



HAL
open science

Urban intensity gradients shape community structure, life-history traits and performance in a multitrophic system

Joan Casanelles-Abella, Loïc Pellissier, Cristiana Aleixo, Marta Alós Orti,
François Chiron, Nicolas Deguines, Lauri Laanisto, Łukasz Myczko, Stefanie
Müller, Ülo Niinemets, et al.

► To cite this version:

Joan Casanelles-Abella, Loïc Pellissier, Cristiana Aleixo, Marta Alós Orti, François Chiron, et al..
Urban intensity gradients shape community structure, life-history traits and performance in a mul-
titrophic system. *Insect conservation and diversity*, 2024, *The Ecology and Conservation of Urban
Insects*, 17 (2), pp.243-258. 10.1111/icad.12728 . hal-04519255

HAL Id: hal-04519255

<https://hal.science/hal-04519255>

Submitted on 3 Apr 2024

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1 **Title:** Urban intensity gradients shape community structure, life-history traits, and performance in a
2 multitrophic system

3

4 **Running title:** Urban intensity effects on food webs

5

6 **Authors:**

7 Joan Casanelles-Abella 1,2,3*

8 Loïc Pellissier 3,4

9 Cristiana Aleixo 5

10 Marta Alós Orti 6

11 François Chiron 7

12 Nicolas Deguines 8

13 Lauri Laanisto 6

14 Łukasz Myczko 9

15 Stefanie Müller 10

16 Ülo Niinemets 6

17 Pedro Pinho 5

18 Roeland Samson 11

19 Piotr Tryjanowski 9

20 Lucía Villarroja-Villalba 2

21 Marco Moretti 2

22

23 **Institutional affiliations:**

24 1 Urban Productive Ecosystems, TUM School of Life Sciences. TUM, Freising, Germany

25 2 Biodiversity and Conservation Biology, Swiss Federal Research Institute WSL, Birmensdorf,
26 Switzerland

27 3 Ecology and Landscape Evolution, ETH Zurich, Zurich, Switzerland

28 4 Land Change Science, Swiss Federal Research Institute WSL, Birmensdorf, Switzerland

29 5 cE3c - Centre for Ecology, Evolution and Environmental Changes & CHANGE - Global Change and
30 Sustainability Institute, Faculdade de Ciências, Universidade de Lisboa, Lisboa, Portugal

31 6 Agricultural and Environmental Sciences, Estonian University of Life Sciences, Kreutzwaldi 5, Tartu,
32 Estonia

33 7 Université Paris-Saclay, CNRS, AgroParisTech, Ecologie Systématique Evolution, Gif-sur-Yvette,
34 France

35 8 Laboratoire Ecologie et Biologie des Interactions, Equipe Ecologie Evolution Symbiose, Université
36 de Poitiers, UMR CNRS, Nouvelle- Aquitaine, France

37 9 Department of Zoology, Poznan University of Life Sciences, Poznan, Poland

38 10 FH Graubünden, Chur, Switzerland

39 11 Laboratory of Environmental and Urban Ecology, Department of Bioscience Engineering,
40 University of Antwerp, Antwerp, Belgium

41

42

43 *Corresponding author

44 **Contact information:** joan.casanelles@wsl.ch; +41 44 739 26 74

45

46

47 **Abstract:**

- 48 1. Urban ecosystems are formed by pronounced socio-ecological gradients, which are distinct
49 from other ecosystems and can simultaneously filter and promote taxa, ultimately affecting
50 their interactions. However, the strength of the effect of filtering and facilitation across the
51 different trophic levels could vary among biotic and abiotic factors.
- 52 2. Here, we investigate the effects of habitat amount, temperature, and host-enemy biotic
53 interactions in shaping communities of cavity-nesting bees and wasps and their natural enemies.
54 We installed trap-nests in 80 sites distributed along urban intensity gradients in 5 European
55 cities (Antwerp, Paris, Poznan, Tartu and Zurich). We quantified the species richness and
56 abundance of hosts and their natural enemies, as well as two performance traits (survival and
57 parasitism) and two life-history traits (sex ratio and number of offspring per nest for the hosts).
58 We analysed the importance of the abiotic and biotic variables using generalized linear models
59 and multi-model inference.
- 60 3. We found that habitat amount was the main driver of multiple host responses, with larger habitat
61 amounts resulting in higher species richness and abundance for hosts and natural enemies, as
62 well as a larger probability of survival and a larger number of broodcells for hosts.
- 63 4. Local resources proxies shaped both bees and wasps and indicate different use of existing
64 vegetation between bees and wasps. Temperature proxies had a minor role in shaping host and
65 natural enemies.
- 66 5. Biotic interactions were a main driver of host and enemy community structure, with natural
67 enemies being strongly affected by host availability, that is, with direct density-dependence
68 between hosts and their natural enemies.
- 69 6. Overall, our study highlights the importance of habitat amount and temperature in shaping
70 urban food webs, as well as on biotic interactions through direct effects on hosts responses and
71 the subsequent consequences for their natural enemies. As cities prepare to tackle the
72 consequences of global change, strategies that make it possible to maintain habitat and mitigate
73 urban overheating emerge as a key urban adaptation for biodiversity conservation.

74

75 **Keywords:** ecological rate, parasitism, survival, sex ratios, trap-nest, urbanization , cavity-nesting bees
76 and wasps

77

78 **1. INTRODUCTION**

79 Urbanization both filters and promotes biodiversity, providing challenges and opportunities for urban
80 wildlife management. Understanding the drivers of urban diversity patterns and ecological processes
81 across urban ecosystems has therefore become a central topic to promote biodiverse cities (Uchida et
82 al. 2021). Understanding the impact of urbanization on multitrophic biodiversity, specifically
83 performance traits (e.g., parasitism, mortality) and life-history traits (e.g., sex ratio, number of eggs),
84 can shed light on species fitness, survival, and occupancy responses. This knowledge is crucial for
85 implementing targeted management strategies. Species assemblages and the fitness of single species
86 are determined by environmental conditions, such as habitat amount (i.e. the total area of suitable
87 habitats at a defined space; sensu Fahrig 2013), food resource availability, and temperature, in
88 combination with biotic interactions, such as top-down control by higher trophic levels (Dainese et al.
89 2018), and bottom-up control by lower trophic levels (Steffan-Dewenter and Schiele 2008). All these
90 drivers are expected to vary substantially along urban intensity gradients.

