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RESEARCH ARTICLE

# No one-size-fits-all: Trait-dependent effects of local plant diversity on pollinators and pollination service in a densifying city

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## Abstract

1. The densification of urban landscapes reshuffles plant–pollinator interactions and affects the provisioning of pollination services. Improving local-scale habitat quality, for example, planting more flowers in urban greenspaces such as gardens, has been proposed to compensate, but effective pollination also depends on trait matching between pollinators and flowers.
2. In an experimental study, we used four phytometer species with differing flower-visitor specificities to assess pollinator visitation, richness and pollination success along independent gradients of landscape-scale densification and local-scale floral richness.
3. Pollinator visitation and richness declined both with increased urban density and lower floral richness. Flower-rich gardens supported more small solitary and large social bees, but not hoverflies, beetles or small social bees.
4. Pollination success declined with densification but was compensated by floral richness only in phytometers with more specialised pollinators.
5. *Synthesis and applications.* Increasing local floral richness can support pollination success of specialised plants in dense urban landscapes. However, a floral enrichment strategy alone is less effective for generalist plants, which are typically more abundant in plant communities. No single strategy can mitigate the loss of pollinators and pollination services in increasingly urbanising environments. Habitat loss in cities should therefore be addressed not only by selectively increasing the quantity of floral resources for pollinators, but also by additional targeted measures in the surrounding landscape, such as creating and connecting specific habitats for different pollinator groups.

KEYWORDS
ecosystem service, effect traits, individual-based traits, pollination, response traits, sentinel plant, urbanisation, voluntary science

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Merin Reji Chacko and David Johannes Frey contributed equally.

## 1 | INTRODUCTION

Urban densification, such as in-fill development and urban consolidation, is an increasingly accepted sustainable development strategy to minimise the negative consequences of urban expansion and sprawl on biodiversity (Teller, 2021; UN-Habitat, 2015). However, if it results in the removal or reduction of urban greenspaces and other open, non-built areas within existing cities, urban densification can have detrimental effects on biodiversity and ecosystem services (Grêt-Regamey et al., 2020; Grimm et al., 2008; Haaland & van den Bosch, 2015), particularly cultural services, providing non-material, intangible benefits to city dwellers (Garfinkel et al., 2024; Miller, 2005). Ideal urban development strategies would allow for planning and management that benefits both nature and humans, such as through the creation of multifunctional urban greenspaces (Alves et al., 2024; Kabisch et al., 2022). Yet, effective implementation requires a clear understanding of biodiversity-ecosystem functioning relationships and underlying services benefiting both nature and humans in cities (Schwarz et al., 2017). Therefore, strategies enabling dense urban living while maintaining biodiversity and ecosystem services are urgently needed (Elmqvist et al., 2013; Gaston et al., 2013; McDonald et al., 2023).

Gardens are prime examples of multifunctional urban greenspaces within cities, provisioning both cultural (e.g. physical and mental health benefits to humans; Keeler et al., 2019) and regulatory (e.g. pollination; Schwarz et al., 2017) services. Globally, urban gardens provide vital secondary habitats for pollinating insects, even serving as refugia for wild pollinators (Goddard et al., 2010; Hall et al., 2017; McFrederick & LeBuhn, 2006). In particular, gardens may offer novel, resource-rich patches of habitat for flower-visiting insects, especially bees (Fortel et al., 2014; Guenat et al., 2019; Hall et al., 2017; Hostetler & McIntyre, 2001; Kendall et al., 2019; Threlfall et al., 2015). However, few studies have investigated both plant–pollinator interactions, how these interactions are mediated by pollinator traits and outcomes for the provision of pollination services simultaneously in urban gardens.

Gardens represent anthropogenic plant assemblages shaped and maintained by horticultural activities, thus consisting of both cultivated and spontaneously growing plant species (Frey & Moretti, 2019; Quigley, 2011). Consequently, the quantity and quality of floral resources may vary strongly depending on the particular selection of plant species grown and maintained by gardeners. Indeed, floral resource availability may range along a broad gradient: from intensively managed grass monocultures to rich mixtures of native and ornamental flowering plants (Frey & Moretti, 2019; Loram et al., 2008; Threlfall et al., 2015). Unsurprisingly, the persistence and abundance of pollinators has been related to floral resource availability (Cohen et al., 2021); moreover, the functional composition of pollinator communities in urban gardens depends on the availability and variety (i.e. trait diversity) of local floral resources (Fournier et al., 2020). For instance, proboscis length (hereafter 'tongue length') determines the range of flower morphologies that can be accessed by pollinators (Rosas-Guerrero et al., 2014). Long-tongued insects can access flowers with deep corollas that are inaccessible to shorter-tongued pollinators, and co-specialisation between long-tongued bees and flowers with deep corollas ensures a more reliable pollination mutualism (Armbruster, 2017). Consequently, pollination success must rely not just on the quantity of floral resources but also on the match between floral traits and pollinator traits.

Spatially heterogeneous urban landscapes favour generalist hymenopteran pollinators (Fournier et al., 2020). This may favour the reproductive success of generalist plants with open nectaries ('halophilous'; Corbert, 2006), which can be visited by many generalistic pollinator taxa (Liang et al., 2023). Contrastingly, other studies have shown that the loss of non-hymenopteran pollinators decreases the visitation frequency of pollinators on halophilous plants in urban landscapes (e.g. Geslin et al., 2013), demonstrating a need for comprehensive studies including multiple pollinator taxa. Plants with hidden nectaries ('euphilous'; Corbert, 2006), which require pollinators with congruent functional traits (e.g. long-tongued bumblebees), exhibited lower reproductive success along an urbanisation gradient (Pellissier et al., 2012; Zink et al., 2024). However, urban landscapes often favour large-bodied pollinators like bumblebees (Benjamin et al., 2014; Gathmann & Tscharntke, 2002; Westphal et al., 2006). These paradoxical outcomes in potential pollination success may be driven by multiple biotic influences, such as local floral resource availability, pollinator abundance and pollinator traits, which often overlap in urban landscapes and must be disentangled to understand their respective contributions (Harrison & Winfree, 2015; Liang et al., 2023; McDougall et al., 2022; Theodorou, 2022; Zink et al., 2024).

Biotic communities are expected to assemble largely based on traits determining the fitness and life history of single individuals in a given environment (McGill et al., 2006; Violle et al., 2007). Pollinator trait changes—especially at the individual level—can have important consequences for population dynamics and ecosystem processes, such as pollination services (Carrié et al., 2017; Eggenberger et al., 2019; Fontana et al., 2018), especially for self-incompatible plants (de Jong et al., 2005), though results have not always been consistent (Bartomeus et al., 2018). Mobility is a key functional trait determining pollination services in spatially heterogeneous environments, as it influences foraging range (e.g. Cote et al., 2017). In pollinating insects, body size is a measure of mobility as it scales with foraging distance (Greenleaf et al., 2007). Since urbanisation can reduce pollinator dispersal and pollen movement (Adedoja & Mallinger, 2024), urban landscapes may favour larger-bodied bee species with high dispersal capability (Buchholz & Egerer, 2020; Fitch et al., 2019; Fournier et al., 2020). However, within those species, limited resources and urban heat island effects can reduce individual body size (Buchholz & Egerer, 2020; Eggenberger et al., 2019). As a result, even when suitable floral resources are present locally, the pollinators best adapted to access them may be absent. They are simply unable to disperse across fragmented urban landscapes dominated by impervious surfaces.

Urban areas are characterised by significant spatial heterogeneity, primarily driven by human activities and manifested across various scales, from individual management units (e.g. gardens), to landscapes encompassing hectares or kilometres (Zhou et al., 2014). The proportion of impervious (i.e. built and paved) surface—a pervasive feature of urban environments—is a suitable and robust proxy for horizontal components of urban densification and loss of concomitant habitat availability at the landscape scale (Harrison & Winfree, 2015). It characterises the landscape context of a focal habitat patch and offers a space-for-time substitute approach to ongoing habitat loss in cities (McDonnell & Hahs, 2008). As urban greenspaces are increasingly replaced with impervious surfaces, pollinator abundance and richness decrease (Liang et al., 2023; Neumann et al., 2024), disrupting trait-matched plant–pollinator interactions (Geslin et al., 2013). While studies have shown that urbanisation and local habitat conditions reshape pollinator communities and flower visitation patterns (Geslin et al., 2013), precious few studies directly measure the consequences for pollination success (e.g. Zink et al., 2024). As flower visitation is an imperfect proxy for pollination service (King et al., 2013), direct measurements of fruit or seed set are needed for a more mechanistic understanding of whether local floral enrichment can offset negative effects on realised pollination, and whether this depends on plant–pollinator trait matching.

