productive during the very early or late flowering season, providing valuable resources in times of scarcity (Baldock et al., 2019; Zaninotto et al., 2023). Including non-native ornamental flowers with extended flowering periods in planting schemes has the added advantage of mitigating against the impact of a changing climate on flower blossom and insect emergence timing (Wyver et al., 2023). Although care must be taken that invasive plant species are not used in ornamental plantings (Aizen et al., 2008; Traveset & Richardson, 2006), non-native ornamental plantings in public green spaces can provide

benefits to pollinator communities. Invasive non-native species were found on some sites (e.g., *Rosa rugosa* Thunb.) planted previously or as garden escapees. Some plants used in the project have become invasive elsewhere (e.g., *Verbena bonariensis* L. (Lamiales: Verbenaceae)) although not in the United Kingdom. This is a particularly sensitive balance, as non-native species used in these settings need to be robust enough to survive light touch management, but not so robust they become invasive. As urban green spaces should provide benefits for wildlife and humans alike, it is important to consider trade-offs between biodiversity-friendly management and recreational purposes for people (Hoyle et al., 2017; Potts et al., 2016). Supplementing native wildflowers with ornamental plantings is likely to strike a balance between potentially conflicting needs. For example, the presence of ornamental borders as signals of 'cues to care', incorporate landscape elements which are designed and signal human management (Hoyle et al., 2017; Nassauer, 2012). The presence of ornamental borders as a signal of management may provide both opportunities for engagement with green spaces via gardening opportunities (Majewska & Altizer, 2020) and increase the tolerance of park users for 'weedy' native plants, which often have high value for biodiversity (Hoyle et al., 2019; Southon et al., 2017).

CONCLUSIONS

There were marked differences in the pollinator communities in enhanced sites compared with control sites, despite a relatively low level of urban densification in small towns. Pollinator groups responded to urbanisation at different scales, with the negative responses from some wild pollinator groups (*Bombus*, Coleoptera and other Hymenoptera), appearing to be reduced on sites with enhancements. The benefits to both pollinators and the wider public are greatest when native wildflower plantings are combined with pollinator-friendly ornamental border plantings. In the context of urban planning, implementation of simple measures, such as the diverse floral plantings in green space enhancements described here, can evidently improve wild pollinator groups to a significant degree despite the degraded agricultural-urban matrix (Blackmore & Goulson, 2014). The enhancement scheme assessed here was implemented by the local county government body making the results of this work relevant to other local authorities which are often tasked with managing green spaces under tight budget restrictions.

AUTHOR CONTRIBUTIONS

Oliver Poole: Conceptualization; methodology; software; data curation; investigation; formal analysis; visualization; writing – original draft; writing – review and editing. **Alba Costa:** Investigation; formal analysis; validation; visualization; supervision; writing – review and editing. **Christopher N. Kaiser-Bunbury:** Conceptualization; methodology; funding acquisition; supervision; writing – original draft; writing – review and editing. **Rosalind F. Shaw:** Conceptualization; formal analysis; validation; supervision; writing – original draft; writing – review and editing; methodology.

ACKNOWLEDGEMENTS

This project was supported by the project ‘Create a Buzz’ funded by the Garfield Weston Foundation to The Eden Project Cornwall. The Making Space for Nature project (Green Infrastructure for Growth 2) was partly funded by the European Regional Development Fund, with match funding from Cornwall Council and the University of Exeter. We thank Rakshita Sah, Lucy Mooney and Frederick Possegger for assistance in data collection. Thanks to Rachel Lennon and Jaimie Barnes for their sound statistical support. We thank the ‘Budding Nature’ team for providing insect identification training, and to our expert entomologists William Hawkes and Sally Luker for help identifying field specimens.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data are freely available to download from figshare: <https://doi.org/10.6084/m9.figshare.24799569.v1>. Insect and plant identification from a sample of the project can be accessed here: <https://www.inaturalist.org/projects/ms4n-flowers>.

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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. Habitat types characterised by management requirements, seed mixtures and indicative ornamental plant lists for phase 1 and 2 MS4N sites. Note that the exact ornamental plants used might vary between sites depending on site characteristics and plant availability. All sites had been managed under these plans for 2–4 years. Phase 1 sites (2017–2019) include those in Camborne, Pool, Redruth, Saltash and Bude. Phase 2 sites (2020–2023) include those in Penryn, Falmouth, St Austell, Bodmin and Launceston.

Table S2. Vegetation type categorisation based on historic plant origin. Native wildflowers and non-native ornamentals plantings for flowering plant taxa surveyed in this study with assigned nectar values and total floral unit counts across all sites per treatment. Some floral units have decimal values due to umbel flowers being recorded as individual florets rather than per umbel, which were converted during analysis to avoid overcounts of these species. Plants are separated into those of native origin and those of which are cultivars or of non-native origin (following Stace, 2001). Note that not all planted species from Table S1 are recorded in Table S2 as they were not necessarily flowering when surveys were carried out.

Table S3. Test for systematic differences in area, urbanisation and floral measures between paired enhanced and control sites, and between phase 1 and phase 2 sites for pollinator measures, floral abundance and nectar production. Floral units (FU) are the total floral unit counts over 10 m² of the transect per site. Visitation frequency (visits) is the total observed pollinating insect flower visits per 200 m² of the transect per site.

Table S4. Model selection statistics of the relationship between visitation frequency (offset by floral units), number of interactions (offset by floral taxon richness) and Shannon diversity of all pollinators combined and separately for taxonomic groups. Model predictors include urbanisation (UP) at four spatial scales (250, 500, 750 and 1000 m), treatment (Enhanced, Control) and interactions as predictors. Values under predictor columns provide the model slope estimate of the variable with the standard error in parentheses, with interactions showing slopes for the control treatment. The 'r.squaredGLMM' function from the 'MuMin' package was used to return r^2 values using the delta method.

Table S5. List of recorded pollinator taxa across all 50 sites. Fine to broad taxonomic resolution provided along with visitation frequency of each distinct taxa.

Table S6. GLMMs to compare the pollinator communities in enhanced sites with and without ornamental plantings across visitation frequency, number of interactions and Shannon diversity for each pollinator group, offset with floral abundance for visitation frequency and floral richness for number of interactions. Significant variables of interest are highlighted in bold.

Figure S1. Mean predicted visitation frequency across the urbanisation gradient and between treatments ($\pm 95\%$ confidence interval), with raw data overlayed for (a) *Bombus* species at 250 m urbanisation radius, (b) other Hymenoptera at 750 m scale, (c) Coleoptera at 750 m scale, (d) *Apis mellifera* at 750 m over both treatments combined. Mean predicted number of interactions of (e) other Hymenoptera over both treatments combined at 750 m scale, (f) Coleoptera at 750 m scale and (g) *A. mellifera* at 500 m scale over both treatments combined. Predictions are derived from the highest ranked models from model averaged sets including treatment and urbanisation predictors in Table S4.

How to cite this article: Poole, O., Costa, A., Kaiser-Bunbury, C.N. & Shaw, R.F. (2024) Pollinators respond positively to urban green space enhancements using wild and ornamental flowers. *Insect Conservation and Diversity*, 1–13. Available from: <https://doi.org/10.1111/icad.12779>