

RESEARCH

Open Access



Local floral resources and edge density within the urban ecosystem promote larger and less variable body size in the great banded furrow bee, *Halictus scabiosae*

Lucie M. Baltz^{1*}, Julianne de Vastey², Hanna Gardein³, Felix Klaus³, Henri Greil³, Robert J. Paxton^{1,4} and Panagiotis Theodorou^{1,4}

Abstract

An organism's body size is a fundamental trait linked to its metabolism, life-history and dispersal. In holometabolous insects, whose size is fixed at adult eclosion, body size can be influenced by environmental factors during development (e.g. nutrition and temperature), or by ecological filtering during adulthood. In bees, larger body size has been linked to advantages in foraging efficiency, thermoregulation, and survival, while excessive variation in body size within populations may indicate developmental instability. Shifts in adult body size have been associated with temperature changes, food resource availability and habitat fragmentation, all of which can be modulated by urbanisation. However, the relationship between urban landscapes and wild bee body size remains poorly understood. In this study we investigated how local floral (food) resources, landscape structure and temperature influence the body size of the great banded furrow bee, *Halictus scabiosae*. Our findings highlight that food resources, semi-natural cover and edge density are the most significant environmental factors influencing body size shifts. Specifically, *H. scabiosae* body size increased with the species richness of flowering host plants at the local patch level. Within sampling sites, body size variation was positively associated with semi-natural cover, suggesting that habitat structure or competition may contribute to size heterogeneity, potentially disrupting size uniformity. Conversely, it was negatively associated with edge density, indicating that a higher amount of ecotones may promote greater size uniformity within populations. Our findings reinforce the idea that enhancing floral resources and improving habitat connectivity through green corridors can support wild bee populations in urban areas.

Keywords Cities, Host plants, Intertergular distance, Urbanisation, Food resources, Semi-natural cover, Edge density

*Correspondence:

Lucie M. Baltz
baltzluce@gmail.com

¹General Zoology, Institute of Biology, Martin Luther University Halle-Wittenberg, Hoher Weg 8, Halle (Saale) 06120, Germany

²Washington & Lee University, 204 W. Washington St, Lexington, VA 24450, USA

³Institute for Bee Protection, Julius Kühn Institute (JKI) – Federal Research Centre for Cultivated Plants, Messeweg 11/12, Braunschweig 38104, Germany

⁴German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Puschstrasse 4, 04103 Leipzig, Germany



© The Author(s) 2025. **Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

Background

Urbanisation is a global phenomenon characterised by the transformation of natural areas and arable land into cityscapes designed to meet human needs, often with negative consequences for biodiversity [1–4]. Urban development is accelerating globally, with urban land cover projected to increase by at least 78% by 2050 [5]. This global urban expansion introduces numerous challenges for living organisms, including increased anthropogenic pollution, the proliferation of impervious surfaces, habitat fragmentation and the loss of semi-natural habitats [6, 7]. Additionally, it contributes to rising local temperatures, a phenomenon known as the urban heat island effect [8]. Collectively, these changes pose significant threats to organisms that are unable to adapt or adjust to these novel and challenging environmental conditions [2].

Nevertheless, urban green spaces can provide suitable habitats for many native species [9, 10], including key ecosystem service providers such as wild bees [3]. The abundance of wild bees is primarily influenced by the availability of suitable nesting and flower (food) resources within their flight range [11]. Therefore, it is not surprising that some wild bee species benefit from the novel nesting opportunities and the high availability and seasonal continuity of flower resources in urban green spaces, including private and public gardens, allotments, parks and cemeteries [4, 12–14]. In fact, previous studies have shown that flower-rich urban sites can support higher abundance and species richness of wild bees compared to agriculture areas [15, 16], rural areas [3] and even nature reserves [15, 17].

However, not all wild bee species benefit from urban areas [4, 18, 19]. Anthropogenic changes, including urbanisation, act as ecological filters, selecting for wild bee species based on their functional traits and ecological requirements, thereby shaping species composition [20, 21]. For example, while cavity-nesting bees may benefit from urban structures such as fences and walls, ground-nesting bees often decline as a result of increased impervious surfaces [4, 22]. Indeed, studies have shown that cavity-nesting bees [14, 22–25], social bees [14, 19, 23, 24, 26] and polylectic bee species [24, 27] tend to benefit from urbanisation. Conversely, urban environments appear to negatively impact the abundance of below-ground, small-bodied bees, early spring-flying species and solitary bees [4, 19, 26, 28, 29].

Body size is one of the most important life-history traits as it is closely linked to fitness [30], including fecundity [31], metabolism, dispersal ability and thermoregulation [32]. In bees, body size is highly correlated with foraging range [33], and the amount of pollen and nectar that an individual can carry [34], which may enhance foraging efficiency and pollination success. Larger bees generally

outperform smaller bees in these aspects, highlighting the advantages of increased body size [33–35]. As a continuous trait, body size varies not only between species but also within species [36], as it responds to changing abiotic and biotic conditions through adaptation and developmental plasticity [30, 37]. Intraspecific variation in body size among wild bees arises primarily due to differences in temperature and food availability during development [35]. Higher temperatures during the larval stage can accelerate development rates, leading to smaller adult body sizes [38]. Conversely, a greater quality and quantity of food resources during the larval stage can result in larger adult bees [39, 40]. Since body size is an important biological trait shaped by environmental factors and physiological constraints, wild bee species are expected to exhibit intraspecific shifts in body size in response to anthropogenic environmental changes, such as climate change and rising temperatures [41], landscape simplification [42] and urbanisation [43]. Furthermore, as individuals within a population tend to be more similar in size under optimal and stable environmental conditions, high variation in body size may indicate variable and stressful conditions, such as elevated temperatures and patchily distributed food resources, which can be the case in urban areas [44, 45].

However, despite a growing body of research, the effects of urbanisation on intraspecific body size in bees remain inconclusive and difficult to predict. Habitat loss and fragmentation caused by impervious surfaces and the urban heat island effect can have contrasting impacts on body size. For instance, Theodorou et al. [46] found that bumble bee body size in cities increases with road density, a proxy of urban fragmentation. Similarly, Brasil et al. [47] found that *Agapostemon virescens* sweat bees were larger in highly urbanised areas. These studies suggest that cities may act as environmental filters favouring large-bodied individuals within a species. In contrast, Eggenberger et al. [48] found that urban bumble bee workers were smaller than their rural counterparts, supporting the hypothesis that higher temperatures and reduced food resources in cities may lead to smaller individuals within a species. Additionally, other studies have reported negative effects [48–51] or no significant effects of urbanisation on bee body size [50, 52].

The inconsistent findings across studies suggests that intraspecific body size responses are not only species-specific but also context- and site-dependent. Furthermore, most research has compared urban ecosystems with rural or agricultural ecosystems, making it difficult to pinpoint the specific urban environmental factors driving body size shifts in bees. To better understand which environmental features within cities influence body size and its variation, studies conducted within the heterogeneous urban landscape are needed. Such research will

help identify how bee body size responds to both local and landscape-level urban factors. Understanding these patterns is crucial for conservation efforts, as body size is a pivotal ecological and evolutionary trait with pervasive effects on individual fitness.

In this study, we extend the research in this field by exploring the relative effects of local floral (food) availability, land surface temperature and landscape composition and configuration on the body size and body size variation of the primitively social wild bee species *Halictus scabiosae*. We hypothesised that these environmental factors would be associated with shifts in *H. scabiosae* body size: specifically, that higher temperatures would correlate with a decrease in body size, while increased floral (food) resources would be associated with an increase in body size. Additionally, we hypothesised that landscape composition and configuration would directly influence body size and body size variation by affecting resource distribution and availability at the landscape level and indirectly by shaping temperature and local floral resource availability.

Methods

Study species

Halictus scabiosae (Rossi, 1790), commonly known as the great banded furrow bee, is a medium sized (12–14 mm in length), polylectic and socially polymorphic wild bee species belonging to the family Halictidae (sweat bees). Mated females emerge in spring and form nests, either alone or with other females, to raise their offspring. Within these nests, some offspring develop into workers, tasked with foraging and brood care, while others become reproductives, which mate and overwinter to start new nests the following year [53, 54]. After the first brood emerges, the founding female typically remains inside the nest, taking on intranidal tasks, rather than participating in foraging [55, 56]. *Halictus scabiosae* is widely distributed across the western Palearctic and is common throughout most of Europe [57]. It is a ground-nesting bee that prefers xerothermic habitats and, in recent decades, its range has expanded northward, likely due to climate warming [58, 59]. Importantly for our study, *H. scabiosae* is very common in anthropogenic habitats, including cities [54, 60].

Study area and sampling

Sampling was conducted in July and August 2021 on artificially planted flower strips in the city of Braunschweig, Germany (Table S1; Fig. 1). The sampling period was chosen to target individuals that developed in 2021 at the study sites, as the egg-laying founding female typically remains inside the nest after the emergence of the first brood early in summer [55, 56], making it unlikely that females from the previous year were collected during this

period. Braunschweig, located in Lower Saxony, has a population of approximately 250,000 inhabitants (braunschweig.de, 2021) and covers an area of 192 km² (north–south: 19.1 km, west–east: 15.7 km), of which 14% is residential, 8.4% consists of industrial and commercial areas, 7.5% is roads, 36% is agricultural land and 26% consists of green areas (parks, gardens, forests and semi-natural cover) (braunschweig.de, 2020). *Halictus scabiosae* was first recorded in Braunschweig in 2018 [58], most likely due to its expansion northwards [59], and is now common and widely distributed throughout the city.