Here, we use a novel experimental approach combining a quasi-orthogonal study design with a system of outcrossing phytometer plant species. We selected 24 gardens in the city of Zurich along independent floral resource availability and densification gradients. Thus, we were able to disentangle the local and landscape-scale drivers of plant–pollinator interactions and pollination services. We set up experimental pots of four focal phytometer plant species along a floral specificity gradient (Albrecht et al., 2007) and measured pollinator visitation frequencies, individual traits and fruit/seed set (i.e. pollination success). Specifically, we aimed to determine: (a) how local floral resource availability and landscape-scale densification in cities influence the flower visitation frequency and richness of various pollinator taxa; (b) how functional traits of pollinators associated with pollination services respond to local floral resource availability and landscape-scale densification; and (c) how floral resource availability and densification interact to influence pollination success.

## 2 | MATERIALS AND METHODS

We performed this study in the central European city of Zurich, Switzerland (47°22′ N, 8°33′ E; Figure 1a). Zurich harbours about 430,000 inhabitants on a surface area of 92 $\mathrm{km}^2$. It comprises the core of the Greater Zurich Area, the largest metropolitan area in Switzerland and home to 1.5 million inhabitants (Federal Statistical Office, 2024).

We considered home gardens (hereafter ‘garden’) as our local habitat patches. To separate local- from landscape-scale effects, we selected 24 gardens to vary independently in their amount of local flowering species richness and landscape-scale proportion of impervious surface cover (Figure 1a,b). Garden selection was based on preliminary assessments using the habitat map of Zurich (Grün Stadt Zürich, 2022) to estimate the surrounding urban density, complemented by field visits to quantify floral richness (Frey & Moretti, 2019). We followed established protocols for the sampling design, site selection and data collection (Reji Chacko et al., 2025a). Garden owners provided permission for access and sampling on their properties. According to Swiss legislation, no special permits were required, as sampling did not involve protected areas nor protected species.

### 2.1 | Local and landscape-scale metrics

We defined the local-scale resource availability (hereafter ‘floral richness’) for pollinators as the species richness of plants producing putatively insect-pollinated flowers, which correlates highly with the abundance and species richness of flower visitors in gardens (e.g. Smith, Gaston, et al., 2006; Smith, Warren, et al., 2006). We considered only plant species flowering in each garden during the experimental period, that is, from early to late summer (Frey & Moretti, 2019). Garden area varied across the gardens, from 135 to 791 $\mathrm{m}^2$. Because species–area relationships could potentially confound patterns of floral richness, we tested for a relationship between garden area and flowering plant species richness and found none (Pearson's $r = -0.21$, $p = 0.32$, $n = 24$), indicating that variation in floral richness primarily reflects garden management rather than garden area per se.

Impervious surface was defined as the proportion of built and paved surface and quantified in ArcGIS (ESRI, 2012) based on the City of Zurich habitat map (Grün Stadt Zürich, 2022) in, 50-, 100-, 250- and 500-m radius sectors around the centre of each focal garden (hereafter ‘densification’). Specifically, we calculated the proportion of area within the ‘versiegelu’ attribute which was classified as ‘versiegelt’ (English: ‘sealed’) (Grün Stadt Zürich, 2022). The combination of several small and one relatively larger spatial scale (500-m) had been found to adequately capture the variation in species composition and ecosystem processes in similar studies in the same city (Frey et al., 2018; Hennig & Ghazoul, 2011; Litteral & Shochat, 2017). The densification variables were highly correlated, the effect strengths of the densification levels (i.e. mean estimates of coefficients) were virtually identical across spatial scales, and the goodness-of-fit was very similar among models (Figures S1 and S2). Thus, results are reported here for the 500-m scale, as it is commonly used in other studies in Zurich (e.g. Casanelles-Abella et al., 2023; Perrelet et al., 2025).

### 2.2 | Phytometer species

We used a phytometer species approach, using species with outcrossing mating systems, either through self-incompatibility or flower morphology preventing self-pollination (Albrecht et al., 2007). Thus, seed and/or fruit set—crucial measures of pollination success—can be largely attributed to pollen transfer and

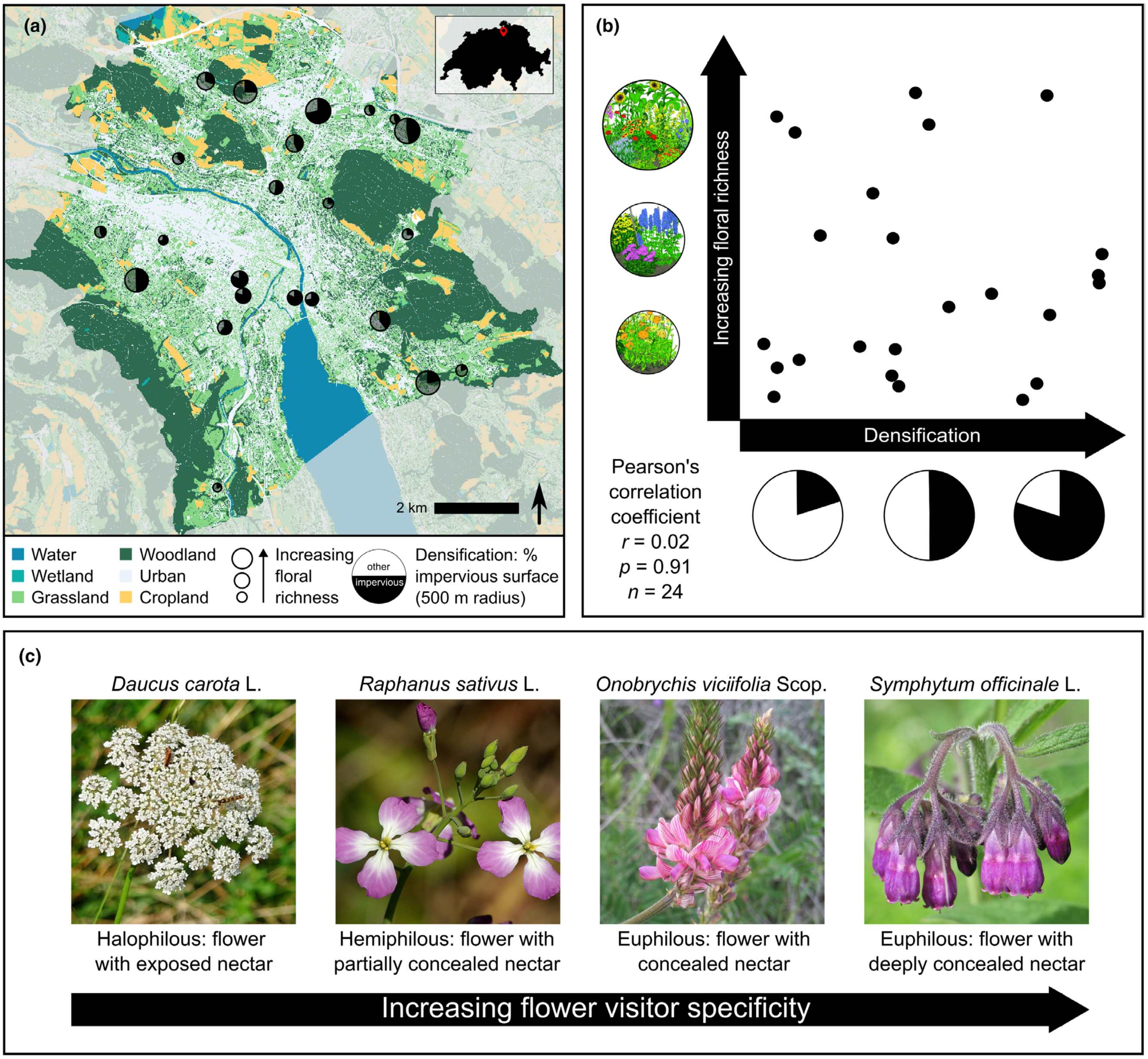

FIGURE 1 Methodological approach. (a) Map of Zurich, Switzerland, with circles representing the 24 gardens in the study. Circle size represents local floral richness; larger circles indicate higher richness. Pie charts represent the proportion of impervious surfaces in a 500 m radius (densification) around the garden. (b) The relationship between floral richness and densification. Black points represent each garden site. Floral richness figures by Esther Schreier. (c) The four phytometer plant species used in this study, from left to right with increasing flower-visitor specificity: *Daucus carota* L. (Photo: Konrad Lackerbeck), *Raphanus sativus* L. (Photo: Alan Schmierer), *Onobrychis viciifolia* Scop. (Photo: Javier Martin) and *Symphytum officinale* L. (Photo: Robert Flogaus-Faust). All photos are sourced via Wikimedia Commons (CC-BY).

insect-driven pollination service (e.g. Albrecht et al., 2007). The four phytometer species had differences in floral types (i.e. access to nectar; sensu Corbert, 2006) which should result in expected variations in their flower-visitor specificity (according to Corbert, 2006; Willmer, 2011): (a) halophilous wild carrot (*Daucus carota* L.) that is primarily visited by wasps, hoverflies and beetles, (b) hemiphilous radish (*Raphanus sativus* L.), typically pollinated by bees, (c) euphilous sainfoin (*Onobrychis viciifolia* Scop.), typically pollinated by long-tongued bees, and (d) deeply euphilous comfrey (*Symphytum officinale* L.), pollinated by long-tongued bees (Figure 1c). We also chose these species due to their numerous flowers/inflorescences per plant, similar plant height and a shared flowering period, that is, May–August.