91 Habitat amount has been identified as a main driver of ecosystem biodiversity (Hutchinson 1957, Fahrig
92 2013), but the relationship between habitat amount and biodiversity might be more complex in cities
93 than in other ecosystems. At the community level, species richness generally increases when the amount
94 of habitat within an appropriately defined area is larger (Fahrig 2013). Moreover, habitat amount can
95 also influence life-history traits. For instance, habitat loss can result in male-biased sex ratios in several
96 Hymenoptera species (Fitch et al. 2019). In cities, as urban intensity increases, the habitat amount
97 becomes scarcer, particularly large patches. However, cities differ from other ecosystems as, rather than
98 being characterized by large habitat patches, habitat is typically distributed in small patches with
99 variable local features (Aronson et al. 2017). Thus, it is unclear what are the effects on the community
100 structure, life history traits and performance traits in urban taxa.

101 The landscape effects of urbanization through habitat amount on biodiversity might be counteracted by
102 the local habitat and resources present in existing patches within the cityscape (Diamond et al. 2023).
103 Greater plant diversity often results in more food resources (e.g. nectar), enhancing the abundance and
104 richness of consumers directly, and of higher trophic levels indirectly (Srivastava and Lawton 1998,
105 Fabian et al. 2014). For example, management activities can alter plant community structure within
106 urban habitats by adding or removing species, also affecting the properties of food webs (Burks and
107 Philpott 2017, da Rocha-Filho et al. 2020). How food resources influence the life-history traits,
108 performance traits and community structure of urban species is less known than in other ecosystems but
109 this is major importance for biodiversity management in urban areas.

110 Temperature gradients and their effects on biodiversity are well documented in communities outside
111 cities (Mayr et al. 2020, Orr et al. 2021). However, cities can also have pronounced local temperature
112 gradients (Zumwald et al. 2021). Different densities and impermeable materials and the presence of

113 blue-green spaces can form urban heat or cooling islands at the points of greatest or fewest accumulation
114 of heat and energy, respectively. High temperatures are expected to favour ectothermic taxa, by
115 increasing insect activity, enhancing interactions, and potentially boosting their diversity (Jamieson et
116 al. 2012, Banaszak-Cibicka 2014, Hamann et al. 2021, Geppert et al. 2022). However, excessively high
117 temperatures, above a species' physiological threshold at different life stages, could enhance desiccation
118 and reduce survival and reproduction success (Dale and Frank 2018), as well as creating a phenological
119 mismatch with the plant hosts (Papanikolaou et al. 2017). Further, because of the positive association
120 between temperature and grey surfaces, warmer areas can correspond to smaller amounts of green
121 habitat and less availability of food resources. The effects of broad temperature gradients on biodiversity
122 have been studied previously (Trøjelsgaard and Olesen 2013), yet local temperature effects, particularly
123 in cities, have been less investigated.

124 Biotic interactions between hosts and their natural enemies are an additional driver of diversity. Natural
125 enemies include predators and parasites, which can indirectly favour species richness by alleviating
126 competitive pressure by dominant species (i.e. top-down regulation Steffan-Dewenter and Schiele 2008,
127 Levi et al. 2019). Focusing on parasitism, interactions between hosts and their natural enemies can be
128 either directly density-dependent (Dainese et al. 2018), when larger numbers of hosts result in increased
129 parasitism (Hassell 2000), or inversely density-dependent, when larger numbers of hosts result in
130 decreased parasitism (Rosenheim 1990, Steffan-Dewenter and Schiele 2008), ultimately affecting the
131 diversity of hosts and natural enemies. The dynamics between hosts and their natural enemies might be
132 altered in cities, as the urban environment can affect the behaviour, distribution, physiology and
133 community structure of both hosts and natural enemies, due to the combined action of multiple socio-
134 ecological factors and processes (Classen-Rodríguez et al. 2021). However, studies on the effects of
135 biotic interactions in cities are still scarce (Theodorou 2022).

136 Here, we studied the effects of habitat amount, resources, temperature and biotic interactions between
137 the hosts and their natural enemies on multitrophic diversity. In particular we considered effects on the
138 community structure (i.e. species richness, abundance) of cavity-nesting bees and wasps (CNBW) and
139 their natural enemies (e.g., parasites, parasitoids, cleptoparasites), as well as on the performance traits
140 (i.e. parasitism, survival) and life-history traits (i.e. sex ratio, number of offspring cells per nest) of
141 CNBW across urban ecosystems. We tested the following non-mutually exclusive hypotheses:

142 1: For hosts and natural enemies, habitat loss at the landscape (i.e. when urban intensity is high) reduces
143 species richness and abundance. This effect might be stronger in wasps than in bees, as loss of habitat
144 particularly affects arthropod prey diversity and abundance at higher trophic levels (Attwood et al. 2008,
145 Mayr et al. 2020). Moreover, for hosts, small amounts of habitat also reduce the number of offspring
146 per nest, the offspring survival, and reduce the number of females.

147 2: Higher local resources (inferred with plant richness and cover of specific habitat types) positively
148 influence community structure, life history traits and survival of hosts. Bees and wasps are central place
149 foragers and thus, the available resources in the vicinity of their nesting sites is critical for their
150 persistence (Rosenberg and McKelvey 1999, Kendall et al. 2022).

151 3: Increasing temperatures, below physiological thresholds where it becomes excessive, positively
152 affect the foraging activity of CNBW. This results in a higher number of eggs laid per nest, offspring
153 survival, number of females, and overall abundance hatched (Mayr et al. 2020, Geppert et al. 2022).
154 Alternatively, excessive temperatures above physiological thresholds will reduce survival (Ricklefs and
155 Wikelski 2002).

156 4: Biotic interactions (host–natural-enemy interactions) might positively shape both hosts and natural
157 enemies. Regarding hosts, higher parasitism rates and a larger number of parasitized brood cells might
158 increase host populations of bees and wasps by reducing competition among dominant species, thus
159 increasing species richness. Regarding natural enemies, increased host availability (i.e. more nests and
160 higher host species richness) increase natural enemy population sizes, resulting in enhanced species
161 richness and the number of parasitized cells by providing more resources (Hassell 1982, Rosenheim
162 1990, Dainese et al. 2018).

163 5: Conversely, biotic interactions might negatively influence both hosts and natural enemies. Regarding
164 hosts, higher parasitism rates and a larger number of parasitized brood cells might reduce host
165 population sizes. Regarding natural enemies, increased host availability (i.e. more nests and higher host
166 species richness) might result in a greater probability of detection of natural enemies by the host, less
167 time for natural enemies to lay eggs, and enhanced collective defences by hosts, ultimately reducing
168 natural-enemy species richness and the number of parasitized cells (Rosenheim 1990).

169 **2. MATERIALS AND METHODS**

170 **2.1. Study cities and sites**

171 Our study was set in five European cities: Antwerp (Belgium), Greater Paris (France, hereafter referred
172 to as Paris), Poznan (Poland), Tartu (Estonia), and Zurich (Switzerland), covering a large part of the
173 climatic variability in mainland Europe (Figure S1). Site selection was done using an orthogonal
174 gradient of patch size and patch isolation (Text S1, see also Casanelles-Abella et al. 2022). Overall, the
175 final selection included 80 sites, 32 in Zurich and 12 in each of the remaining four cities (Figure S1;
176 Table S1). Sites were at least 500 m apart from each other, except for two sites in Zurich that were 260
177 m apart (see Text S1 for additional details).