Using hand-nets, we sampled 158 female *H. scabiosae* individuals from 16 sites (10 individuals per site, one site with 8 individuals). To capture a gradient of urbanisation, these sites were distributed from the city centre to the outskirts (Fig. 1). To ensure independent sampling, sites were spaced at least 1 km apart, a distance exceeding the foraging range of most bee species [33]. Sampling was conducted between 09:00 and 15:00 on days with good weather conditions (sunny, >16 °C, low wind; Table S1). Due to the distinct morphological characteristics of *H. scabiosae*, individuals were identified in the field. Collected bees were kept in 100% ethanol and stored at –20 °C for further analysis.

Body size measurements

We used the intertegular distance (ITD), the distance between the two wing bases (tegulae) on the thorax, as a proxy for body size [46, 61, 62]. ITD is strongly correlated with the dry body mass of bees [63] and a good predictor of flight ability as it is associated with flight muscle volume [63] and foraging distance [33]. ITD measurements were taken once per individual by J. de V. using a stereo microscope (Olympus SZX7) with an integrated camera, connected to a computer with the cellSens software v.1.6 digital measurement tool. Additionally, we calculated the percentage coefficient of variation ($CV = 100 \cdot \sigma/\mu$, where σ is the standard deviation and μ is the mean value) of ITD per sampling site.

Environmental data collection

To determine the main environmental factors influencing body size, we collected various environmental data. To ensure sufficient sample size and consistency, bees were collected from planted flower strips, which served as standardized foraging sites. These strips were established in early 2020, except for one planted in early 2021, all using the same seed mix (Table S2). However, at the time of our sampling, they varied in flower richness and abundance (Table S1). Since body size is primarily influenced by the amount of food available to developing larvae [35], we estimated the availability of floral resources at each sampling site. Although *H. scabiosae* is polylectic, it shows a preference for Asteraceae, Plantaginaceae,



Fig. 1 Map of **A** Germany, where the black dot marks the city of Braunschweig, and **B** where the red dots mark the 16 sampling sites in the city of Braunschweig. The ochroid shading represents agricultural areas, the green shading represents semi-natural, forest, and urban green land uses, the grey shadings represent residential area and the black lines represent roads and railway tracks. The map was created with free vector map data licenced by OpenStreetMap Foundation (OSMF) under ODbL (<https://opendatacommons.org/licenses/odbl/>)

Campanulaceae, Convolvulaceae and Dipsacaceae flowers [57, 64]. Therefore, we quantified both flower coverage and species richness, focusing specifically on its main host plants (Tables S2 and S3).

To assess floral resource availability, we placed a 20 m x 20 m quadrat within the flower strip at each site, divided it into four 10 m x 10 m squares. Within each square, we identified the area of 1 m x 1 m with the highest floral resource availability (Fig. S1). For each site, we counted the number of flowering host plant species across all four

1 m x 1 m squares to determine species richness. Flower coverage was assessed by visually estimating the percentage cover of each flowering plant species within each of the four 1 m x 1 m quadrats per site. For each quadrat, the total flower cover was calculated by summing the cover values across all flowering species. The final flower coverage per site was then calculated by averaging the total cover values across the four quadrats. Flowering plants were identified to species level using the *Flora incognita* app (floraincognita.com), which has a 93%

accuracy when multiple images are provided [65]. Floral resource availability was quantified in June, as this period likely influences the development of adult *H. scabiosae* females that were raised in the current year at those sites and subsequently collected in July and August. Across all sites, we identified ten main host flowering plant species, 40% of which were not included in the original seed mix of the flower strips (Table S3). The flower resources measured within the quadrat represent a subset of the total floral availability in the surrounding landscape, but provide a standardised basis for comparing resource availability across sites. Flower species richness and coverage of *H. scabiosae*'s main host plants were used as predictors in subsequent statistical analyses (Tables S2 and S3).

Roads fragment the landscape and may impact bee densities by acting as barriers to foraging and dispersal [66, 67]. A previous study has also found a positive correlation between road density and bee body size [46]. To quantify road density, we measured the total length of roads within multiple spatial radii, increasing in 100 m increments from 100 m to 1,500 m around the centre of each sampling site. Analyses were conducted using Quantum GIS v.3.16.3 (QGIS.org) with road network data obtained from Geofabrik GmbH (download.geofabrik.de).

Land surface temperature (LST) data were obtained using Landsat 8 (landsat.gsfc.nasa.gov/satellites/landsat-8/) using the code provided by Ermida et al. [68]. The Landsat 8 is a thermal infrared sensor with a spatial resolution of 100 m and a 16-day revisit cycle. To capture the main larval development period of *H. scabiosae*, we used median LST data from April to August 2021. LST data were processed using the R packages “terra” [69], “sf” [70] and “exactextractr” [71]. We quantified LST at multiple spatial radii, increasing in 100 m increments from 100 m to 1,000 m around the centre of each sampling site.

We quantified landscape heterogeneity with several metrics that may impact *H. scabiosae* body size and foraging: (i) the proportion of semi-natural cover (e.g. remnant vegetation, shrub land, meadows), (ii) the proportion of managed urban green land uses (e.g. public parks, botanical gardens, allotments, recreation ground like playgrounds and sport fields) and (iii) edge density (i.e. ecotones; transition between two habitat types). These variables were analysed using Quantum GIS with data obtained from Geofabrik GmbH and quantified at multiple spatial radii in 100 m increments from 100 m to 1,500 m.

The effects of landscape on bee body size are likely scale-dependent, as different environmental factors influence body size at varying spatial scales. For instance, local-scale floral resource availability can directly impact larval nutrition and development by determining the immediate foraging success of provisioning females. In

contrast, broader landscape features such as semi-natural areas, managed green spaces, road density and edge density, which affect habitat connectivity, as well as nesting opportunities and foraging range operate at larger spatial scales. These broader-scale factors influence overall resource accessibility and movement potentially shaping bee body size through ecological sorting. Since each predictor may exert its influence at a distinct spatial scale, selecting a single scale risks overlooking key relationships. For example, road density may act as a movement barrier at smaller scales (100–500 m) but serve as an indicator of urban fragmentation at larger scales ($\geq 1,000$ m), potentially filtering for larger-bodied bees that can traverse fragmented landscapes [46]. Similarly, semi-natural areas and managed green spaces may provide critical nesting and foraging habitats at intermediate scales, influencing bee populations differently depending on spatial context.

Studies have shown that a multi-scale approach improves ecological modelling by capturing the most relevant spatial scales for each variable, enhancing our ability to detect patterns and mechanisms driving species responses [72, 73]. By integrating multiple spatial scales, we can better account for the ecological processes influencing *H. scabiosae* body size, ensuring a more comprehensive understanding of how landscape structure affects bee populations. This approach enables us to identify the most predictive scale for each environmental factor, ultimately providing stronger insights into the spatial dynamics of habitat suitability, temperature and fragmentation effects on bee body size.

To identify the spatial scales with the most predictive power for body size shifts in *H. scabiosae*, we correlated our response variables (ITD and CV of ITD) with each of our predictors (road density, LST, proportion of semi-natural cover, proportion of managed green spaces and edge density, Tables S4 and S5). For ITD, the correlation coefficient peaked at the following distances: 1,000 m for road density, 600 m for LST, 900 m for semi-natural cover, 1,500 m for managed green spaces and 1,300 m for edge density. For the CV of ITD, correlation coefficients peaked at 700 m for road density, 600 m for LST, 600 m for semi-natural cover, 1,300 m for managed green spaces, and 1,100 m for edge density. These radii were used in subsequent analyses.

Statistical analysis

All statistical analyses were performed using the R statistical software v.4.3.1 [74]. We used structural equation modelling (SEM), to visualise and statistically test for the importance of predictors and their interrelations in a logical, causal framework. To investigate the effects of road density, LST, proportion of semi-natural cover, proportion of managed green spaces, edge density, main host

flower coverage and main host flower species richness on *H. scabiosae* body size, we constructed models based on directed acyclic graphs (DAGs). First, we created a DAG representing our hypotheses (Fig. 2) and then applied piecewise structural equation modelling (piecewise SEM) using the R package “piecewiseSEM” [75]. In piecewise SEM, paths are estimated in individual models and then integrated into a causal model [75].

To build our piecewise SEMs, we first defined our response variables. For our analyses, we used LST, proportion of semi-natural cover, proportion of managed green spaces, edge density, main host flower coverage, main host flower species richness, body size and body size variation as response variables. We then fitted component models to each of the response variables according to their relationships with road density and each other within our full causal path model. We included a potential landscape and LST influence on floral resources, as many of *H. scabiosae*'s host plants were not part of the seed mixes used in the flower strips. For the response variables: landscape, local floral resources, LST and body size variation we used linear models (LMs). For body size we used linear mixed models (LMMs) with site as a random factor. To avoid any potential effects of seasonality and caste on the body size of *H. scabiosae*, we

included the day of the year as an additional fixed factor in the models of body size and body size variation. Since we sampled some sites over multiple days, we used the median sampling day of the year for each site.