In each garden, we placed a standardised array of 19 pots comprising all four phytometer species: five pots of carrot, six of radish, five of sainfoin and three of comfrey, totalling 456 pots across 24 gardens, on 9 June 2016. Pots were arranged centrally, rather than along any borders, in order to minimise potential edge effects. Plants were sourced from certified nurseries or grown from seed, hardened outdoors and watered regularly. In each round, we counted all flowers or inflorescences per plant, with carrot assessed by counting umbels. Planting protocols and species-specific arrangements followed established procedures (Reji Chacko et al., 2025a).

## 2.3 | Flower visitation frequency and diversity

A total of 37 pre-trained volunteers sampled up to nine gardens in parallel per day using previously established protocols (Reji Chacko et al., 2025a). Volunteers were randomly assigned to different gardens for each sampling round, but no individual sampled the same garden more than once. We conducted pollinator observations during peak flowering (15 June–20 July 2016), under standardised weather conditions: ≤6 okta cloud cover (Meteorological Office, 2000) and ≤3 Beaufort wind force scale (World Meteorological Organization, Commission for Maritime Meteorology, 1970). In each garden, two to three trained volunteers recorded weather conditions and collected flower visitors on all phytometer plants for nine consecutive hours (9:00–18:00) per day, repeated across at least three rounds. Thus, we determined flower visitation frequency (i.e. pollinator abundance, 'where it counts'), per insect species or group during each of nine consecutive hours per sampling day.

Flower visitors were collected individually after landing on open flowers using a small hand-held collection tube, transferred and stored in cooled containers, and later identified to the species level and sexed by taxonomic experts (see Reji Chacko et al. (2025a) for further details). The four most abundant visitor groups (bees, hoverflies, wasps and beetles) were identified to species level. Lepidopterans were not included due to extremely low visitation rates. Illegitimate pollinators (e.g. nectar robbers) were also recorded but excluded from analyses.

## 2.4 | Measurement of pollinator functional traits

We selected traits that are known to influence flower visitation and are sensitive to urban densification: body size and tongue length (Fournier et al., 2020; Merckx et al., 2018). For body size, we used the well-established proxies intertegular distance and wingspan for bees and hoverflies, respectively (Kendall et al., 2019). We measured the tongue length of bees as the sum of the prementum and glossa lengths and of hoverflies as the labellum/prementum ratio (Gilbert, 1981), according to Reji Chacko et al. (2025a). Pollinators were analysed separately by functional groups, separating hoverflies, wasps, beetles, wild bees and honeybees. Following Albrecht et al. (2007) bee pollinators were further analysed separately according to their level of sociality (i.e. solitary vs. social bees). Sociality is an important additional trait, as it can influence pollination outcome via behavioural differences (Albrecht et al., 2012; Moretti et al., 2017; Williams et al., 2010). Sociality was taken from the European bee species database compiled by Stuart Roberts (see: Code and data availability). Social bees encompassed both eusocial and semi-social species.

## 2.5 | Measurement of pollination success

Fruit set (proportion of fertilised flowers) and seed set (number of seeds per flower or inflorescence) served as proxies for pollination success. We collected all plant pots after the end of flowering: 3–4 August 2016. Flowers produced after the experimental period were marked and excluded from all analyses. Fruits and seeds were left to mature in the greenhouse, and fruit and/or seed set was quantified by species-specific protocols completed before 5 September, according to Reji Chacko et al. (2025a).

## 2.6 | Statistical methods

### 2.6.1 | Local- and landscape drivers of pollinator visitation frequency and species richness

First, we determined whether pollinator visitation frequency and species richness changed with urban densification and floral richness. Pollinator visits were analysed for each pollinator group separately, but pollinator groups were pooled over phytometer plants. To achieve this, we fitted Poisson generalised linear models (GLMs) to analyse the change in flower visitation frequency and species richness of pollinator groups (response variables) as a function of floral richness, urban densification and their interaction (explanatory variables). All models were checked for over-dispersion that, if present, was accounted for by adding an observation-level random factor to models (Korner-Nievergelt et al., 2015). Sampling effort, that is, the time each field worker monitored flowers of phytometer species, could not be standardised perfectly, so we included sampling time as an offset term in the models (Korner-Nievergelt et al., 2015). Hence, we modelled the rates of pollinator visits rather than the absolute counts. We excluded one garden from the analyses, as the sampling effort was significantly lower than the others.

### 2.6.2 | Local- and landscape drivers of pollinator trait response

To determine whether floral richness mediates variation in relative tongue length of bees and tongue shape of syrphid flies we used linear mixed effect models with floral richness, urban densification and their interaction; phytometer species and their interaction with floral richness, and sex as fixed effects; and garden, sampling date and time window as crossed random effects. To account for phylogenetic relationships among pollinators, a nested random effect term with species within genus and genus within family (family/genus/species) entered the model assuming that taxa correctly reflect phylogenetic relationships (i.e. monophyly). In contrast to the body size models, time window was considered a random factor since no direct causal link was expected between daytime and the relative tongue length of a pollinator. Response variables were log-transformed if this improved the normality of the residuals.

To determine whether body size is associated with urban densification and whether floral richness mediates variation in body size, we fitted Gaussian linear mixed effect models with floral richness, urban densification and their interaction; floral richness, phytometer species and their interaction; time window, wind speed, cloudiness and sex as fixed effects, and garden and sampling date as crossed random factors. Phylogenetic structure was corrected for as described above.

### 2.6.3 | Pollination success

Pollination success (i.e. fruit and seed set) was analysed as a function of floral richness, urban densification and their interaction as explanatory variables. Poisson generalised linear mixed effect models were used if response variables were counts (i.e. seed set), and binomial generalised linear mixed effect models were used if the response variables were ratios between fertilised versus non-fertilised flowers (i.e. fruit set). Depending on the sampling units, models were run at the level of individual plants, flowering units (e.g. umbels) or fruits by including plant and garden as nested random factors. To quantify the role of visitation frequency and species richness of pollinator groups driving the observed patterns of pollination success across gardens, Poisson generalised linear mixed effect models were run using the same random term structure.

The flowering of sainfoin was poorly synchronised with that of other phytometer species and thus, three gardens had to be excluded from the analysis due to only one plant being in flower.

### 2.6.4 | Bayesian inference

We used a Bayesian approach to estimate model parameters and their uncertainty. To achieve this, the results from the (G)LMM fits were used to calculate their joint posterior distribution based on improper prior distributions (Korner-Nievergelt et al., 2015). Mean parameter estimates were then obtained by 10,000 random samples from their joint posterior distributions, together with their 95% credible intervals, which express that the range is expected within the true parameter value with a probability of 0.95. The latter was calculated as the 2.5% and 97.5% quantiles of the posterior distributions. Before drawing Bayesian inference, model assumptions and goodness-of-fit were tested in all models. All continuous explanatory variables were *z*-transformed to mean zero and one standard deviation prior to analysis.

We tested model residuals for spatial autocorrelation using Moran's *I* based on simulated residuals using the *DHARMa* package (Hartig, 2025). In the few cases where significant spatial autocorrelation was detected, we fitted models including Moran's eigenvector maps (Tables S1–S6). Details of the spatial diagnostics and sensitivity analyses are provided in Supporting Information and Tables S1–S6. Because effect sizes and statistical inferences for our predictors were qualitatively unchanged, we retained the original model without spatial eigenvectors for presentation and interpretation.

All analyses were run in the software R version 3.5.1 (R Development Core Team, 2023). Models were run with the package *lme4* (Bates et al., 2015), and Bayesian inferences were made using the R package *arm* (Gelman & Hill, 2006).