178 **2.2. Insect sampling**

179 We sampled cavity-nesting bees and wasps (CNBW) and their natural enemies (parasites, parasitoids,
180 kleptoparasites, nest destroyers; see Text S2) using trap-nests, which were placed in the study sites.
181 This enabled us to study their individual- and community-level responses in standardized nesting
182 conditions (Figure 1b; Tschardt et al. 1998, Staab et al. 2018). To avoid vandalism, we installed trap-
183 nests at 2.5–3.5 m height in sun-exposed SE or SW expositions for the period of January to October
184 2018. In October, we collected the trap-nests and stored them at c. 5°C. Between November and
185 December 2018, we opened all reed internodes to detect brood cells. We counted the number of brood
186 cells in the bee and wasp nests and noted the occurrence of natural enemies (cleptoparasites, parasites,
187 parasitoids and predators). We then placed the reeds individually into glass tubes and closed the tubes
188 with cotton wadding to collect emerging insects. We stored the tubes at 5°C until February 2019, when
189 we transferred the tubes to a room at ambient temperature.

190 During spring and summer 2019, bees, wasps and their natural enemies emerged. We identified bees,
191 wasps and enemies to the species level or to the lowest taxonomic rank possible (Table S2), using
192 existing identification keys (Text S3). In addition, we identified the sex of all emerged bees and wasps
193 and calculated the sex ratio at the nest level (i.e. for each reed tube). When no adult hosts emerged from
194 a nest, we used the nest features (sealing material, diameter, larval food type) to identify the host genus
195 or the family. Finally, some natural enemy species could only be identified to morphospecies (Table
196 S3).

197 **2.3. Community structure, performance traits, and life history traits**

198 We calculated community structure, performance traits, and life-history traits (sensu Violle et al. 2007)
199 to study the effects of habitat amount, resources, temperature and biotic interactions between the hosts
200 and their natural enemies on multitrophic community diversity. Concerning the community structure,
201 at each site we calculated species richness, abundance of hatched hosts, and number of nests of the
202 hatched hosts separately for bees and wasps. We calculated the abundance of hatched hosts as the
203 number of brood cells where an individual emerged, i.e. the total number of brood cells minus the
204 number of parasitized cells and the number of cells with no emergence for reasons other than parasitism.
205 Abundance was calculated as the total community abundance. We calculated the number of nests as the
206 total number of colonized reeds. The abundance of hatched hosts and number of nests were highly
207 correlated (Pearson correlations from 0.81 to 0.92). Thus, we only included the abundance of hatched
208 hosts in the analyses, as it reflects the actual number of individuals that will constitute the next
209 generation. For natural enemies, we calculated the species richness and abundance. We estimated the
210 abundance of natural enemies as the number of parasitized brood cells rather than the total number of
211 emerging individual enemies, to account for differences in the number of eggs laid per cell across
212 different enemy species.

213 We assessed performance traits, i.e. survival and parasitism, at the individual cell level. Specifically,
214 for each cell within a nest, we noted whether the cell was alive or dead (survival; Figure 1c), and whether
215 it had a parasite or not (parasitism; Figure 1c). Further, we calculated the parasitism rate as the number
216 of cells with a parasite divided by the total number of cells. However, the scales at which parasitism
217 operates can vary among natural enemies. For instance, some might attack the first or last cells in a nest,
218 whereas other might attack an entire sequence of cells in a nest. Therefore, to account for the variability
219 in the parasitism modes of the natural enemy community, we also calculated and studied parasitism at
220 the nest level, as the number of cells parasitized.

221 Concerning life-history traits, we calculated the total number of brood cells per nest as the total number
222 of brood cells within a single nest, regardless of whether the larvae were dead, alive or parasitized
223 (Figure 1c). Finally, we used the probability that a female host emerged from a given cell as a proxy for
224 sex ratio. To do so, we first identified the sex of the individual hosts. Then, we noted it in a binary way
225 to indicate whether the host was a female or not (Figure 1c). We could identify the sex of all hatched
226 hosts. Further, because CNBW first lay females and then males, on some occasions we could also
227 identify the host sex in dead and parasitized cells, that is, when we had already identified the sex of the
228 preceding and the following cells.

229 **2.4. Predictors**

230 We used four sets of variables representing (1) habitat amount at the landscape scale, (2) local habitat
231 and resources, (3) temperature and (4) biotic interactions (Figure S2).

232 We inferred habitat amount at the landscape scale using a combination of landcover data and remote-
233 sensing-based indices. First, we estimated habitat amount using metrics based on land-cover data. Using
234 the European Urban Atlas (EEA 2012), we calculated the local patch size (total area of the study site)
235 and patch isolation (using the proximity index, which weights the contribution of the area of
236 neighbouring patches by the distance to the focal patch within a given search radius) (Gustafson and
237 Parker 1994). We considered as favourable habitat all patches with high probability of having trees (that
238 is, UGAs, urban forest and grey urban land-cover with less than 30% impervious surface, as defined in
239 EEA, 2012). Further, following the *habitat amount hypothesis* (Fahrig 2013), which defines habitat
240 amount as the total area of habitat at a defined distance from the nest, we used the European Land Cover
241 Map at 10 m resolution (Venter and Sydenham 2021), which enable accounting for small habitat
242 patches. We calculated the amount of green and gray covers using 50, 100, 200, 400 and 800 m buffers
243 from the focal trap-nests, to infer the habitat amount at each site. The selected buffer sizes are expected
244 to be relevant for the studied organisms (Gathmann and Tschardt 2002). Due to the high correlations
245 between buffers, we used 100 and 800 m in our analyses. Additionally, we also used remote-sensing-
246 based indices, calculated at the same buffers. In particular, we used the normalized difference vegetation

247 index (NDVI) and the Urban Index (UI) within the five buffers (Text S4). Due to the high correlations
248 with the amount of green surfaces, the amount gray surfaces, NDVI and UI (Figures S3-S4), we only
249 used the amount of green surfaces at 100 and 800 m in our analyses.