Once we had created our full model, we used a multi-step model selection process to determine the best, most parsimonious model. We removed weak paths and reassessed the model fit using Fisher's C test and Shipley's test of directed separation (d-separation), both implemented in the R package “piecewiseSEM”. To find the best, most parsimonious model, we dropped predictors and compared the Akaike Information Criterion for small sample sizes (AICc), choosing the model with the lowest AICc. All model assumptions were checked visually with the R package “DHARMa” [76] and were found to conform to expectations (normally distributed residuals, homoscedasticity, linearity, no outliers). Furthermore, we checked for collinearity among the predictors with variance inflation factors (VIFs) with a cut-off of five [77]. No multicollinearity was detected in our models. For the LMMs, we report marginal R^2 , which reflects the variance explained by the fixed effects, and conditional R^2 , which includes both fixed and random effects [78].

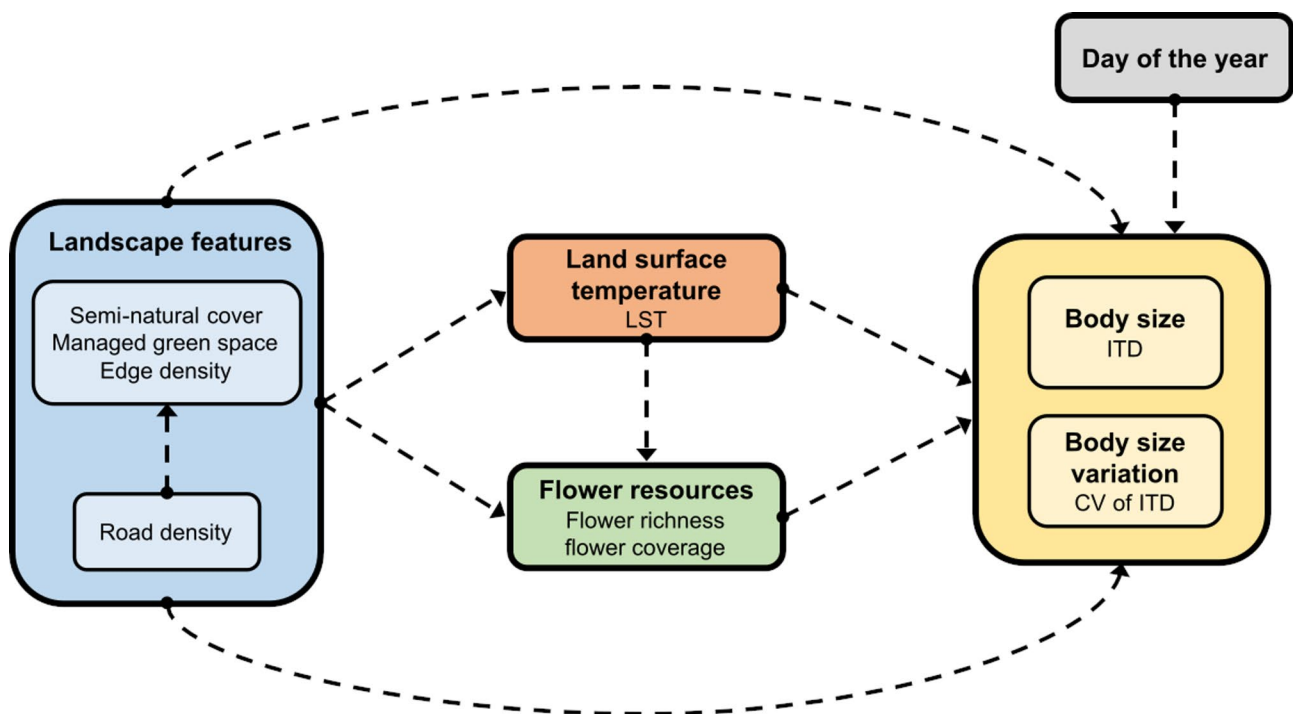


Fig. 2 Conceptual directed acyclic graph (DAG) of all hypothesised links among road density and landscape features, temperature (land surface temperature, LST), flower resources, day of the year and body size (ITD in mm) and coefficient of variation of body size (CV of ITD). Road density is hypothesised to affect ITD and CV of ITD either directly or through effects on landscape heterogeneity, temperature and floral resources. Other landscape features (proportion of semi-natural cover, proportion of managed green spaces and edge density) are hypothesised to affect ITD and CV of ITD either directly or through effects on LST and floral resources. LST is hypothesised to affect ITD and CV of ITD either directly or through effects on flower resources. Flower resources and day of the year are hypothesised to affect ITD and CV of ITD directly

Results

In total, 158 *H. scabiosae* females were measured. The intertegular distance ranged from 1.99 mm to 2.86 mm ($\bar{x} = 2.39 \pm 0.17$ SD, Table S6) and was normally distributed (Fig. S2). The CV of ITD ranged from 3.3 to 9.4% ($\bar{x} = 6.3 \pm 1.6$ SD, Table S6). We tested our hypothesis of indirect causal effects of urbanisation on body size with a piecewise SEM. Our best causal model (Fisher's $C = 11.49$, $P = 0.321$, $df = 10$; Table S8) included an effect of road density on edge density, semi-natural cover and flower richness and an effect of flower richness on body size (Fig. 3). Road density had a negative effect on the proportion of semi-natural cover (LM; $\beta = -0.587$, $P = 0.019$; Fig. 4A, Table S8) and a positive effect on edge density (LM; $\beta = 0.576$, $P = 0.019$; Fig. 4A, Table S8). In addition, the best model included a non-significant negative effect of the proportion of semi-natural cover (LM; $\beta = -0.066$, $P = 0.78$; Fig. S3, Table S8) and a positive effect of edge density, though only marginally significant, on *H. scabiosae* host flowering plant species richness (LM; $\beta = 0.487$, $P = 0.058$; Fig. 4C, Table S8). The main host flowering plant richness had a positive effect on the body size of *H. scabiosae* (LMM; $\beta = 0.212$, $P = 0.028$; Figs. 4D, Table S8).

We tested our hypothesis of indirect causal effects of urbanisation on the coefficient of variance of body size,

i.e. CV of ITD, with a piecewise SEM. Our best causal model (Fisher's $C = 5.434$, $P = 0.71$, $df = 8$; Fig. 5, Table S9) included an effect of road density on edge density and proportion of semi-natural cover and an effect of edge density, proportion of semi-natural cover and day of the year on the CV of ITD. Road density had a negative effect, although not statistically significant, on the proportion of semi-natural cover (LM; $\beta = -0.254$, $P = 0.343$; Fig. S4B, Table S9) and a positive effect on edge density (LM; $\beta = 0.52$, $P = 0.039$; Fig. S4A, Table S9). We found a positive effect of the proportion of semi-natural cover ($\beta = 0.529$, $P = 0.022$; Fig. 6A, Table S9) and a negative effect of edge density (LM; $\beta = -0.511$, $P = 0.031$; Fig. 6B, Table S9) on the CV of ITD. The best model further included a non-significant positive effect of day of the year on the CV of ITD (LM; $\beta = 0.377$, $P = 0.101$; Fig. S4B, Table S9).

Discussion

In this study, we examined the *H. scabiosae* body size as a response variable within a cityscape. Our findings indicate that host flowering plant richness, the extent of semi-natural cover and edge density are key drivers of *H. scabiosae* body size and its variation. Our best models revealed that *H. scabiosae* body size increases with greater host plant richness. Additionally, body size