## 3 | RESULTS

We sampled 5504 native insect pollinators belonging to 157 species over 1244 sampling hours across 92 observation rounds on 18 sampling dates. We additionally captured 256 illegitimate pollinators (i.e. nectar robbers) on comfrey (222 individuals) and sainfoin (34 individuals). The majority of pollinators were bees (Hymenoptera: Anthophila, 66%). European honeybees (*Apis mellifera* L.) represented 9% of all pollinators. For the remaining bee (Hymenoptera: Anthophila) pollinators (54%), 98% were social or solitary species. The remaining 2% either demonstrated parasitic (6 individuals) and/or facultatively social (54 individuals) lifestyles and were not analysed separately. Hoverflies (Diptera: Syrphidae) made up the majority of the remaining non-bee pollinators (29%). The remaining 5% of sampled pollinators were composed of beetles (Coleoptera: Elateriformia, Cucujiformia, Scarabaeiformia) and wasps (Hymenoptera: Chrysididae, Crabronidae, Pompilidae, Sapygidae, Sphecidae, Vespidae). We assessed seed/fruit sets in 14,673 observations in 456 pots across the 24 gardens.

### 3.1 | Influence of local and landscape-scale drivers on pollinator flower visitation frequency and species richness

When analysed separately, densification was associated with a net negative effect on all groups, except for solitary bees and honeybees (Figures 2 and 3). Densification was associated with declines in overall flower visitation frequency when pollinators were pooled ($\beta = -0.33$, 95% CI [−0.26, −0.18], $n = 23$; Figures 2i and 3i). For honeybees, densification was positively associated with their abundance ($\beta = 0.34$, 95% CI [0.14, 0.54], $n = 23$; Figures 2b and 3b), while for solitary bees, no response was detected. Moreover, pollinator richness across all investigated pollinator groups and phytometer species was negatively related to densification (Figures S3 and S4). Pollinators were also analysed separately for each phytometer species; these results were generally consistent with the pooled data (Figure S5).

Floral richness credibly increased wild bee pollinator abundance ($\beta = 0.23$, 95% CI [0.10, 0.36], $n = 23$; Figures 2a and 3a), and to a lesser extent, pollinator species richness (Figures S3 and S4). This effect was independent from those of densification, that is, no credible effect detected from the local by landscape interaction (Figure 3a). The effect on overall pollinator visitation frequency (Figure 2a–i)

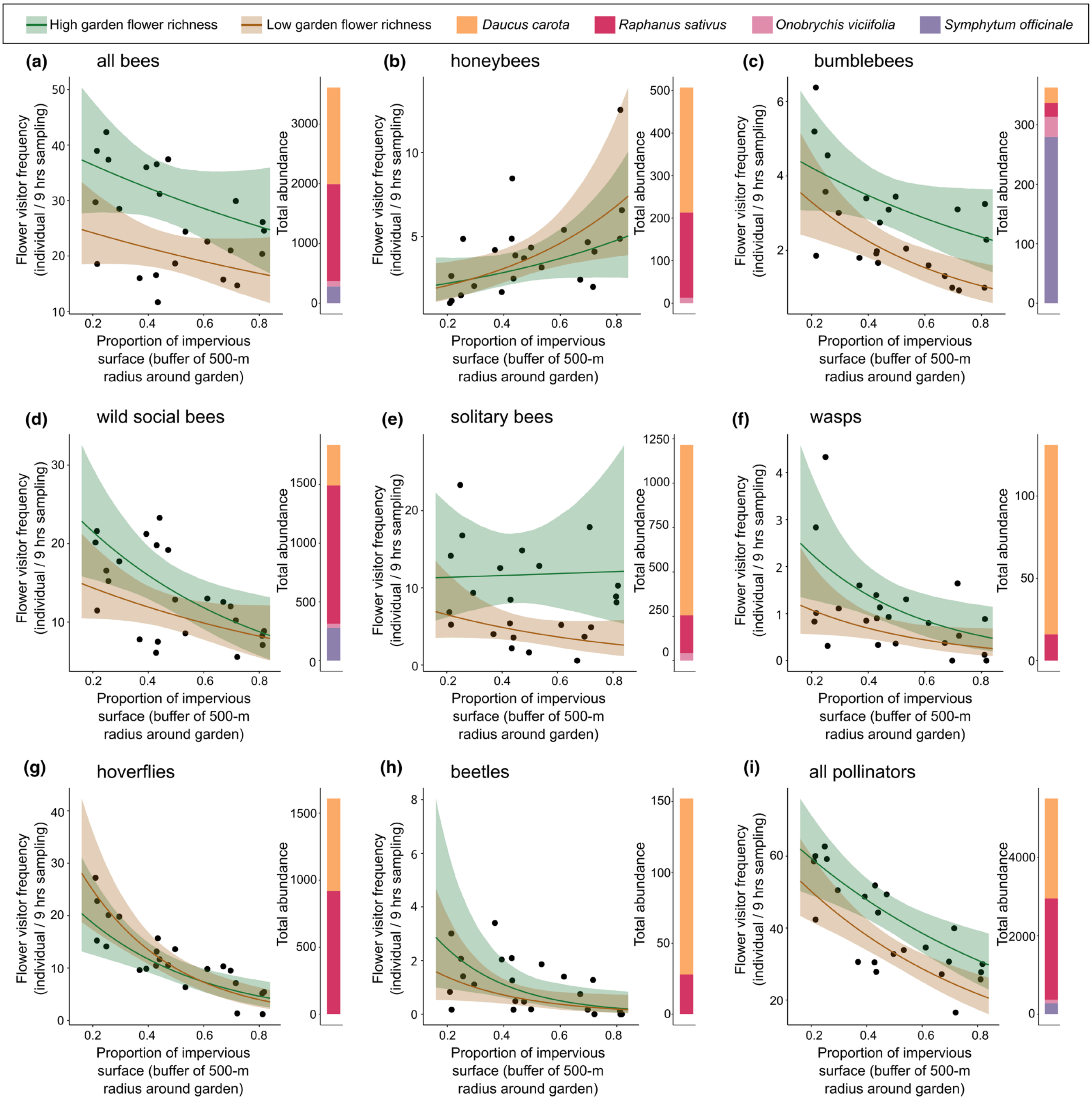

FIGURE 2 Bayesian effect plots depicting the effects of landscape-scale habitat loss (i.e. the proportional area of impermeable surface within 500-m radius circles) on the pollinator abundance (flower visitation frequency in individuals per 9 h of sampling) across all phytometer plants for (a) all bees without honeybees, (b) honeybees, (c) bumblebees, (d) wild social bees, (e) solitary bees, (f) wasps, (g) hoverflies, (h) beetles and (i) all pollinators. Mean values and their 95% credible intervals (CI) were predicted for low and high garden-scale plant species richness of insect-pollinated plants, corresponding to the 20% (brown CI) and the 80% (green CI) percentiles of the observed floral richness. The barplots represent the abundance of the group between the four phytometer plant species (orange: *Daucus carota*, fuchsia: *Raphanus sativus*, light pink: *Onobrychis viciifolia*, purple: *Symphytum officinale*).

was mainly driven by bumblebee ($\beta$=0.25, 95% CI [0.09, 0.40], $n$=23; Figures 2c and 3c), solitary bee ($\beta$=0.48, 95% CI [0.21, 0.75], $n$=23; Figures 2e and 3e) and wasp visitation ($\beta$=0.32, 95% CI [0.05, 0.60], $n$=23; Figures 2f and 3f), while honeybee, hoverfly and beetle visitation frequencies were not affected by floral richness (Figures 1b,g,h and 2b,g,h).

## 3.2 | Local and landscape drivers of pollinator trait variation

Variation in body size and relative tongue length of flower visitors was not primarily driven by floral richness or densification. Instead, the main drivers were sex, phytometer plant species identity and