250 We used the floristic inventories from Casanelles-Abella, Frey et al. (2021) to further characterize
251 habitat amount in terms of food resource availability, inferred as plant species richness. Additionally,
252 we computed plant Shannon diversity but due to the high correlations with species richness we did not
253 include it in the models. Briefly, we performed the floristic inventories in standardized plots,
254 documenting the occurrence of all entomophilous plants (excluding families Poaceae and Cyperaceae)
255 within a 100 m buffer of the trap-nests. Floristic inventories took place on four occasions between April
256 and July 2018. In addition, we used the local landcover map developed by Alós-Ortí et al. (2022). This
257 local landcover map distinguishes between vegetation and build-up types (grasslands, woody
258 vegetation, and impervious surfaces within 32 m) and can be used an indirect proxy for food resource
259 availability for bees and wasps as both taxa are central-place foragers and thus highly affected by the
260 vegetation composition and availability within the vicinity of their nesting sites (see also, Text S5). Due
261 to the high correlation between the proportion of woody vegetation and grasslands at 32 m, we only
262 used the proportion of grasslands in our models.

263 We measured temperature at the trap-nest level and within a 800 m buffer from the trap-nests. At the
264 trap-nest level, data loggers (1-Wire/Data Logger model DS1921G-F5, Analog Devices, Wilmington,
265 MA, USA) recorded temperature hourly between February and June 2018 overlapping with the nesting
266 activity of the majority of CNBW species, and we calculated the mean temperature per study site over
267 this period (local temperature). We expect this scale of measurement to reflect the local thermal nesting
268 conditions. However, because the studied cities followed a latitudinal gradient, we further transformed
269 the local temperature by computing temperature anomalies for each city, by subtracting the
270 temperature measurement in a site by the average from all the sites in each city (hereinafter referred as
271 local temperature). Within the 800 m buffer (landscape temperature), we inferred temperature using
272 remote sensing indices of land surface temperature (LST; Text S4), from the USGS/Earth Explorer
273 website (<https://earthexplorer.usgs.gov/>). We expect this scale of measurement to reflect the thermal
274 landscape surrounding our study sites. Additionally, we calculated LST for 50, 100, 200 and 400 m
275 buffers, but ultimately did not use these estimates due to high inter-correlations (Pearson $r > 0.8$). The
276 distribution of values of the used predictors can be found in Figure S2.

277 To assess the role of biotic interactions on the studied responses, we used both top-down and bottom-
278 up proxies. Specifically, we used the number of parasitized cells and the species richness of natural
279 enemies as top-down proxies. Moreover, as bottom-up proxies, we used the number of nests and the
280 species richness of hosts.

281 Finally, we performed a principal component analysis (PCA) on the explanatory variables to define new
282 meaningful underlying variables while reducing the dimensionality of the data set. The first PCA axis
283 explained ca. 40% of the variation in the data, and was largely influenced by landscape level variables,
284 that is, the amount of green areas at 100 and 800 m, and LST at 800 m (Figure S5). Thus, we referred
285 to this first PCA axis as “urban intensity”, and used it for data visualisation, while we used the specific
286 proxies of habitat amount, local resources, temperature and biotic interactions for modelling..

287 **2.5. Statistical analyses**

288 We used R version 4.0.2 (R Core Team 2022) and RStudio v.07.1 (RStudio Team 2020) for all analyses
289 and statistical figures, using the packages glmmTMB v.1.1.3 (Brooks et al. 2017), MuMIn v.1.46.0
290 (Barton and Šímová 2015), evaluate v.0.15 (H and Y 2022), performance v.0.9.2 (Lüdtke et al. 2021),
291 DHARMA v.0.4.5 (Hartig 2022), and ggplot2 v.3.3.6 (Wickham 2016).

292 We used generalized linear mixed-effects models (GLMMs) to assess the influence of temperature,
293 habitat amount, and host–natural-enemy interactions (biotic interactions) on host and natural-enemy
294 responses. For hosts, we considered the response variables species richness, abundance hatched,
295 survival (probability that the host in a cell survived), parasitism at the cell level (probability that the
296 host in a cell was parasitized), parasitism at the nest level (number of parasitized cells in a nest), sex
297 ratio (probability that the host in a cell was female) and number of brood cells per nest. For natural
298 enemies, we considered the response variables species richness and number of parasitized cells (proxy
299 for enemy abundance). We modelled each response in hosts and natural enemies individually. One site
300 in Antwerp (An057) was not colonized and was excluded from the analyses, leading to a sample size
301 of 79 sites.

302 We ran models separately for bees and wasps and for the natural enemies of bees and wasps. We
303 modelled species richness and abundance responses with a Poisson error structure when there was no
304 overdispersion, and a negative binomial error structure and a log-link when we detected overdispersion.
305 In the end, all species richness models were modelled with a Poisson error structure, and all abundance
306 models were run with a negative binomial error structure. We built the models using city as a random
307 term and a variable number of fixed effects (see below). For host parasitism, host survival, and host
308 sex-ratio, we used cell-level data, encoding each variable as a binary output (1 = non-
309 parasitized/alive/female; 0 = parasitized/dead/male). We used a binomial distribution with a logit-link
310 (Zuur et al. 2010), using a nested random term (individual nest within site within city) and a variable
311 number of fixed effects. For the number of brood cells per nest and parasitism at the nest level, we used
312 a negative binomial error structure, as overdispersion was detected, using a nested random term (site
313 within city) and a variable number of fixed effects (see below).

314 For all variables, we ran all possible combinations of models using the function *dredge* from the
315 MuMIN package. Then, we used the Akaike information criterion corrected for small sample sizes
316 (AICc; Burnham et al. 2011) and selected the model with the lowest score. While we concentrate our
317 inference on the best supported model, to account for model uncertainty all models with $\Delta AICc < 3$
318 (following prior studies, Mayr et al., 2020) were also considered plausible and are presented in the
319 Supplementary Information. Furthermore, in the additional models, we performed model averaging,
320 computing the full-model averaged parameter estimates for each predicting variable in the candidate
321 model set, using zero when predictors were not included in a particular model (Symonds and Moussali,
322 2011). We checked collinearity among the predictors using the variance inflation factor (VIF) and the
323 Pearson correlation coefficient. We discarded variables with $VIF > 3$ and a Pearson correlation
324 coefficient > 0.7 (Zuur et al. 2010, Dormann et al. 2013, Text S6, Figure S2). Prior to the analyses, we
325 standardized all predictors by z-transformation (Schielzeth 2010). We calculated the pseudo- R^2
326 following Nakagawa & Schielzeth (2013). We used diagnostic plots to estimate model performance and
327 test for spatial autocorrelation. All p-values were adjusted with the Holm correction (Holm 1979) to
328 correct for multiple comparisons.