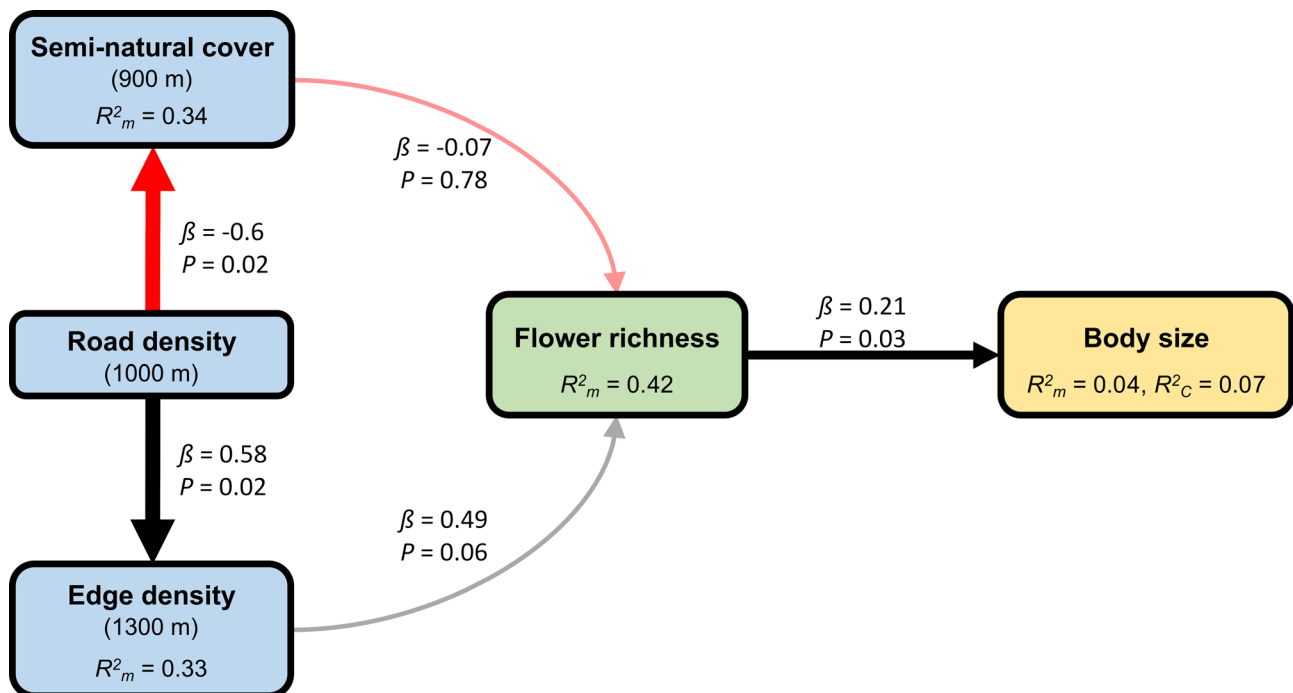


Fig. 3 Directed acyclic graph (DAG) of the best piecewise SEM of the hypothesised indirect effect of road density (radius 1,000 m) on body size (ITD, mm) through semi-natural cover (radius 900 m), edge density (radius 1,300 m) and flower richness. The boxes show the measured variables. The red arrows show negative relationships, and the black arrows show positive relationships, as derived from the piecewise SEM analysis. Non-significant ($P > 0.05$) paths are semi-transparent. The thickness of the arrows represents the magnitude of the standardised regression coefficient. Standardised path coefficients and P -values are reported next to the arrows, and conditional (with all factors, R^2_C) and marginal (only fixed factors, R^2_m) R^2 values are reported for all response variables

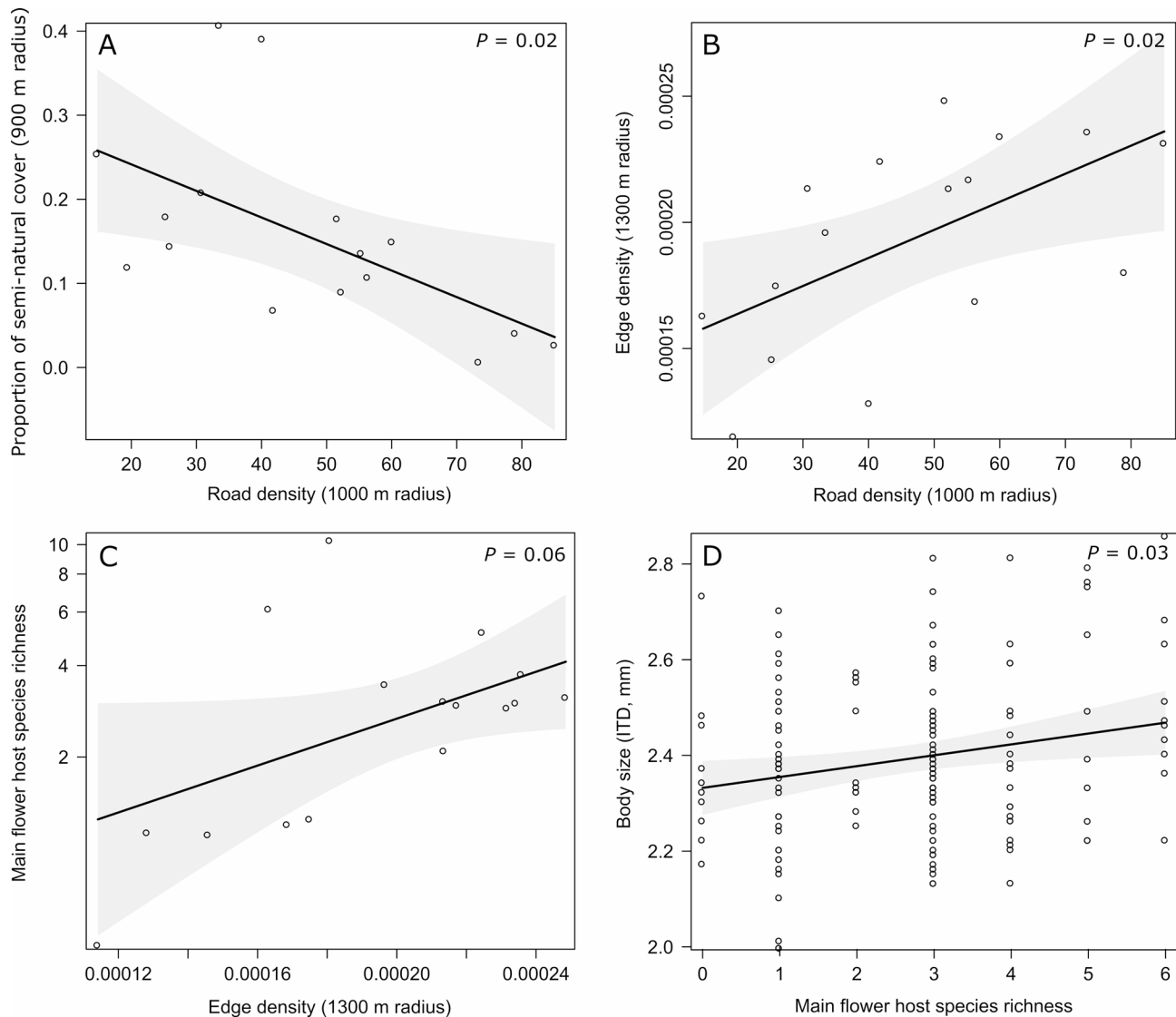


Fig. 4 Relationships resulting from the piecewise SEM between **A** the proportion of semi-natural cover at the 900 m radius and road density at the 1,000 m radius, **B** edge density at the 1,300 m radius and road density at the 1,000 m radius, **C** main host flowering plant species richness of *H. scabiosae* and edge density at the 1,000 m radius, **D** *H. scabiosae* body size (ITD, mm) and its main host flowering plant species richness. Plotted lines show predicted relationships. Shaded areas show 95% confidence interval. P -values are given in the right, upper corner.

variation increases with higher semi-natural cover and lower edge density. Below we expand on these results and discuss their ecological and conservation implications.

Flower richness affects body size

For bees, the quantity and quality of food resources are crucial determinants of body size, as the amount, composition, as well as the nutritional value of larval food directly impact adult size [35, 79]. Several studies have shown that increased pollen quantity and flower abundance lead to larger bee body sizes [40, 80, 81]. However, despite variation in flower abundance among our sample sites, we did not observe a significant effect of flower coverage on *H. scabiosae* body size. This could be because

all samples were collected from flower strips where food quantity was likely sufficient.

Food quality is another important component of dietary resources, as low food quality can limit adult body size [79, 82, 83]. Nutritional composition plays a significant role in bee development. For example, the polylectic sweat bee *Lasioglossum zephyrum* produced larger offspring when larvae were fed a protein-rich diet [39]. Similarly, increased protein supply correlated with larger body sizes in the stingless bee *Nannotrigona perilampoides* [40]. Beyond proteins, nutrients like sodium (Na) and zinc (Zn) are also critical for bee body mass [83, 84]. While specific host plants may provide essential nutrients [85], greater flower richness