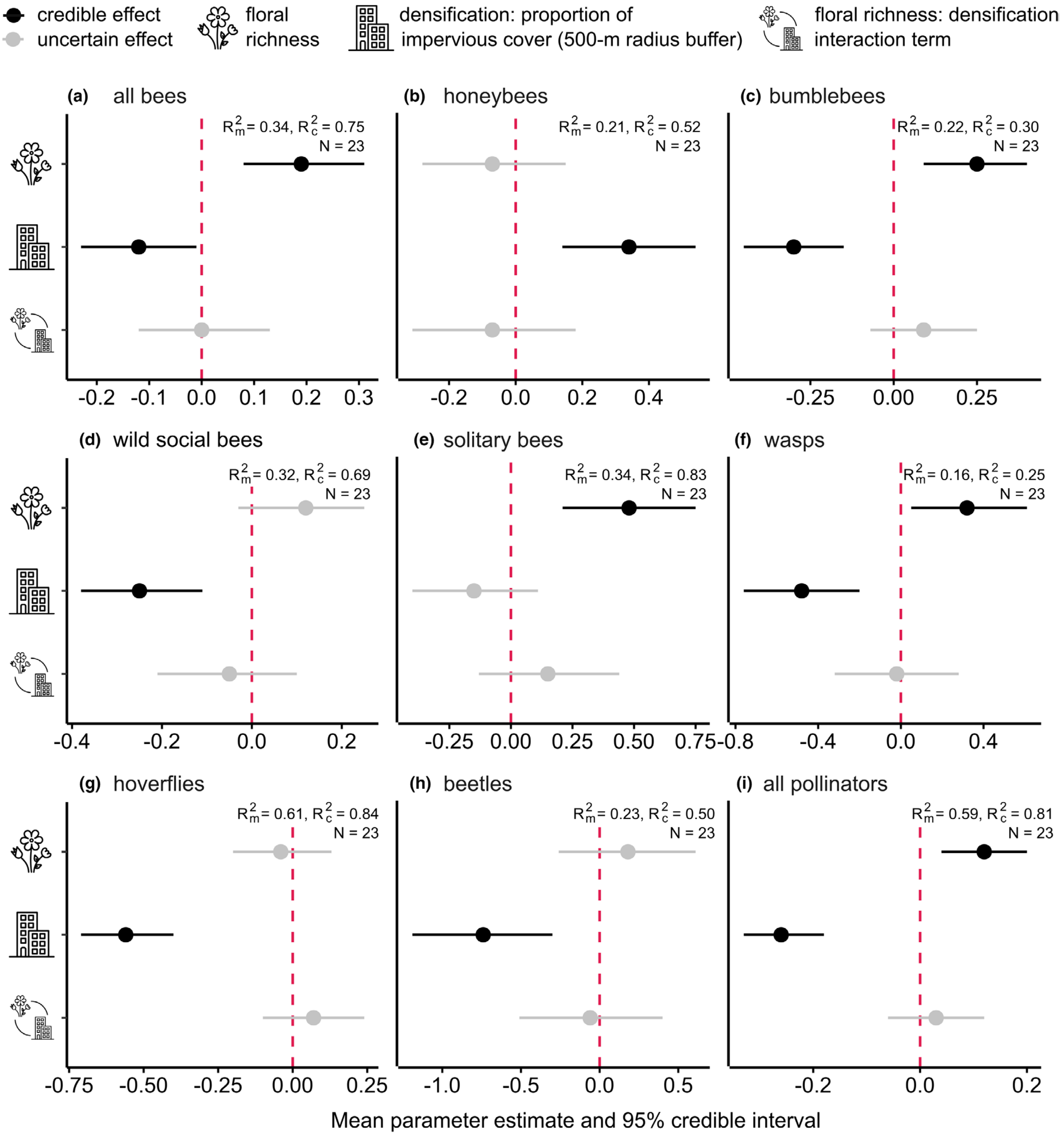

FIGURE 3 Parameter estimates of local (floral richness) and landscape (densification) characteristics and their interaction affecting the abundance of pollinators across all phytometer species for (a) all bees, (b) honeybees, (c) bumblebees, (d) wild social bees, (e) solitary bees, (f) wasps, (g) hoverflies, (h) beetles and (i) all pollinators. Parameter estimates are based on 10,000 random samples from the posterior distributions. Significant effects, that is, credible intervals that do not include zero, are in black, while uncertain effects are given in grey. Floral richness represents the local-scale flowering plant species richness, densification represents the proportion of impervious surfaces in a 500-m radius around the garden. Interaction represents the interaction term between the local and landscape-scale metrics. For the generalised linear mixed effect models, the percentage of explained variance is given for the fixed part (marginal $R^2_m$) and for the entire model (conditional $R^2_c$). For the generalised linear models, the percentage of explained variance is given as $R^2_c$. Number of observations: *N*. Icon attributions: Flaticon.com.

local environmental conditions (e.g. time of day, wind speed, etc.) at the time of sampling (Figures 4 and 5). Densification was slightly negatively associated with the body size for all bees when analysed without honeybees ($\beta = -0.003$, 95% CI [−0.006, 0.000], $n = 2976$; Figure 4a), but not for social or solitary bees alone (Figure 4b,c) nor hoverflies (Figure 4d). The interaction term between floral richness

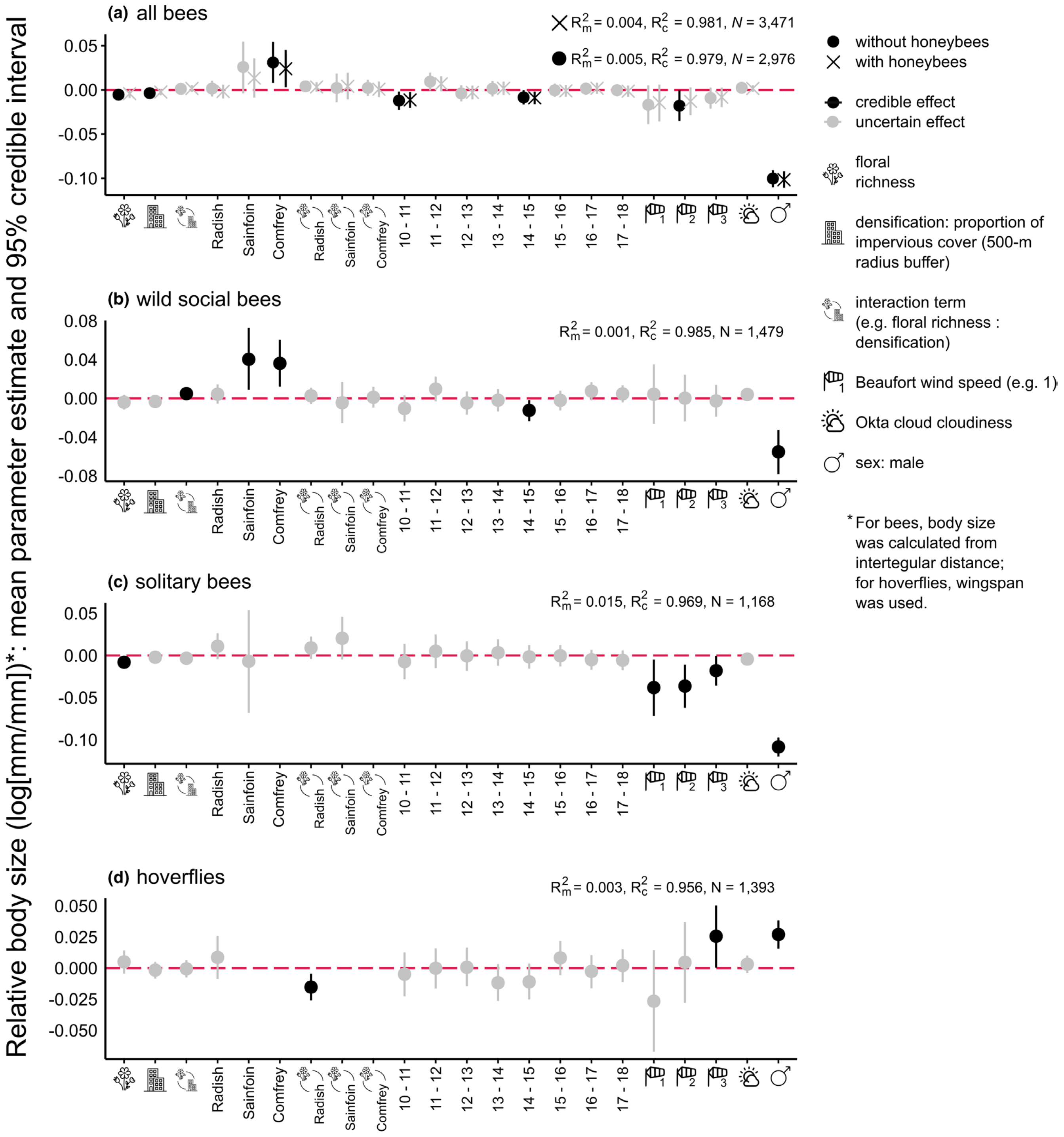

**FIGURE 4** Parameter estimates and 95% credible intervals of local (floral richness) and landscape (densification) characteristics affecting the individual body size of pollinators in five functional groups: (a) all bees (circles) and all bees without honeybees (crosses), (b) social bees, (c) solitary bees and (d) hoverflies. Body size was measured as intertegular distance in bees and as wing length in hoverflies. Mean parameter estimates were obtained by 10,000 random samples from their joint posterior distributions, together with 95% credible intervals, expressing the range expected to contain the true value with 0.95 probability. Significant effects, that is, credible intervals that do not include zero, are given in black (uncertain effects in grey). Percentage of explained variance is given for the fixed part (marginal $R^2_m$) and for the entire model (conditional $R^2_c$), as well as the number of observations (*N*). If the effect of a phytometer plant is lacking, no flower visitors were observed. Plant species effects of *Raphanus sativus* (radish), *Onobrychis viciifolia* (sainfoin) and *Symphytum officinale* (comfrey) are shown relative to *Daucus carota* (wild carrot).