329 **3. RESULTS**

330 Our trap-nests sampled a total of 4392 nests of cavity-nesting bees (1998 nests) and wasps (2394 nests),
331 containing 16,617 brood cells from 16 bee and 45 wasp species (Table S5), and 4 bee and 14 wasp
332 morphospecies (Figure S6). Four species (*Chelostoma florissomne*, *Hylaeus communis*, *Osmia bicornis*
333 and *Osmia cornuta*) accounted for about 80% of the total number of bee brood cells (Table S2), whereas
334 for wasps the total number of brood cells was more evenly distributed across species. *Passaloecus*
335 *eremita* was the only species representing more than the 10% of the total wasp brood cells, indicating a
336 greater dominance of certain species in cavity-nesting bees than in wasps (Table S2). All species were
337 native, with the exception of the sphecid wasp *Isodontia mexicana* (Saussure, 1867), which was
338 recorded in Antwerp, Paris and Zurich. Further, we identified a total of 47 natural enemy species or
339 morphospecies in 812 nests and 1500 brood cells (Table S3-S4), representing taxa from three insect
340 orders (Hymenoptera, Coleoptera, Diptera) and mites (*Chaetodactylus* spp.).

341 **3.1. Effect of urbanization**

342 A first exploration of the data revealed that several of the community structure metrics, performance
343 traits and life history traits of CNBW and their natural enemies to be structured along urban intensity
344 gradients (i.e., with increasing temperature and grey surfaces in the landscape Figure 2). Urban intensity
345 tended to decrease the community structure (i.e., richness and abundance) of CNBW and their natural
346 enemies, as well as reducing host survival rates and altering sex ratios to more male-biased (Figure 2).

347 Conversely, parasitism at the cell and nest level were relatively unaffected by urban intensity (Figure
348 2)

349 **3.2. Effect of habitat amount at the landscape scale**

350

351 We found host community structure (species richness and abundance hatched) to be strongly associated
352 with proxies for habitat amount (i.e., amount of green spaces within a given buffer from the trap-nest)
353 for both bees and wasps (Table 1, Figure 3). In particular, sites surrounded by larger amounts of green
354 areas (i.e., with less urbanization) had higher host species richness and abundance of the hatched hosts
355 (Tables 1 and S6, Figure 3). Moreover, habitat amount proxies had the largest estimate for host species
356 richness, when compared with proxies for local resources or biotic interactions (Table 1). The influence
357 of habitat amount proxies was also supported by multimodel inference, where these proxies were
358 retained in most plausible models (Table S7, Data S1-S2). In addition, the amount of green areas also
359 influenced the species richness for natural enemies of bees and wasps and the abundance for the natural
360 enemies of wasps (Table 1 and S6, Figure 3), but the effect of habitat amount proxies were less clear
361 after averaging plausible models. Specifically, park size and the amount of green areas in 800 m were
362 retained in the vast majority of plausible models for the species richness of natural enemies of bees
363 (Table S7, Data S1-S2).

364 Habitat amount also shaped several of the performance traits and life-history traits of hosts. Habitat
365 amount proxies (i.e., the amount of green areas at 100 and 800 m) were the main drivers of bee and
366 wasp survival, having the highest estimates (Table 1 & S6, Figure 3). However, the spatial scales were
367 different for bees (800 m) and wasps 100 m). Particularly, the probability of survival increased with
368 higher amounts of green areas (Figure 3).

369 Moreover, we found habitat amount to have the largest effect (based on the estimate, Table 1) on both
370 parasitism at the nest level (i.e., number of parasitized cells per nest) and number of cells per nests in
371 bees), with a positive effect (Table 1 and S6, Figure 3). The influence of habitat amount on these
372 performance and life-history traits was confirmed with multimodel inference, with the proxies selected
373 in all plausible models and significant in the averaged model (Table S7, Data S2). Strikingly, while we
374 found habitat amount proxies to also have the largest effect on the sex ration of wasps, we found it
375 reduced the probability of a cell being a female (Tables 1 and S6). However, it's important to note that
376 effect of habitat amount was lost after averaging the other plausible models (Table S7, Data S1-S2).

377 **3.3 Local resources**

378 We found local resources to influence host and natural enemy responses. Regarding bees, plant species
379 richness had a positive effect on bee species richness in both GLMMs (Tables 1 and S6, Figure S7) and
380 after model averaging (Table S6), with a similar effect size to habitat amount proxies (i.e., similar

381 estimate, Table 1 and S6). In contrast, we found the abundance of natural enemies of bees were
382 negatively influenced by plant species richness (Table 1). Regarding wasps, local resources proxies had
383 a negative effect on wasp responses. Higher plant species richness led to male-biased sex ratios and to
384 a reduced number of cells per nests (Tables 1 and S6). However, these effects were lost after model
385 averaging (Table S7, Data S2). Furthermore, we found the amount of grasslands within 32 m to
386 negatively influence wasp abundance, whereas positively boosting parasitism at the nest level (Table 1
387 and S6, Figure S7) in both GLMMs and after model averaging (Table S7, Data S2).

388 **3.4. Effect of temperature**

389 Temperature was an important driver of some of the host and enemy responses (Figure 4). First, we
390 found local temperature negatively influenced the number of cells per nests for wasps in the GLMMs
391 (Table 1 and S6, Figure 4), but the effect was lost after model averaging. Second, temperature at the
392 landscape scale increased the number of parasitised cells per nests for bees (Table 1 and S6, Figure 4).
393 Regarding natural enemies, temperatures at the local scale reduced the abundance of the natural enemies
394 of wasps, and at the landscape scale (LST at 800 m), increased the richness of bee natural enemies
395 (Table 1 and S6, Figure 4), both for GLMMs and after model averaging (Table S6).

396 **3.5. Effect of biotic interactions**

397 Biotic interactions shaped host and enemy community structure both in GLMMs and after model
398 averaging (Table 1, S6 and S7, Figure 5). Furthermore, proxies of biotic interactions had the largest
399 effect on bee and wasp abundances (Table 1). Specifically, larger parasitism rate negatively impacted
400 the abundance of both bees and wasps (Table 1 and S6, Figure 5). Conversely, a larger number of
401 parasites was positively associated with host species richness and abundance (Table 1 and S6, Figure
402 5). Finally, both the abundance and the species richness of natural enemies of both bees and wasps
403 increased with a larger number of nests per site and with a higher host species richness (Table 1 and S6,
404 Figure 5).