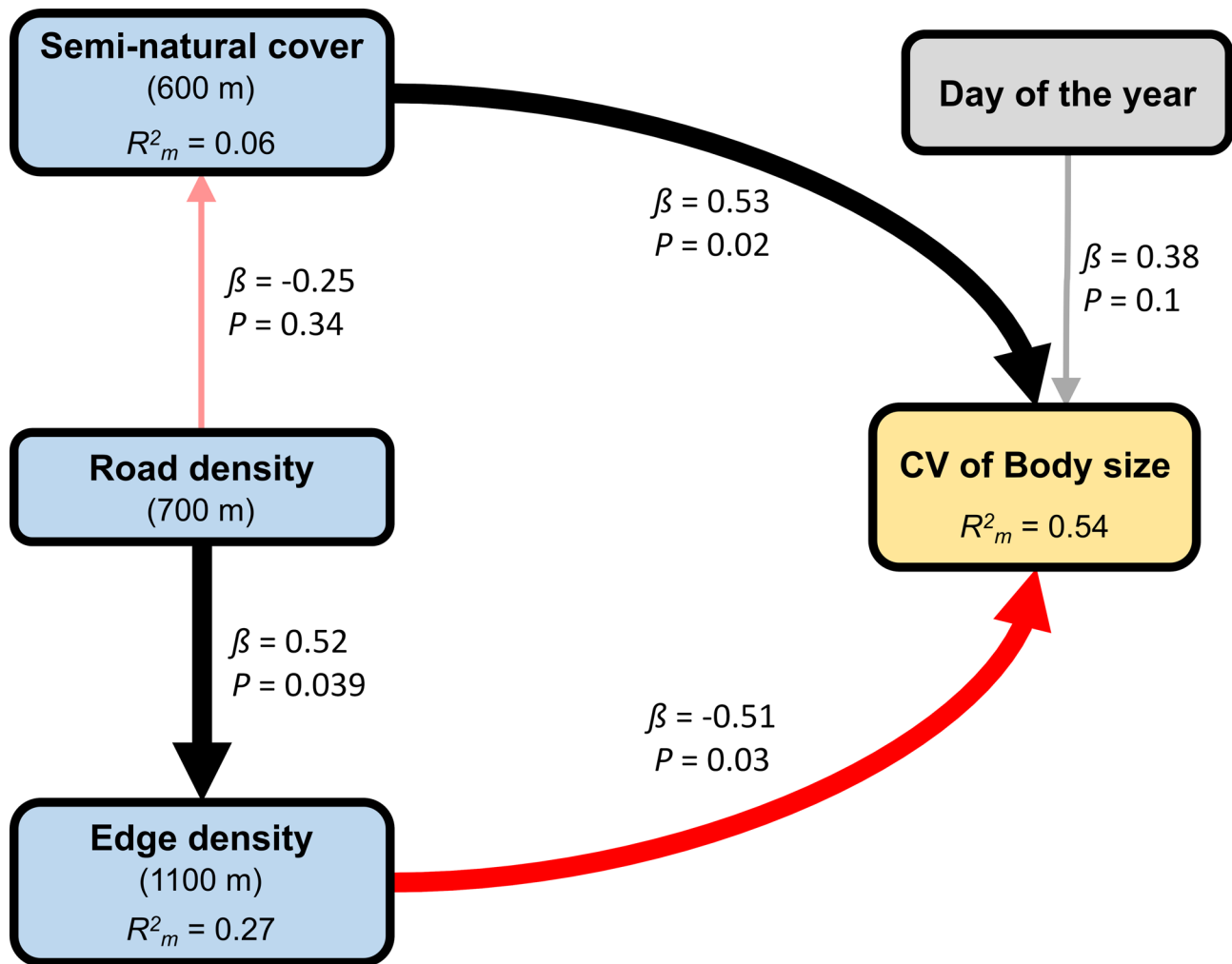


Fig. 5 Directed acyclic graph (DAG) of the best piecewise SEM of the hypothesised indirect effects of road density (radius 700 m) on the coefficient of variance (CV) of body size through edge density (radius 1,100 m) and proportion of semi-natural cover (radius 600 m). The boxes show the measured variables. The red arrows show negative relationships, and the black arrows show positive relationships, as derived from the piecewise SEM analysis. Non-significant ($P > 0.05$) paths are semi-transparent. The thickness of the arrows represents the magnitude of the standardised regression coefficient. Standardised path coefficients and P -values are reported next to the arrows, and marginal R^2 (only fixed factors, R^2_m) values are reported for all response variables

likely increases the probability of balanced larval nutrition. Indeed, *Tetragonula carbonaria* body size has been shown to increase with flower richness [81]. Consistent with these findings, our results show that *H. scabiosae* females exhibited larger body sizes with increasing host plant richness, likely due to enhanced and more diverse larval nutrition i.e. higher food quality.

In our study, the majority of *H. scabiosae*'s primary host plants belonged to the Asteraceae family, which also dominated the floral cover across all sites. Given this consistent dominance, variation in body size is unlikely to result from shifts in plant family composition. Moreover, Asteraceae pollen is generally considered relatively low in protein compared to pollen from other families [86, 87], making it improbable that the body size increase is driven by greater access to high-protein resources.

Instead, we propose that greater species richness, even within a single dominant family like Asteraceae, enhances the nutritional diversity available to developing larvae. A more diverse floral assemblage likely provides a broader spectrum of amino acids, micronutrients, lipids, and beneficial secondary metabolites, which together support improved larval development [88] and ultimately lead to larger adult body sizes. Other urban bee studies also support the relationship between food resources and body size. For example, Tommasi et al. [51] found a positive correlation between floral abundance and *Bombus terrestris* body size along an urbanisation gradient. Additionally, our findings align with the hypothesis that shifts in wild bee body size in urban environments, whether increasing [89] or decreasing [48, 49, 90, 91], are primarily driven by floral resource availability.

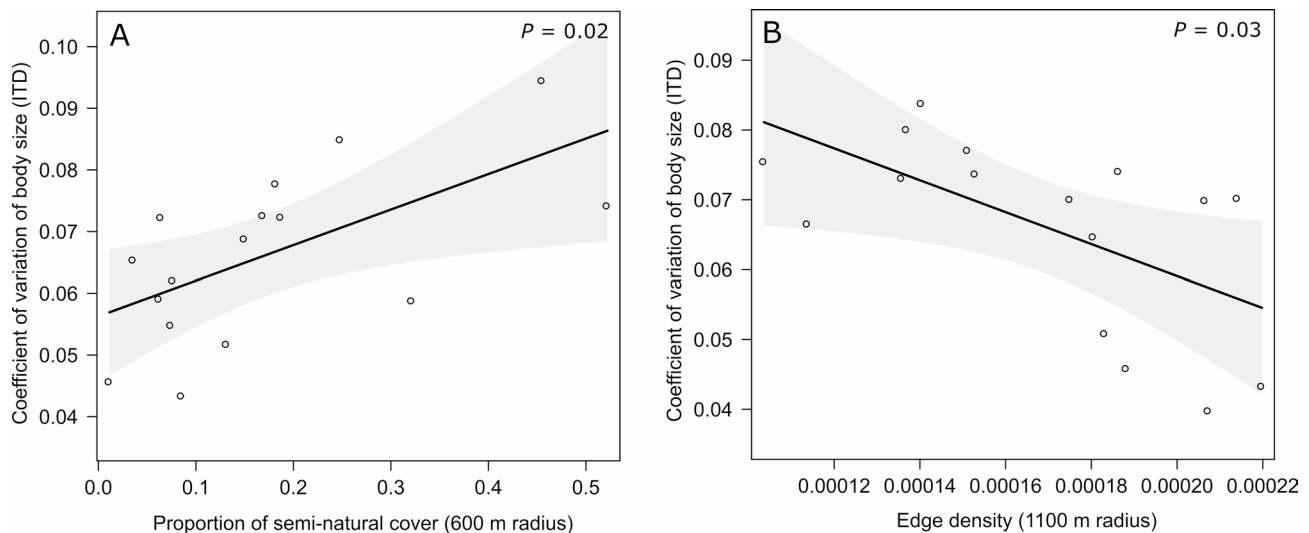


Fig. 6 Relationships resulting from the piecewise SEM between **A** the coefficient of variation of body size (CV of ITD) of *H. scabiosae* and the proportion of semi-natural cover at the 600 m radius, **B** the coefficient of variation of body size (CV of ITD) and edge density at the 1,100 m radius. Plotted lines show predicted relationships. Shaded areas show 95% confidence interval. *P*-values are given in the right, upper corner

However, bee body size is also influenced by other environmental factors beyond floral resources. Fragmentation (e.g. road density) and temperature have been shown to affect bee body size [46, 92]. Along an urbanisation gradient, Merckx et al. [93] found a positive correlation between impervious surfaces and micromoth body size, while Tommasi et al. [51] found a negative effect of temperature on *B. pascuorum* body size. However, in our study, neither road density nor temperature significantly influenced *H. scabiosae* body size. This could be due to species-specific responses to urban environmental factors or context-dependent effects of the surveyed city. Notably, *H. scabiosae* is a thermophilic species expanding northward [59, 94, 95] and constructs nests up to 30 cm deep in the ground [53]. Its preference for warm conditions and the insulating effect of subterranean nests may buffer the impact of temperature fluctuations, potentially explaining why surface temperature as determined by us at the landscape level did not affect body size in our study. Future studies should experimentally rear *H. scabiosae* under different food and temperature conditions to better understand their relative influences on body size.

Overall, we did not find a significant direct or indirect effect of urban landscape heterogeneity on body size. While edge density had a marginally significant effect on flowering plant richness, its indirect effect on body size was not significant. Ecotones, characterised by local vegetation, can serve as foraging and nesting habitats for bees [3, 96, 97] and act as pollen transportation corridors, facilitating plant reproduction and connectivity between plant populations [98–100]. In our study, flowering plant richness was not limited to the species included in the

seed mix of the flower strips but also included other spontaneously growing species. This suggests that higher edge density may have enhanced landscape connectivity, potentially facilitating seed dispersal and contributing to greater floral richness at these sites.

Proportion of semi-natural cover and edge density affect variation in body size

Body size variation in a population tends to be higher under stressful environmental conditions [44, 45]. Stressors for wild bees are, for example, increased temperatures due to climate change, exposure to pesticides and pathogens and nutritional stress due to food scarcity and competition [101]. Since adult body size is primarily determined by food during the larval stage, greater size variation may reflect inconsistent food resource availability [35] or competition with other species, e.g. honeybees [102]. In general, increased body size variation may indicate greater environmental instability, shaped by factors like food availability and temperature.