and densification had a slight (though uncertain) positive effect on social bee body size (Figure 4b). Floral richness showed a credible, negative association with the body size of solitary bees ($\beta = -0.008$, 95% CI [−0.013, −0.003], $n = 1479$; Figure 4c) and of all bees when analysed without honeybees, albeit with only a slight effect ($\beta = -0.005$, 95% CI [−0.010, −0.001], $n = 2976$; Figure 4a). Finally,

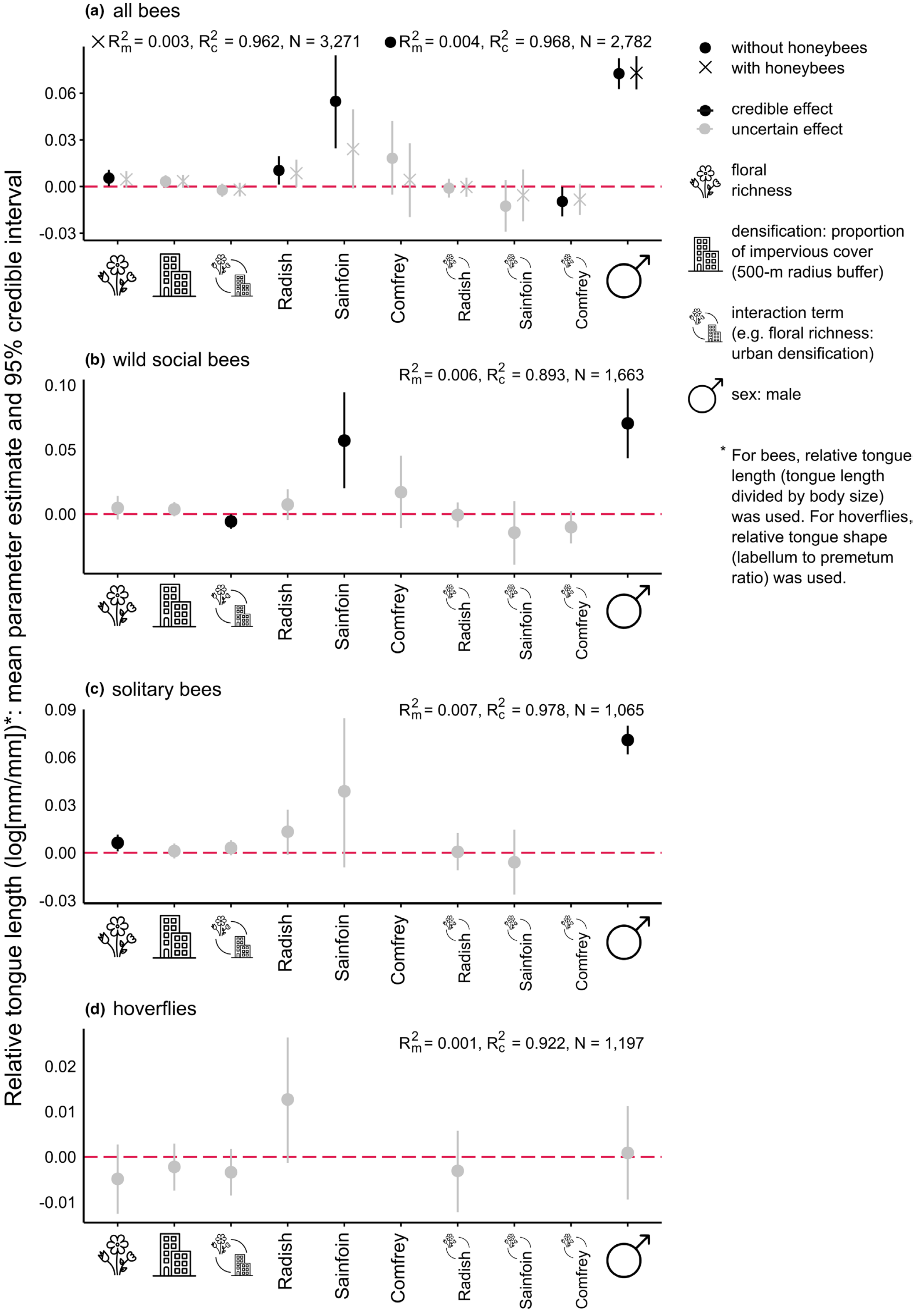
(a) all bees
× $R^2_m$ = 0.003, $R^2_c$ = 0.962, N = 3,271
● $R^2_m$ = 0.004, $R^2_c$ = 0.968, N = 2,782
0.06
0.03
0.00
-0.03
Radish
Sainfoin
Comfrey
Radish
Sainfoin
Comfrey
(b) wild social bees
$R^2_m$ = 0.006, $R^2_c$ = 0.893, N = 1,663
0.10
0.05
0.00
(c) solitary bees
$R^2_m$ = 0.007, $R^2_c$ = 0.978, N = 1,065
0.09
0.06
0.03
0.00
-0.03
(d) hoverflies
$R^2_m$ = 0.001, $R^2_c$ = 0.922, N = 1,197
0.02
0.01
0.00
-0.01
Relative tongue length (log[mm/mm])*: mean parameter estimate and 95% credible interval
● without honeybees
× with honeybees
credible effect
uncertain effect
floral richness
densification: proportion of impervious cover (500-m radius buffer)
interaction term (e.g. floral richness: urban densification)
sex: male
* For bees, relative tongue length (tongue length divided by body size) was used. For hoverflies, relative tongue shape (labellum to premetum ratio) was used.

**FIGURE 5** Parameter estimates and 95% credible intervals of local and landscape characteristics affecting the individual tongue length of pollinators of five functional groups: (a) all bees (circles) and all bees without honeybees (crosses), (b) social bees, (c) solitary bees and (d) hoverflies. In bees, relative tongue length is the proboscis length divided by intertegular distance. In hoverflies, tongue shape is the labellum/prementum ratio. Mean parameter estimates were obtained by 10,000 random samples from their joint posterior distributions, together with 95% credible intervals, expressing the range expected to contain the true value with 0.95 probability. Significant effects, that is, credible intervals that do not include zero, are given in black (uncertain effects in grey). Percentage of explained variance is given for the fixed part (marginal $R^2_m$) and for the entire model (conditional $R^2_c$), as well as the number of observations ($N$). If the effect of a phytometer plant is lacking, no flower visitors were observed. Plant species effects of *Raphanus sativus* (radish), *Onobrychis viciifolia* (sainfoin) and *Symphytum officinale* (comfrey) are shown relative to *Daucus carota* (wild carrot).