405 **4. DISCUSSION**

406 Our results stress the importance of habitat amount, temperature, resources, and biotic interactions in
407 enhancing multitrophic biodiversity in urban ecosystems. However, the size of the effect of the different
408 drivers varied depending on the response. Habitat amount turned to have a larger effect on several
409 responses of cavity-nesting bees and wasps (CNBW) than temperature, local resources and biotic
410 interactions. For example, sites covered by larger amounts of green surfaces, and thus, with higher
411 vegetation cover and heterogeneity, had more CNBW species and individuals, with higher survival
412 rates. Greater vegetation cover has been found to be linked with higher abundances and richer
413 communities of insect pollinators (Albrecht et al. 2007) and predators (Fabian et al. 2014). Moreover,
414 our study supports the relevance of focusing on overall habitat amount, as proposed by Fahrig (Fahrig

415 2013), rather than on specific, more classical metrics of patch size and isolation (e.g., the proximity
416 index), which in our study had a much minor role in shaping the CNBW and their natural enemies. The
417 *habitat amount hypothesis* (Fahrig 2013) is very useful for understanding urban biodiversity patterns,
418 as cities are characterized by a large number of relatively small, diverse, not necessarily adjacent patches
419 (Aronson et al. 2017), explaining why certain cityscapes can still harbour relatively high diversity levels
420 (Fournier et al. 2020, Vega and Küffer 2021). Our research reinforces the notion that, particularly in
421 cities with a long urban history like ours, the entirety of urban habitats—rather than just natural ones—
422 plays a vital role in preserving diverse species assemblages across various trophic levels. This occurs
423 through habitat supplementation and complementation, as discussed by Colding in 2007. This contrasts
424 with what has been observed in regions or cities with shorter land-use-change histories (e.g., Brazil; da
425 Rocha-Filho et al. 2017, 2020), where the amount of natural habitat, rather than overall urban habitats,
426 has been found to strongly shape bee and wasp diversities.

427 The effects of habitat amount are complex and often indirect, and can vary across trophic levels
428 (Steffan-Dewenter and Schiele 2008, Mayr et al. 2020). In our study, habitat affected the richness of
429 bee and wasp enemies and the abundance of bee enemies. However, the magnitude of the effects was
430 always smaller than the ones for proxies for biotic interactions with their hosts, assessed using metrics
431 representing the availability of hosts (i.e. number of nests, host species richness) as observed in other
432 studies (Fabian et al. 2014, Dainese et al. 2018). Nonetheless, the effects of habitat amount cannot be
433 disregarded, as host communities depended strongly on the amount of habitat, hence indirectly affecting
434 higher trophic levels. Indirect effects of habitat loss have been documented across food webs
435 (Bascompte et al. 2003, Ryser et al. 2019), with negative effects occurring particularly for taxa from
436 higher trophic levels (Melian and Bascompte 2002).

437 Our metrics of plant diversity and vegetation composition, which we used as local resources, shaped
438 several wasp responses and strikingly, only bee species richness. In the case of wasps, higher amounts
439 of grasslands and plant species richness had a negative effect on wasp community structure, life history
440 traits and performance traits. Larger amounts of grasslands imply lower amounts of woodlands (i.e.,
441 shrubs and trees). Similarly, larger plant species richness might be occurring in local landscapes with
442 larger cover of grasslands. Cavity-nesting wasp prey on several insects to feed their larvae and often
443 require certain compounds to build their nest (e.g., resin; Requier and Leonhardt 2020) that are found
444 in woodlands (Beyer et al. 2023), which might explain our results. In any case, local food resource
445 availability has been found to have a variable effect on the structure of CNBW communities in non-
446 urban ecosystems, with studies finding positive effects of plant species richness on CNBW (Tschardt
447 et al. 1998, Albrecht et al. 2007, Mayr et al. 2020) and no effects (Ebeling et al. 2012, Fabian et al.
448 2014). In that regard, the quantity and quality of the food resource (e.g., in terms of nutritional values)
449 might mediate the effects of plant diversity on higher trophic levels (Raubenheimer et al. 2009, Lihoreau
450 et al. 2015, Vaudo et al. 2015, Parreño et al. 2022).

451 Temperature can directly influence insect metabolism (Zuo et al. 2012) and can further regulate species
452 richness and abundance, yet we only found evidence of temperature effects in a handful of responses
453 and with complex and contrasting effects. Moreover, the magnitude of the effect was always smaller
454 than habitat amount, local resources and biotic interaction drivers. Warmer environments have been
455 found to enhance wild bee diversity in cities (e.g., in Rome; Geppert et al. 2022), while less is known
456 about wasps. However, temperatures in cities are highly influenced by the amount and distribution of
457 impervious surfaces, the density of buildings and the type of artificial materials. Therefore, higher
458 temperatures, can be also indicative of smaller habitat amounts and likely of lower food resource
459 availability, which ultimately negatively impact biodiversity responses across ecological levels, as we
460 observed. Finally, while our results provide new evidence on the effects of local temperature, there are
461 some limitations. Particularly, we did not measure the temperature during the months when the larval
462 or pupal stages of many species are developing, i.e. from late summer to the following spring.
463 Temperature sensitivity can vary during ontogeny (Rombough 2003), and thermal conditions during
464 the larval and pupal stages can therefore be critical for later CNBW development and emergence
465 (Rombough 2003, Ostap-Chec et al. 2021). Hence, future studies should extend temperature
466 measurements to also include all developmental stages of CNBW.

467 How biotic interactions influence the properties of host communities in cities remains poorly
468 understood. In our study, biotic interactions had the largest effect on several host community
469 structure responses. This contrasts with findings from prior studies on cavity-nesting wasps in
470 non-urban ecosystems, where resource availability (Steffan-Dewenter and Schiele 2008)
471 together with temperature (Mayr et al. 2020) were stronger drivers of CNBW diversity. In
472 addition, our results showed that wasp richness is positively regulated by their natural enemies,
473 which could indicate a possible top-down regulation from natural enemies for wasps through
474 reduced competition (Levi et al. 2019). However, it is worth noticing that the effect size was
475 much smaller than other drivers, limiting the importance of the top-down regulation of wasp
476 diversity. Regarding bees, our finding of a lack of influence of top-down controls on bee
477 richness should be interpreted with caution, as other top-down factors, such as predation, were
478 not assessed and could be more important (Vidal and Murphy 2018). It is also possible that
479 habitat, and subsequently resource availability, represent a greater limitation than parasitism
480 pressure on bee hosts. In this regard, we only find evidence of the effects of habitat amount and
481 local resources on bee species richness, which had a similar estimate. For example, our results
482 agree with a study on populations of the cavity-nesting bee *Osmia bicornis* in agricultural areas
483 in Germany showed that resource availability was the primary driver, rather than regulation
484 from natural enemies (Steffan-Dewenter and Schiele 2008).

485 Biotic interactions exerted also the largest pressure in the species richness and abundance of natural
486 enemies, with a direct density-dependence on their hosts. Previous studies have also reported direct

487 density-dependence (Krewenka et al. 2011, Mayr et al. 2020). Thus, this suggests that the factors
488 thought to promote inversely density-dependent parasitism, like limited handling time by natural
489 enemies or improved defense and guarding capacities of aggregated hosts (Rosenheim 1990), do not
490 apply to the organisms studied. Moreover, our findings underpin the dependence of natural enemies on
491 their resources (hosts), supporting the idea that higher trophic levels are severely limited by their food
492 resources (Mayr et al. 2020). In that regard, natural enemies are vulnerable to the decline in host
493 availability and to the drivers responsible for these declines, such as habitat reduction, loss of key
494 resources, and the spread of novel pathogens or diseases, which are well-known drivers of insect decline
495 and are becoming more severe worldwide (Wagner et al. 2021).