Semi-natural areas are often considered less stressful environments for wild bees because they provide abundant food and nesting resources, supporting higher wild bee diversity and abundance [103–105]. Additionally, they may buffer the negative effects of climate change on wild bee populations [106]. However, we observed that increased semi-natural cover was associated with greater body size variation in *H. scabiosae* females. At a 900 m scale, this effect may be driven by the heterogeneous nature of urban semi-natural areas and the distribution of resources across microhabitats. Variability in vegetation structure and floral resource availability within those semi-natural areas can lead to differences in nutritional

intake during larval development, contributing to body size variation. Additionally, while semi-natural areas provide more floral resources, they support higher bee densities and increased species diversity [107, 108], potentially intensifying competition for high-quality or preferred food sources [109]. This competition could lead to uneven access to resources, amplifying differences in body size among individuals. Furthermore, due to increased host density in areas with greater semi-natural cover, bees may experience higher parasite pressures [110, 111], which could impose differential selection on body size [112, 113]. These stressors could alter developmental trajectories and influence parental investment strategies, further shaping body size variation in bee populations. In contrast, higher edge density was associated with decreased body size variation. This could be explained by ecotones promoting plant diversity [98, 99, 114], thereby stabilising food availability and reducing foraging trip duration [115]. Additionally, wild bees frequently use habitat edges as foraging and dispersal routes [116], potentially leading to more stable environmental conditions for *H. scabiosae* in areas of high edge density.

More broadly, it is important to recognize that increased body size variation does not necessarily reflect environmental stress alone. In primitively eusocial species such as *H. scabiosae*, body size variation may also carry adaptive significance by enabling flexible task allocation and division of labour within colonies [35]. In some populations, larger individuals may be better suited to tasks such as long-distance foraging or handling specific floral resources, while smaller individuals may focus more on intranidal tasks such as brood care, nest maintenance, or guarding [35, 117]. This variation can enhance colony resilience, particularly in heterogeneous or unpredictable environments where resource availability and competition fluctuate [35]. However, evidence for size-based division of labour in *H. scabiosae* is mixed; while some populations exhibit clear size-related roles [118], others show no significant size differences between foraging and egg-laying females [53]. This suggests that body size variation in *H. scabiosae* likely reflects a combination of environmental stressors and adaptive developmental plasticity, with the expression of these dynamics varying by ecological context. Importantly, these mechanisms are not mutually exclusive. Furthermore, the threshold at which variation shifts from being adaptive to maladaptive, indicating stress rather than functional flexibility, is context-dependent and remains poorly defined in the current literature [35]. This dual interpretation is particularly relevant to our finding that body size variation increased with greater semi-natural cover, potentially reflecting both the adaptive benefits of task flexibility in heterogeneous environments and the developmental

costs associated with uneven or unpredictable resource distribution.

Conclusion

Wild bees are vital ecosystem service providers with significant ecological and economic value. *Halictus scabiosae* is likely a key pollinator for Asteraceae plants, making its response to urban environments particularly relevant. Body size is one of the most important life-history traits as it is closely linked to fitness, metabolism and dispersal ability [30]. Our findings suggest that, within the urban ecosystem, the availability of diverse or high-quality food resource is a major driver of body size shifts in *H. scabiosae*. To support wild bee populations in urban areas, future conservation efforts should focus on enhancing floral resources and improving habitat connectivity by increasing the amount of ecotones. Specifically, city planners and policymakers should increase and diversify urban floral resources by promoting native plant species, enhance green corridors to provide foraging routes and habitat connectivity. Given that cities can serve as critical refuges for wild bee species, integrating these measures into urban planning will be essential for maintaining pollinator diversity and sustaining ecosystem services in an increasingly urbanised world.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s12862-025-02416-5>.

Supplementary Material 1.

Acknowledgements

We are grateful to the Lower Saxon State Department for Waterway, Coastal and Nature Conservation (NLWKN) for permission to sample wild bees.

Authors' contributions

L.M.B. participated in study design, collected and analysed the data and drafted the manuscript. J.d.V. collected data. H. Ga., F.K. and H.Gr. participated in plant data collection and bee sampling. R.J.P. participated in study design and data interpretation and P.T. participated in study design, drafted the manuscript and data interpretation. All authors contributed in drafting and finalizing the manuscript.

Funding

Open Access funding enabled and organized by Projekt DEAL. This study is part of the BeesUp project, which is funded by the German Federal Agency for Nature Conservation (within the Federal Biological Diversity Programme) with funds from the Federal Ministry for the Environment, Nature Conservation, Nuclear Safety and Consumer Protection (Grant Number: 3520685A29).

Data availability

All data are available as supplementary material.

Declarations

Ethics approval and consent to participate

Collecting females of *Halictus scabiosae* does not require ethical approval.

Consent for publication

All authors approved the text.

Competing interests

The authors declare no competing interests.