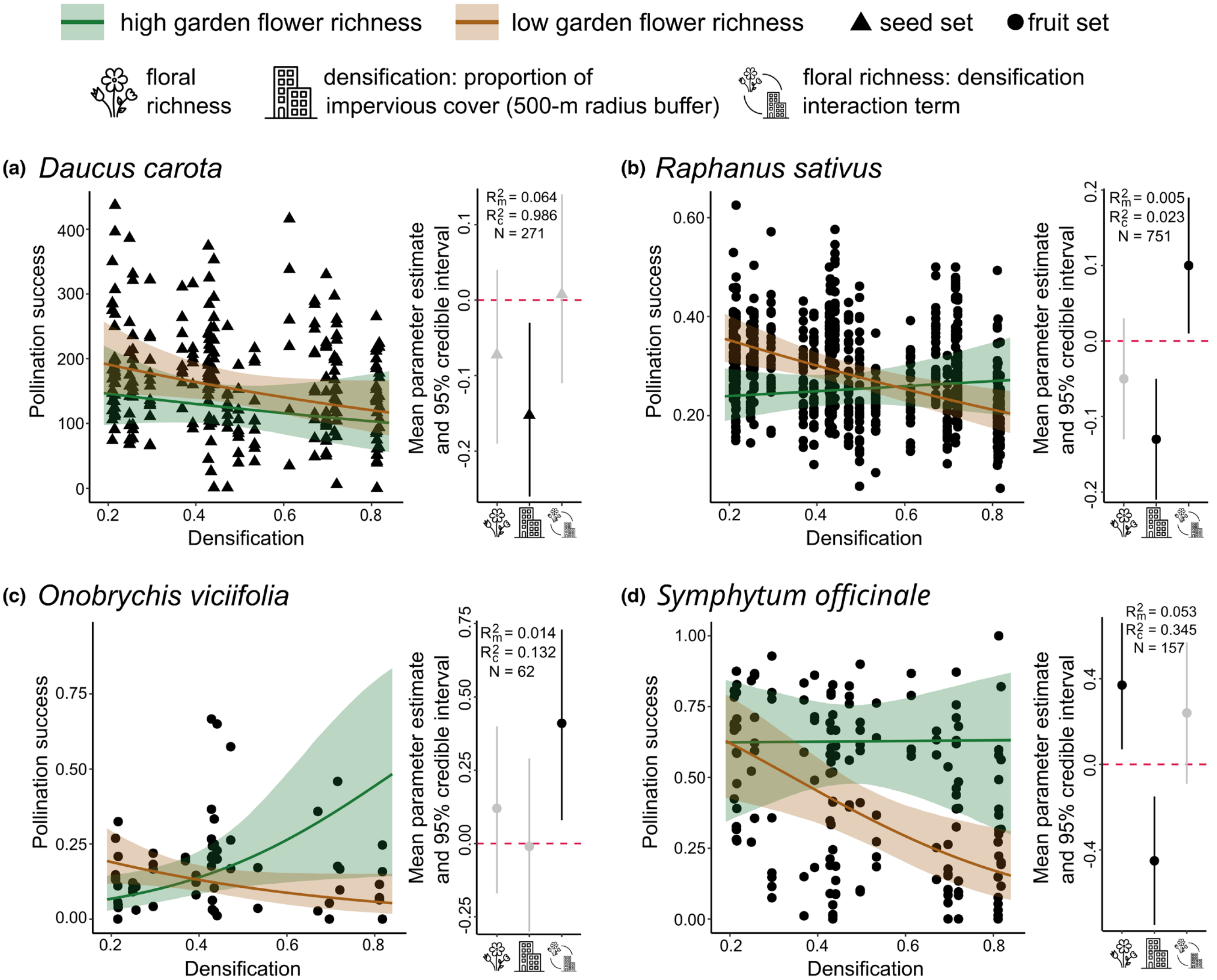

**FIGURE 6** Bayesian effect and coefficient plots illustrating the effects of local flowering species richness and landscape-scale habitat loss on the reproductive success of four phytometer species: (a) seed set of *Daucus carota* as a function of hoverfly abundance, (b) fruit set of *Raphanus sativus* as a function of social bee abundance, (c) fruit set of *Onobrychis viciifolia* as a function of total bee abundance and (d) fruit set of *Symphytum officinale* as a function of social bee abundance. For the effect plots, mean values and their 95% credible intervals (CI) were predicted for low and high garden-scale plant species richness of insect-pollinated plants, corresponding to the 20% (brown CI) and the 80% (green CI) percentiles of the observed local-scale flowering plant species richness. Parameter estimates are based on 10,000 random samples from the posterior distributions. In the coefficient plots, significant effects, that is, credible intervals that do not include zero, are in black, while uncertain effects are given in grey. Local represents the local-scale flowering plant species richness, landscape represents the landscape-scale habitat loss metric (proportion of impervious surfaces in a 500-m radius around the garden). Interaction represents the interaction term between the local and landscape-scale metrics. Percentage of explained variance is given for the fixed part (marginal $R^2_m$) and for the entire model (conditional $R^2_c$), as well as the number of observations ($N$). If the effect of a phytometer plant is lacking, no flower visitors were observed. Icon attributions: Flaticon.com.

the relative tongue length of solitary bees showed a weak but positive relationship with floral richness ($\beta = 0.006$, 95% CI [0.001, 0.011], $n = 1065$; Figure 5c).

### 3.3 | Local and landscape-scale drivers of pollination success

We found that the response of each phytometer plant's pollination success to floral richness and densification paralleled that of pollinator functional groups. The reproductive success of all but comfrey was negatively affected by densification (Figure 6a–d). Floral richness was positively associated with reproductive success in comfrey ($\beta = 0.37$, 95% CI [0.08, 0.67], $n = 157$; Figure 6d) and positive interactive effects were observed between floral richness and densification in both radish ($\beta = 0.01$, 95% CI [0.01, 0.19], $n = 751$; Figure 6b) and sainfoin ($\beta = 0.41$, 95% CI [0.09, 0.73], $n = 62$; Figure 6c).

## 4 | DISCUSSION

Using a quasi-orthogonal experimental design with individual trait-based analyses and direct measurements of pollination success, we show densification had predominantly negative effects on wild pollinator visitation, particularly for non-bee taxa. We found no interactive effects of local and landscape factors on pollinator visitation, but their interaction did influence pollination success—specifically in hemiphilous and euphilous plants. Our results underscore the importance of accounting for both local and landscape drivers and how their interplay shapes pollination outcomes through shifts in trait-dependent plant–pollinator interactions.

We demonstrate that increasing densification and associated loss of pollinator habitat in urban areas results in shifts in pollinator communities, disrupting plant–pollinator interactions and, furthermore, pollination success. In our experimental plant community, pollinator visitation frequencies more than halved between densely built urban landscape sectors (80% of impervious surface), when compared to more loosely built urban landscape sectors (20% of impervious surface). Our results are in line with the existing literature, demonstrating that the richness and abundance of arthropod pollinators decrease at high levels of urbanisation, as pollinator habitats are replaced by impervious surfaces in which neither floral nor nesting resources are available (Fortel et al., 2014; Glaum et al., 2017; Lagucki et al., 2017; Liang et al., 2023; Wenzel et al., 2020).

Body size is expected to be an important trait in mediating such relationships (Harrison & Winfree, 2015; Wenzel et al., 2020). Large-bodied pollinators with large potential foraging ranges should have an advantage over small pollinators in fragmented (urban) landscapes where habitats are few and scattered, and resource locations are difficult to predict due to regular plant biomass removal (e.g. mowing; Carrié et al., 2017; Cote et al., 2017; Wenzel et al., 2020). Conversely, smaller-bodied pollinators have lower energetic requirements and may persist in small, previously colonised, high-quality habitat patches, but only if these patches are sufficiently numerous and well-connected (Baldock et al., 2019; Donkersley et al., 2023; Harrison & Winfree, 2015). Still, while some studies report community-level shifts towards larger actively dispersing insects along an urbanisation gradient (Merckx et al., 2018) while others find taxa-dependent trends in the opposing direction (Hahs et al., 2023) or no significant effects at all (Fortel et al., 2014). Indeed, a recent meta-analysis found no consistent relationship between body size and urbanisation (Liang et al., 2023), a conclusion also corroborated by other syntheses (Buchholz & Egerer, 2020; Wenzel et al., 2020). We found that body size and tongue length or shape were mostly determined by intrinsic biological factors (e.g. sex), the time of day, weather conditions and the plant–pollinator interaction, but less by densification. This supports the idea that traits involved in species interactions play a major role in shaping communities at the local scale of a habitat patch rather than landscape-scale urbanisation (Aronson et al., 2016). This may be especially relevant for central place foragers like bees (Hahs et al., 2023).

The role of body size likely interacts with other traits, such as sociality, leading to inconsistent results (Bartomeus et al., 2018; Moretti et al., 2017; Wenzel et al., 2020; Williams et al., 2010). Due to their restricted mobility and risks for offspring survival during foraging, small solitary bees may depend more on feeding resources that are close to their nesting sites (Hahs et al., 2023). In contrast, large and mobile social bees such as bumblebees gather resources over larger areas (Benjamin et al., 2014; Gathmann & Tscharntke, 2002; Westphal et al., 2006). Notably, bumblebees have been reported to decrease in body size with increasing urban density, either as a result of reduced floral resource availability or as a direct adaptation to more limited resource availability (Austin et al., 2022; Eggenberger et al., 2019; Selva et al., 2025; Theodorou et al., 2021). We found that floral richness promoted both small solitary and large social bees (i.e. bumblebees): the latter mostly when urbanisation levels were high. In contrast, small social bees were mainly landscape-dependent. Our findings suggest that gardens with high floral richness may simultaneously support resident small-bodied bee pollinators and serve as foraging hotspots for large, mobile species in areas where landscape-level habitat is scarce. This highlights the importance of flower-rich gardens as foraging habitats for mobile species in densely built areas where the amount of suitable landscape-scale habitat is low (Harrison & Winfree, 2015). A similar mechanism likely underlies the increased honeybee visitation observed with urban densification, reflecting a concentration of foraging activity by highly mobile social bees into isolated, flower-rich gardens rather than increased colony density (Garbuzov et al., 2015; Hennig & Ghazoul, 2012).

Visitation frequency and richness of non-hymenopteran pollinators did not respond to floral richness: hoverflies and beetles were more negatively affected by increasing densification than any other group. This may not be surprising given their dependence on diverse micro- and macro-habitats as adults and larvae (e.g. Neumann et al., 2024). For instance, many flower-visiting beetles develop in dead wood as larvae, a rare resource in densely built areas (Foster et al., 2019). It might also suggest a stronger dependence on spillover (i.e. mass effects) from semi-natural, woody and more humid habitats when compared to bees (Guenat et al., 2019; Kleijn & van Langevelde, 2006; Meyer et al., 2009; Verboven et al., 2014).