496 Finally, our study opens some questions regarding other dimensions and scales of diversity that could
497 not be developed here. First, regarding scale, studying how community restructuring (i.e., beta diversity
498 metrics) occurs along urban socio-ecological gradients could help assess the degree of filtering of the
499 communities of hosts and enemies across the studied cities, as shown in other studies (Fournier et al.
500 2020). Second, because biodiversity conservation and management requires information on all its
501 complexity (Villalta et al. 2022), adding additional dimensions, such as functional and phylogenetic
502 diversity, could provide complementary information on how diversity is structured within and among
503 cities.

504 **5. CONCLUSIONS**

505 Our study shows how urban intensity shapes multitrophic diversity through different drivers.
506 Particularly, our study highlights the importance of habitat amount and temperature in urban food webs,
507 through the direct effects on hosts responses and the subsequent consequences on their natural enemies.
508 Ongoing climate change and its interaction with the urban fabric (Müller et al. 2014), together with
509 urban intensification scenarios in the face of a growing urban population (Liu et al. 2020), therefore
510 represent two main challenges for the survival of urban CNBW communities, as well as the interacting
511 species in higher or lower trophic levels. Ongoing adaptation plans to reduce overheating through
512 targeted greening and the expansion of novel and restored habitats represent an opportunity to maintain
513 urban biodiversity (Butt et al. 2018), including the studied food webs. Overall, the study of multitrophic
514 diversity improves our understanding of the contributions of different drivers to multiple dimensions of
515 biodiversity, which in turn helps us to monitor ecological conditions and anticipate future challenges
516 for biodiversity conservation.

517 **ACKNOWLEDGEMENTS**

518 This research was supported by the Swiss National Science Foundation (project 31BD30_172467)
519 within the ERA-Net Bio-divERsA project “BioVEINS: Connectivity of green and blue infrastructures:
520 living veins for biodiverse and healthy cities” (H2020 BiodivERsA32015104) and by the Swiss Federal

521 Office for the Environment (FOEN) in the framework of the project “City4Bees” (contract no.
522 16.0101.PJ/S284-0366). We also acknowledge Göhner Stiftung for supporting this project (2019-
523 2917/1.1). CA was supported by the FCT (SFRH/BD/141822/2018). P.T. and Ł.M. acknowledge Polish
524 funding through NCN/2016/22/Z/NZ8/00004. PP to FCT (CEECIND/03415/2020,
525 DivRestore/001/2020). We thank the local authorities of Zurich (particularly Grün Stadt Zurich [GSZ]),
526 Antwerp, Paris, Poznan and Tartu for supporting this study. Moreover, we acknowledge L. Roquer, J.
527 Bosch and A. Rodrigo for their input on the trap-nest collection. We thank S. Müller, E. Eggenberg, K.
528 Kilchhofer, P. Bischof, R. Veenstra, Ł. Myczko, A. Zanetta and D. Frey for help collecting and
529 processing the bee data. We are grateful to S. Fontana and F. Duchenne for their guidance with the
530 statistical analyses.