Received: 8 March 2025 / Accepted: 3 July 2025

Published online: 31 July 2025

References

- Grimm NB, Faeth SH, Golubiewski NE, Redman CL, Wu J, Bai X, et al. Global change and the ecology of cities. *Sci*. 2008;319:756–60.
- Elmqvist T, Fragkias M, Goodness J, Güneralp B, Marcotullio PJ, McDonald RI, Parnell S, Schewenius M, Sendstad M, Seto KC, Wilkinson C. Urbanization, biodiversity and ecosystem services: challenges and opportunities: a global assessment. *Springer Nature*; 2013. <https://doi.org/10.1007/978-94-007-7088-1>.
- Theodorou P, Radzevičiūtė R, Lentendu G, Kahnt B, Husemann M, Bleidorn C, et al. Urban areas as hotspots for bees and pollination but not a panacea for all insects. *Nat Commun*. 2020;11:576.
- Liang H, He Y, Theodorou P, Yang C. The effects of urbanization on pollinators and pollination: A meta-analysis. *Ecol Lett*. 2023;26:1629–42.
- Huang K, Li X, Liu X, Seto KC. Projecting global urban land expansion and heat Island intensification through 2050. *Environ Res Lett*. 2019;14:114037.
- Seto KC, Güneralp B, Hutyra LR. Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. *Proc Natl Acad Sci U S A*. 2012;109:16083–8.
- Ren Q, He C, Huang Q, Zhang D, Shi P, Lu W. Impacts of global urban expansion on natural habitats undermine the 2050 vision for biodiversity. *Resour Conserv Recycl*. 2023;190:106834.
- Rizwan AM, Dennis LYC, Liu C. A review on the generation, determination and mitigation of urban heat Island. *J Environ Sci*. 2008;20:120–8.
- McKinney ML. Effects of urbanization on species richness: A review of plants and animals. *Urban Ecosyst*. 2008;11:161–76.
- Aronson MFJ, La Sorte FA, Nilon CH, Katti M, Goddard MA, Lepczyk CA, et al. A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. *Proc R Soc B Biol Sci*. 2014;281:20133330.
- Westrich P. Habitat requirements of central European bees and the problems of partial habitats. In *Linnean Society symposium series* 1996;18:1–16.
- Baldock KCR, Goddard MA, Hicks DM, Kunin WE, Mitschunas N, Morse H, et al. A systems approach reveals urban pollinator hotspots and conservation opportunities. *Nat Ecol Evol*. 2019;3:363–73.
- Theodorou P, Herbst S-C, Kahnt B, Landaverde-González P, Baltz LM, Osterman J, et al. Urban fragmentation leads to lower floral diversity, with knock-on impacts on bee biodiversity. *Sci Rep*. 2020;10:21756.
- Weber M, Diekötter T, Dietzsch AC, Erler S, Greil H, Jütte T, et al. Urban wild bees benefit from flower-rich anthropogenic land use depending on bee trait and scale. *Landsc Ecol*. 2023;38:2981–99.
- Baldock KCR, Goddard MA, Hicks DM, Kunin WE, Mitschunas N, Osgathorpe LM, et al. Where is the UK's pollinator biodiversity? The importance of urban areas for flower-visiting insects. *Proc R Soc B Biol Sci*. 2015;282:20142849.
- Theodorou P, Albig K, Radzevičiūtė R, Settele J, Schweiger O, Murray TE, et al. The structure of flower visitor networks in relation to pollination across an agricultural to urban gradient. *Funct Ecol*. 2017;31:838–47.
- Theodorou P, Osterman WH, Mrozek JH, Wild BS, Beckmann M, Osterman J, Paxton RJ. Protected areas do not outperform urban wastelands in supporting insect pollinators and pollination in central Germany. *Basic Appl Ecol*. 2025;84:29–39.
- Bates AJ, Sadler JP, Fairbrass AJ, Falk SJ, Hale JD, Matthews TJ. Changing bee and hoverfly pollinator assemblages along an Urban-Rural gradient. *PLoS ONE*. 2011;6:e23459.
- Banaszak-Cibicka W, Żmihorski M. Wild bees along an urban gradient: winners and losers. *J Insect Conserv*. 2012;16:331–43.
- Buchholz S, Egerer MH. Functional ecology of wild bees in cities: towards a better Understanding of trait-urbanization relationships. *Biodivers Conserv*. 2020;29:2779–801.
- Wenzel A, Grass I, Belavadi VV, Tscharnke T. How urbanization is driving pollinator diversity and pollination—A systematic review. *Biol Conserv*. 2020;241:108321.
- Fortel L, Henry M, Guilbaud L, Guirao AL, Kuhlmann M, Mouret H, et al. Decreasing abundance, increasing diversity and changing structure of the wild bee community (Hymenoptera: Anthophila) along an urbanization gradient. *PLoS ONE*. 2014;9:e104679.
- Cardoso MC, Gonçalves RB. Reduction by half: the impact on bees of 34 years of urbanization. *Urban Ecosyst*. 2018;21:943–9.
- Banaszak-Cibicka W, Dylewski Ł. Species and functional diversity — A better Understanding of the impact of urbanization on bee communities. *Sci Total Environ*. 2021;774:145729.
- Cane JH, Minckley RL, Kervin LJ, Roulston TH, Williams NM. Complex responses within a desert bee guild (Hymenoptera: Apiformes) to urban habitat fragmentation. *Ecol Appl*. 2006;16:632–44.
- Villalta I, Bouget C, Lopez-Vaamonde C, Baude M. Phylogenetic, functional and taxonomic responses of wild bee communities along urbanisation gradients. *Sci Total Environ*. 2022;832:154926.
- Buchholz S, Gathof AK, Grossmann AJ, Kowarik I, Fischer LK. Wild bees in urban grasslands: urbanisation, functional diversity and species traits. *Landsc Urban Plan*. 2020;196:103731.
- Ahrné K, Bengtsson J, Elmqvist T. Bumble bees (*Bombus* spp.) along a gradient of increasing urbanization. *PLoS ONE*. 2009;4:e5574.
- Wray JC, Neame LA, Elle E. Floral resources, body size, and surrounding landscape influence bee community assemblages in oak-savannah fragments. *Ecol Entomol*. 2014;39:83–93.
- Brown JH, Marquet PA, Taper ML. Evolution of body size: consequences of an energetic definition of fitness. *Am Nat*. 1993;142:573–84.
- Honěk A, Honek A. Intraspecific variation in body size and fecundity in insects: A general relationship. *Oikos*. 1993;66:483.
- Calder WA. Ecological consequences of body size. *Encyclopedia of life sciences*. Wiley. 2001.
- Greenleaf SS, Williams NM, Winfree R, Kremen C. Bee foraging ranges and their relationship to body size. *Oecologia*. 2007;153:589–96.
- Kerr NZ, Crone EE, Williams NM. Integrating vital rates explains optimal worker size for resource return by bumblebee workers. *Funct Ecol*. 2019;33:467–78.
- Chole H, Woodard SH, Bloch G. Body size variation in bees: regulation, mechanisms, and relationship to social organization. *Curr Opin Insect Sci*. 2019;35:77–87.
- Chown SL, Gaston KJ. Body size variation in insects: A macroecological perspective. *Biol Rev*. 2010;85:139–69.
- Day T, Rowe L. Developmental thresholds and the evolution of reaction norms for age and size at Life-History transitions. *Am Nat*. 2002;159:338.
- Radmacher S, Strohm E. Factors affecting offspring body size in the solitary bee *Osmia bicornis* (Hymenoptera, Megachilidae). *Apidologie*. 2010;41:169–77.
- Roulston TH, Cane JH. The effect of pollen protein concentration on body size in the sweat bee *Lasioglossum zephyrum* (Hymenoptera: Apiformes). *Evol Ecol*. 2002;16:49–65.
- Quezada-Euán JG, López-Velasco A, Pérez-Balam J, Moo-Valle H, Velazquez-Madrado A, Paxton RJ. Body size differs in workers produced across time and is associated with variation in the quantity and composition of larval food in *Nannotrigona perilampoides* (Hymenoptera, Meliponini). *Insectes Soc*. 2011;58:31–8.
- Gardner JL, Peters A, Kearney MR, Joseph L, Heinsohn R. Declining body size: a third universal response to warming? *Trends Ecol Evol*. 2011;26:285–91.
- Grab H, Brokaw J, Anderson E, Gedlinske L, Gibbs J, Wilson J, et al. Habitat enhancements rescue bee body size from the negative effects of landscape simplification. *J Appl Ecol*. 2019;56:2144–54.
- Merckx T, Souffreau C, Kaiser A, Baardsen LF, Backeljau T, Bonte D, et al. Body-size shifts in aquatic and terrestrial urban communities. *Nature*. 2018;558:113–6.
- Molet M, Péronnet R, Couette S, Canovas C, Doums C. Effect of temperature and social environment on worker size in the ant *temnothorax nylanderii*. *J Therm Biol*. 2017;67:22–9.
- Tammaru T, Teder T. Why is body size more variable in stressful conditions: an analysis of a potential proximate mechanism. *Evol Ecol*. 2012;26:1421–32.
- Theodorou P, Baltz LM, Paxton RJ, Soro A. Urbanization is associated with shifts in bumblebee body size, with cascading effects on pollination. *Evol Appl*. 2021;14:53–68.
- Brasil SNR, Ayers AC, Rehan SM. The effect of urbanisation and seasonality on wild bee abundance, body size and foraging efforts. *Ecol Entomol*. 2023;48:499–507.
- EGgenberger H, Frey D, Pellissier L, Ghazoul J, Fontana S, Moretti M. Urban bumblebees are smaller and more phenotypically diverse than their rural counterparts. *J Anim Ecol*. 2019;88:1522–33.