Densification, as measured by the proportion of impervious surface around the garden, led to landscape-scale declines in vegetation cover, which was generally associated with decreased pollination success in all phytometer species. Moreover, in all four phytometer species, we found positive associations between fruit and seed sets and abundance or richness of one or several pollinator functional groups (Figure S6). In addition, the response of phytometer species to floral richness and densification matched their pollinators' response. Taken together, these findings indicate that the loss of flower visitation by pollinators and the loss of pollinator species along densification gradients can impact fruit or seed sets of associated plants, thereby potentially reducing their reproductive success and survival over the longer term. Overall, our results agree with the few existing studies investigating the functional consequences of pollinator loss along habitat loss gradients in cities (Andrieu et al., 2009; Pauw, 2007; Williams & Winfree, 2013; Zink et al., 2024). For instance, Pauw (2007) demonstrated that the loss of specific pollinator species from small patches of remnant native vegetation, which were embedded in an urban matrix, caused pollen limitation in dependent plant species. Similarly, Williams and Winfree (2013) found reduced pollinator abundance, pollinator species richness and pollination services in one but not another woodland herb along an urbanisation gradient of decreasing forest patch size. More recently, Zink et al. (2024) found that reproductive success of two crop species (squash and the buzz-pollinated tomato) decreased with a greater proportion of impervious surface, but potentially due to shifts in pollinator community composition. Contrastingly, Liang et al. (2023) found evidence for increased pollination services with urbanisation in non-tropical regions, likely due to the abundance of both generalistic flower morphologies and pollinators. However, they noted that this increase was likely driven by increased visitation rates of managed pollinators on generalistic flowers (Liang et al., 2023). A direct measurement, such as single-visit effectiveness (King et al., 2013), of pollination service and its relationship along environmental and biodiversity gradients remains an exciting field of exploration, especially under controlled experimental conditions.

Increasing floral richness has been hypothesised to mitigate the negative impacts of urban densification on pollinator diversity and pollination services (Liang et al., 2023; Wenzel et al., 2020). Testing this hypothesis, we found that floral richness can indeed mitigate landscape-driven loss of potential pollination services, at least in hemiphilous and euphilous plants. Floral richness positively correlated with fruit or seed set in all phytometer species that showed positive associations with bees (i.e. radish, sainfoin and comfrey). The strongest and densification-independent effect of floral richness was found in the bumblebee-pollinated comfrey. In flower-rich gardens, the pollination success of more specialised plants (sainfoin and comfrey) did not decrease along the densification gradient, despite the marked decrease in their pollinator group (wild bees and bumblebees, respectively) abundances along the same gradient, even in flower-rich gardens. Feeding niche partitioning of the honeybee and wild bees has been shown to increase with increased proportion of impervious surfaces in the same city (Casanelles-Abella et al., 2023). Therefore, we hypothesise that euphilous plants may have been more preferentially pollinated in flower-rich gardens where both abundance and richness of other pollinators (especially honeybees) and the proportion of impervious surfaces are higher, to avoid competition with other generalist pollinators on plant species with low flower-visitor specificity. Future studies should explore how such shifts in foraging behaviour of entire pollinator communities—possibly mediated by intraspecific and interspecific competition—may also affect pollination success along local and landscape-level resource gradients.

Our study highlights that local floral richness in gardens has a great potential to buffer landscape-driven losses in bee pollinators and pollination service in urban environments expected to undergo densification. Thus, besides maintaining large flower-rich areas such as parks in cities (Fairbairn et al., 2024), managing and maintaining small-scale pollinator habitats, such as gardens, may increase overall pollinator habitat in urban landscapes. We show that this could potentially also have positive outcomes for the flow and provisioning of pollination services across urban landscapes, especially those provided by highly mobile pollinator species (Braaker et al., 2014; Frey et al., 2018; Gaston et al., 2013; Grafius et al., 2016). However, it must be recognised that small-scale habitats should be numerous and well-connected to allow for the long-term persistence of pollinator communities (Baldock et al., 2019; Donkersley et al., 2023; Vega & Küffer, 2021). Yet, non-bee pollinators, such as beetles and flies, are still often neglected, notwithstanding the increasing evidence that they are both important for pollination services and decreasing in abundance despite local resource availability (Dunn et al., 2020; Liang et al., 2023; Muinde & Katumo, 2024; Rader et al., 2016; Wenzel et al., 2020). To favour pollinators across the full taxonomic range and functional spectrum, semi-natural, woody and more humid habitats are also needed. One strategy to achieve this is by landscape complementation and supplementation (Colding, 2007). To support the full diversity of pollinators and the ecosystem services they provide, cities must offer a mosaic of high-quality greenspaces—from flower-rich gardens to semi-natural, woody and humid habitats, including nesting sites and other feeding resources than nectar and pollen along the life cycle. In the face of growing urban densification, ensuring these habitats are well-connected is key to enabling pollinator persistence and maintaining pollination services within increasingly compact urban landscapes. Densification is becoming an increasingly widespread strategy to curb sprawl. Our study offers a case study from Zurich, where densification is an explicit development strategy, and thus provides a useful basis for understanding how it may affect pollinator communities and pollination success. Future studies across multiple cities will be needed to assess the generality of these patterns and to identify the urban contexts in which local resources, together with landscape connectivity and habitat complementation, can best sustain pollinators and the ecosystem services on which growing urban populations depend.

## AUTHOR CONTRIBUTIONS

David Johannes Frey, Marco Moretti, Jaboury Ghazoul and Matthias Albrecht designed the experiment. David Johannes Frey and Marco Moretti developed the protocols, guided the field- and lab work, and participated in the sampling campaign. David Johannes Frey and Merin Reji Chacko performed data analyses and wrote the paper. All authors contributed critically to the drafts and gave final approval for publication.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

## DATA AVAILABILITY STATEMENT

Sampling protocols and raw data are available here: https://doi.org/10.16904/envidat.676 (Reji Chacko et al., 2025b). Scripts to prepare and analyse the data are archived on Zenodo: https://doi.org/10.5281/zenodo.19354924 (Reji Chacko & Frey, 2026). The source code repository is maintained at: https://github.com/mrejichacko/BetterBlooms.

## STATEMENT OF INCLUSION

Our study brings together authors from a number of different countries, including scientists based in the country where the study was carried out, with local garden owners, volunteers and taxonomic experts. Volunteers were trained in ecological monitoring, and outcomes were shared with participants and made openly available, ensuring stakeholder engagement and accessibility of results.

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## SUPPORTING INFORMATION

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

**Figure S1.** (A) Coefficient plots visualising the effects of the strength of densification level on flower visitation frequency (capture rates per 9 h) at different spatial scales. (B) Pearson *r* correlation plot showing pairwise correlations between densification levels measured as the proportion of impervious surface at 50, 100, 250 and 500 m radius buffers around each garden.

**Figure S2.** Percentage of explained variance of Poisson generalised linear mixed effect models having flower visitor frequencies (i.e. capture rates of individuals) as response variable.

**Figure S3.** Bayesian effect plots depicting the effects of densification in cities (i.e. the proportional area of impermeable surface within 500-m radius circles) on the pollinator richness across all phytometer plants for (a) all bees, (b) all bees without honeybees, (c) bumblebees, (d) wild social bees, (e) solitary bees, (f) wasps, (g) hoverflies, (h) beetles and (i) all pollinators.

**Figure S4.** Parameter estimates of local and landscape characteristics affecting the richness of pollinators across all phytometer species for (a) all bees, (b) all bees without honeybees, (c) bumblebees, (d) wild social bees, (e) solitary bees, (f) wasps, (g) hoverflies, (h) beetles and (i) all pollinators.

**Figure S5.** Estimated effects of landscape densification (500 m radius) on pollinator abundance across phytometer species and pooled data.

**Figure S6.** Bayesian effect plots illustrating the effects of pollinator abundance on the pollination success of four phytometer species: (a) seed set of *Daucus carota* as a function of hoverfly visitation frequency (i.e. abundance), (b) fruit set of *Raphanus sativus* as a function of social bee abundance, (c) fruit set of *Onobrychis viciifolia* as a function of total bee abundance and (d) fruit set of *Symphytum officinale* as a function of social bee abundance.

**Table S1.** Results of Moran's *I* tests for residual spatial autocorrelation in pollinator abundance models.

**Table S2.** Moran's *I* tests for hoverfly and beetle abundance models before and after inclusion of Moran's Eigenvector Map (MEM) variables.

**Table S3.** Fixed-effect estimates and *p*-values from original and Moran's Eigenvector Map (MEM)-augmented abundance models for hoverflies and beetles.

**Table S4.** Moran's *I* tests for pollination success models before and (when necessary) after inclusion of Moran's Eigenvector Map (MEM) variables.

**Table S5.** Fixed-effect estimates and *p*-values from original and Moran's Eigenvector Map (MEM)-augmented pollination success models.

**Table S6.** Results of Moran's *I* tests for residual spatial autocorrelation in pollinator trait models.

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