49. Garlin J, Theodorou P, Kathe E, Quezada-Euán JG, Paxton RJ, Soro A. Anthropogenic effects on the body size of two Neotropical Orchid bees. *BMC Ecol Evol*. 2022;22:94.
50. Austin MW, Tripodi AD, Strange JP, Dunlap AS. Bumble bees exhibit body size clines across an urban gradient despite low genetic differentiation. *Sci Rep*. 2022;12:4166.
51. Tommasi N, Pioletti E, Biella P, Labra M, Casiraghi M, Galimberti A. Effect of urbanization and its environmental stressors on the intraspecific variation of flight functional traits in two bumblebee species. *Oecologia*. 2022;199:289–99.
52. Banaszak-Cibicka W, Fliszkiewicz M, Langowska A, Żmihorski M. Body size and wing asymmetry in bees along an urbanization gradient. *Apidologie*. 2018;49:297–306.
53. Batra SWT. Nesting behavior of *Halictus scabiosae* in Switzerland (Hymenoptera, Halictidae). *Insectes Soc*. 1966;13:87–92.
54. Ulrich Y, Perrin N, Chapuisat M. Flexible social organization and high incidence of drifting in the sweat bee, *Halictus scabiosae*. *Mol Ecol*. 2009;18:1791–800.
55. Fabre J-H. Bramble-bees and others. Mead: Dodd; 1915.
56. Gogala A. Initiation of new nests in a social bee, *Halictus scabiosae* Rossi (Hymenoptera: Halictidae). *Opusc Zool Flumin*. 1991;67:1–7.
57. Westrich P. Die Wildbienen Deutschlands. 2nd edition. Stuttgart: Verlag Eugen Ulmer; 2019.
58. Schweitzer L, Theunert R. Zum Vorkommen von *Halictus scabiosae* (Rossi, 1790) und *Megachile pilidens* (Alfken, 1924) in Niedersachsen (Hymenoptera: Apidae). *Peiner Biol ogische Arbeitsgemeinschaft-Online*; 2019;1:1–9.
59. Gil-Tapetado D, Ferrari A, Ronchetti F, Polidori C. Distribution widening of a ground-nesting social bee across Europe favored by climate change and urban setting. *Apidologie*. 2024;55:35.
60. Ropars L, Dajoz I, Geslin B. La diversité des abeilles parisiennes. *Osmia*. 2018;7:14–9.
61. Willmer P, Finlayson K. Big bees do a better job: intraspecific size variation influences pollination effectiveness. *J Pollinat Ecol*. 2014;14:244–54.
62. Brant RA, Camilo GR. Body size variation in a social sweat bee, *Halictus ligatus* (Halictidae, Apoidea), across Urban Environments. *Insects*. 2021;12:1086.
63. Cane JH. Estimation of bee size using intertegular span (Apoidea). *J Kans Entomol Soc*. 1987;60:145–7.
64. Fortunato L, Zandigiacomo P. Fenologia e preferenze florali di *Halictus scabiosae* (Rossi) in Friuli Venezia Giulia. *Boll Soc Nat Silvia Zenari*. 2013;36:147–56.
65. Mäder P, Boho D, Rzanny M, Seeland M, Wittich HC, Deggelmann A, et al. The flora incognita app—Interactive plant species identification. *Methods Ecol Evol*. 2021;12:1335–42.
66. Andersson P, Koffman A, Sjödin NE, Johansson V. Roads May act as barriers to flying insects: species composition of bees and wasps differs on two sides of a large highway. *Nat Conserv*. 2017;18:47–59.
67. Bhattacharya M, Primack RB, Gerwein J. Are roads and railroads barriers to bumblebee movement in a temperate suburban conservation area? *Biol Conserv*. 2003;109:37–45.
68. Ermda SL, Soares P, Mantas V, Götsche F-M, Trigo IF. Google Earth engine Open-Source code for land surface temperature Estimation from the landsat series. *Remote Sens*. 2020;12:1471.
69. Hijmans RJ. Terra: Spatial data analysis. CRAN: Contributed Packages; 2023.
70. Pebesma E, Bivand R. Spatial Data Science: With applications in R. Chapman and Hall/CRC. 2023.
71. Baston D, exactextractr. Fast extraction from raster datasets using polygons. CRAN: Contributed Packages; 2023.
72. Martin AE, Fahrig L. Measuring and selecting scales of effect for landscape predictors in species–habitat models. *Ecol Appl*. 2012;22:2277–92.
73. McGarigal K, Wan HY, Zeller KA, Timm BC, Cushman SA. Multi-scale habitat selection modeling: a review and outlook. *Landscape Ecol*. 2016;31:1161–75.
74. Team RC. R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing; 2023.
75. Lefcheck JS, piecewiseSEM. Piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods Ecol Evol*. 2016;7:573–9.
76. Hartig F, DHARMa. Residual diagnostics for hierarchical (Multi-Level / Mixed) regression models. CRAN: Contributed Packages; 2022.
77. Zuur AF, Ieno EN, Walker N, Saveliev AA, Smith GM. Mixed effects models and extensions in ecology with R. New York, NY: Springer New York; 2009.
78. Nakagawa S, Schielzeth H. A general and simple method for obtaining R² from generalized linear mixed-effects models. *Methods Ecol Evol*. 2013;2:133–42.
79. Halvorson HM, Sperfeld E, Evans-White MA. Quantity and quality limit detritivore growth: mechanisms revealed by ecological stoichiometry and co-limitation theory. *Ecology*. 2017;98:2995–3002.
80. Lawson SP, Helmreich SL, Rehan SM. Effects of nutritional deprivation on development and behavior in the subsocial bee *Ceratina calcarata* (Hymenoptera: Xylocopinae). *J Exp Biol*. 2017;220:4456–62.
81. Kaluza BF, Wallace HM, Heard TA, Minden V, Klein A, Leonhardt SD. Social bees are fitter in more biodiverse environments. *Sci Rep*. 2018;8:12353.
82. Filipiak M. A better Understanding of bee nutritional ecology is needed to optimize conservation strategies for wild bees—The application of ecological stoichiometry. *Insects*. 2018;9:85.
83. Filipiak ZM, Denisow B, Stawiarz E, Filipiak M. Unravelling the dependence of a wild bee on floral diversity and composition using a feeding experiment. *Sci Total Environ*. 2022;820:153326.
84. Filipiak ZM, Filipiak M. The scarcity of specific nutrients in wild bee larval food negatively influences certain life history traits. *Biology (Basel)*. 2020;9:462.
85. Filipiak M. Key pollen host plants provide balanced diets for wild bee larvae: A lesson for planting flower strips and hedgerows. *J Appl Ecol*. 2019;56:1410–8.
86. Vaudo AD, Patch HM, Mortensen DA, Tooker JF, Grozinger CM. Macronutrient ratios in pollen shape bumble bee (*Bombus impatiens*) foraging strategies and floral preferences. *Proc Natl Acad Sci U S A*. 2016;113:E4035–42.
87. Roulston TH, Cane JH, Buchmann SL. What governs protein content of pollen: pollinator preferences, pollen-pistil interactions, or phylogeny? *Ecol Monogr*. 2000;70:617–43.
88. Vaudo AD, Tooker JF, Grozinger CM, Patch HM. Bee nutrition and floral resource restoration. *Curr Opin Insect Sci*. 2015;10:133–41.
89. Kardum Hjort C, Smith HG, Allen AP, Dudaniec RY. Morphological variation in bumblebees (*Bombus terrestris*) (Hymenoptera: Apidae) after three decades of an Island invasion. *J Insect Sci*. 2023;23:10.
90. Ab Hamid S, Salleh MS, Thevan K, Hashim NA. Distribution and morphometrical variations of stingless bees (Apidae: Meliponini) in urban and forest areas of Penang island, Malaysia. *J Trop Resour Sustain Sci*. 2021;4:1–5.
91. May-Itzá W, de Araujo-Freitas J, de Paxton C, Moo-Valle RJ, Medina-Medina H, Quezada-Euán LA. Stingless bees in urban areas: low body size and high frequency of diploid males at mating congregations of *Nannotrigona perilampoides* (Hymenoptera: Meliponini) in Mérida, Yucatán, México. *Apidologie*. 2021;52:755–66.
92. Warzecha D, Diekötter T, Wolters V, Jauker F. Intraspecific body size increases with habitat fragmentation in wild bee pollinators. *Landscape Ecol*. 2016;31:1449–55.
93. Merckx T, Kaiser A, Van Dyck H. Increased body size along urbanization gradients at both community and intraspecific level in macro-moths. *Glob Chang Biol*. 2018;24:3837–48.
94. Westrich P. Die Wildbienen Baden-Württembergs. 2nd edition. Verlag Eugen Ulmer; 1989.
95. Scheuchl E, Willner W. Taschenlexikon der Wildbienen Mitteleuropas: Alle Arten im Porträt. Quelle & Meyer; 2016.
96. Hass AL, Kormann UG, Tscharnkte T, Clough Y, Baillod AB, Sirami C, et al. Landscape configurational heterogeneity by small-scale agriculture, not crop diversity, maintains pollinators and plant reproduction in Western Europe. *Proc R Soc B Biol Sci*. 2018;285:20172242.
97. Hopwood JL. The contribution of roadside grassland restorations to native bee conservation. *Biol Conserv*. 2008;141:2632–40.
98. Kumar S, Stohlgren TJ, Chong GW. Spatial heterogeneity influences native and nonnative plant species richness. *Ecology*. 2006;87:3186–99.
99. Liu R, Yan X, Lin X, Sun Y, Zhang T, Xiao J. Urban spontaneous plant richness in response to the 2D/3D Building and green space patterns in a highly urbanized area. *Ecol Indic*. 2023;154:110852.
100. Gao Z, Song K, Pan Y, Malkinson D, Zhang X, Jia B, et al. Drivers of spontaneous plant richness patterns in urban green space within a biodiversity hotspot. *Urban Urban Green*. 2021;61:127098.
101. Goulson D, Nicholls E, Botias C, Rotheray ELL. Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. *Science*. 2015;347:1255957.
102. Goulson D, Sparrow KR. Evidence for competition between honeybees and bumblebees; effects on bumblebee worker size. *J Insect Conserv*. 2009;13:177–81.
103. Ojija F, Adam Silabi L. Bees and their interactions with flowering plants in disturbed and semi-natural settings. *J Asia Pac Entomol*. 2024;27:102225.
104. Eraerts M, Van Den Berge S, Proesmans W, Verheyen K, Smaghe G, Meeus I. Fruit orchards and Woody semi-natural habitat provide

- complementary resources for pollinators in agricultural landscapes. *Landsc Ecol.* 2021;36:1377–90.
105. Twerd L, Banaszak-Cibicka W, Wastelands. Their attractiveness and importance for preserving the diversity of wild bees in urban areas. *J Insect Conserv.* 2019;23:573–88.
106. Papanikolaou ADD, Kühn I, Frenzel M, Schweiger O. Semi-natural habitats mitigate the effects of temperature rise on wild bees. *J Appl Ecol.* 2017;54:527–36.
107. Beninde J, Veith M, Hochkirch A. Biodiversity in cities needs space: A meta-analysis of factors determining intra-urban biodiversity variation. *Ecol Lett.* 2015;18:581–92.
108. Cloutier S, Mendes P, Cimon-Morin J, Pellerin S, Fournier V, Poulin M. Assessing the contribution of lawns and semi-natural meadows to bee, wasp, and flower fly communities across different landscapes. *Urban Ecosyst.* 2024;27:1417–34.
109. Theodorou P. The effects of urbanisation on ecological interactions. *Curr Opin Insect Sci.* 2022;52:100922.
110. Theodorou P, Radzevic R, Murray E, Paxton RJ, Schweiger O. Pollination services enhanced with urbanization despite increasing pollinator parasitism. *Proc R Soc B.* 2016;283:20160561.
111. Anderson RM, May RM. The population dynamics of microparasites and their invertebrate hosts. *Philos Trans R Soc Lond B Biol Sci.* 1981;291:451–524.
112. Gerard M, Michez D, Debat V, Fullgrabe L, Meeus I, Piot N, et al. Stressful conditions reveal decrease in size, modification of shape but relatively stable asymmetry in bumblebee wings. *Sci Rep.* 2018;8:1–10.
113. Smith AR, Wcislo WT, O'Donnell S. Body size shapes caste expression, and cleptoparasitism reduces body size in the facultatively eusocial bees *Megalo*ptera (Hymenoptera: Halictidae). *J Insect Behav.* 2008;21:394–406.
114. Šálek M, Kučera T, Zimmermann K, Bartůšková I, Plátek M, Grill S, et al. Edges within farmland: management implications of taxon specific species richness correlates. *Basic Appl Ecol.* 2015;16:714–25.
115. Theodorou P, Kühn O, Baltz LM, Wild C, Rasti SL, Bucksch CR, et al. Bumble bee colony health and performance vary widely across the urban ecosystem. *J Anim Ecol.* 2022;91:2135–48.
116. Brebner JS, Makinson JC, Bates OK, Rossi N, Lim KS, Dubois T, et al. Bumble bees strategically use ground level linear features in navigation. *Anim Behav.* 2021;179:147–60.
117. Free JB. The division of labour within bumblebee colonies. *Insectes Soc.* 1955;2:195–212.
118. Quénu C. Étude systématique des apides du périgord Noir Le genre *Halictus* (Printemps-Été 1953). *Ann La Société Entomol Fr.* 1954;123:157–63.

Publisher's Note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.