531 **CONFLICT OF INTEREST**

532 The authors declare no conflict of interest.

533 **DATA AVAILABILITY**

534 Data will be made available from the repository ENVIDAT (www.envidat.ch) if the article is accepted.

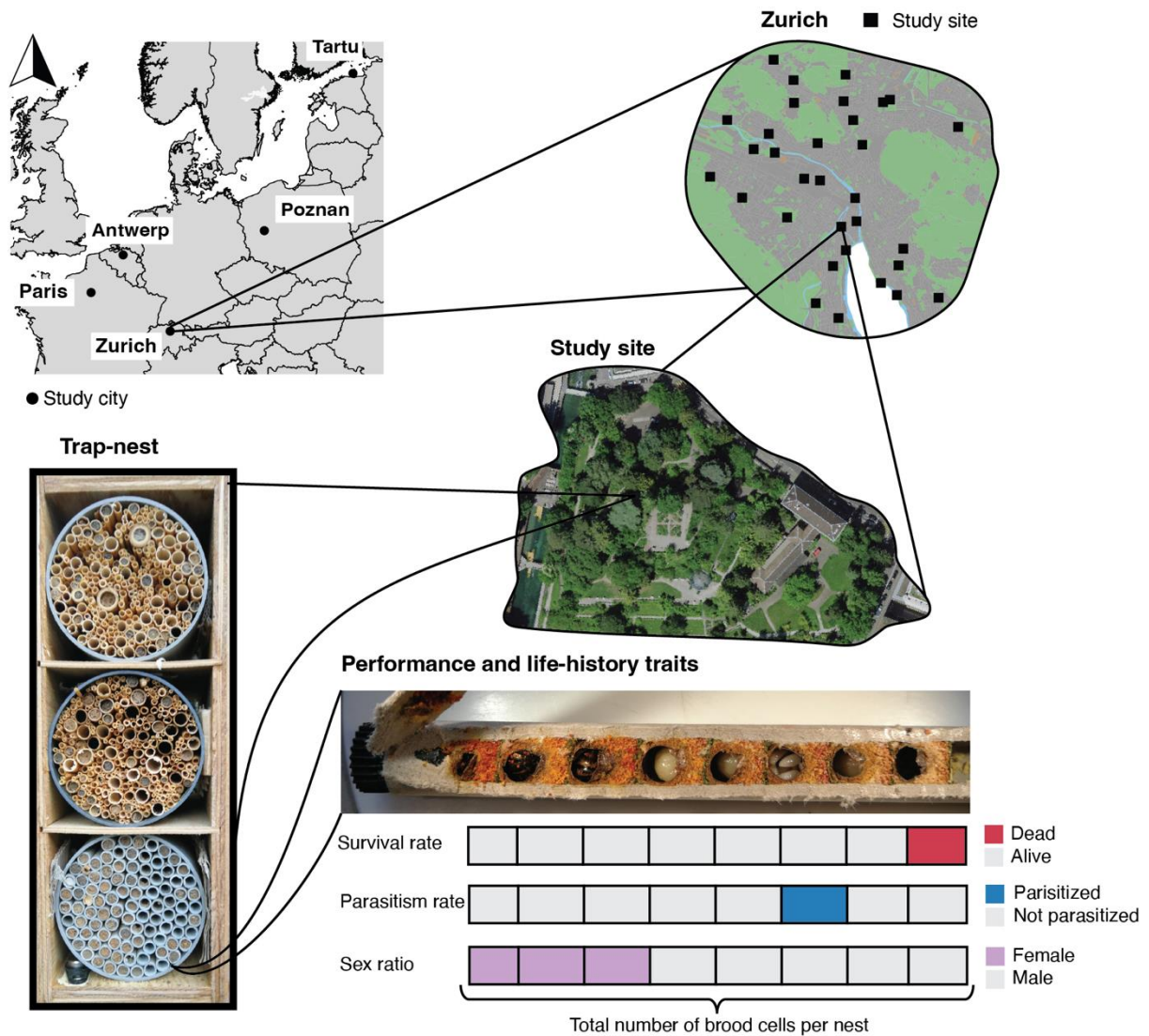
535

Tables and Figures

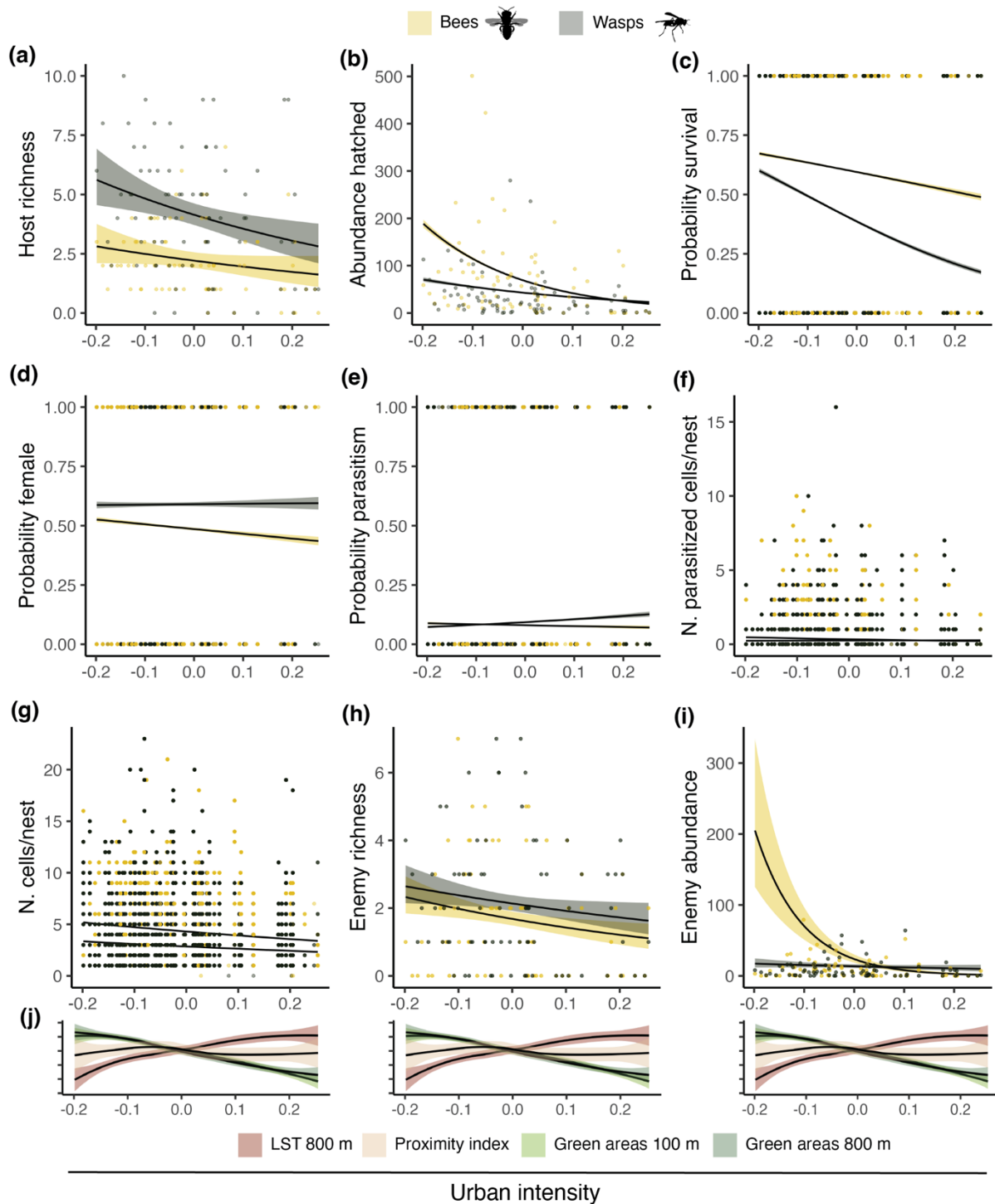
TABLE 1. Summary of the significant effects ($p < 0.05$) of the proxies for temperature, habitat amount, resource availability and biotic controls from the GLMMs on the responses of cavity-nesting bees and wasps and their natural enemies. Plus signs indicate a positive estimate whereas minus signs indicate a negative estimate. For each model, the delta corrected Akaike Information Criterion ($\Delta AICc$) between the best and the second best performing model, and the marginal R^2 and conditional R^2 are provided. Model estimates are provided in Table S5. For the results on multimodel inference, see Table S6 and Data S1 and S2.

		Temperature		Habitat amount		Local resources		Biotic interactions		$\Delta AICc$	R^2_m	R^2_c			
		Local temperature LST 800	Park area	Prox. Index	Green areas 100	Green areas 800	Grasslands 32	Impervious 32	S				Par. rate	N. parasites	Host richness
Hosts	Bees	Richness			0.234				0.210			0.153	0.207	0.207	
		Abundance		-0.294		0.374				-0.659	0.911		0.046	0.520	0.573
		Survival	0.223		0.234	0.717							0.099	0.052	0.676
		Parasitism cell											1.291	0.000	0.956
		Parasitism nest	0.356	0.079	-0.205	0.409		-0.196					1.067	0.020	0.792
		Sex ratio		-0.145									0.015	0.021	0.443
		Wasps	N. cells			0.11		-0.054					0.426	0.038	0.452
	Richness			-0.210	0.341		-0.116			0.013			0.754	0.449	0.548
	Abundance		-0.175		0.422		-0.298			-0.705	1.004		0.304	0.718	0.722
	Survival				0.532		-0.389	-0.324					0.576	0.062	0.592
	Parasitism cell		0.119					0.029					0.080	0.002	0.258
	Parasitism nest		-0.184	-0.201			0.318		-0.211				1.134	0.070	0.269
	Sex ratio		-0.155			-0.203			-0.170				0.214	0.015	0.217
	N. cells		-0.072	-0.095	-0.076				-0.107				0.027	0.053	0.519
Enemies	Bees	Richness	0.338			0.352				0.473	0.330	0.414	0.469	0.469	
		Abundance		-0.498		0.258		-0.36				1.79	0.099	0.658	0.658
	Wasps	Richness			0.197						0.397	0.141	0.625	0.459	0.459
		Abundance	-0.303	0.214			0.301				0.503	0.49	1.186	0.622	0.627

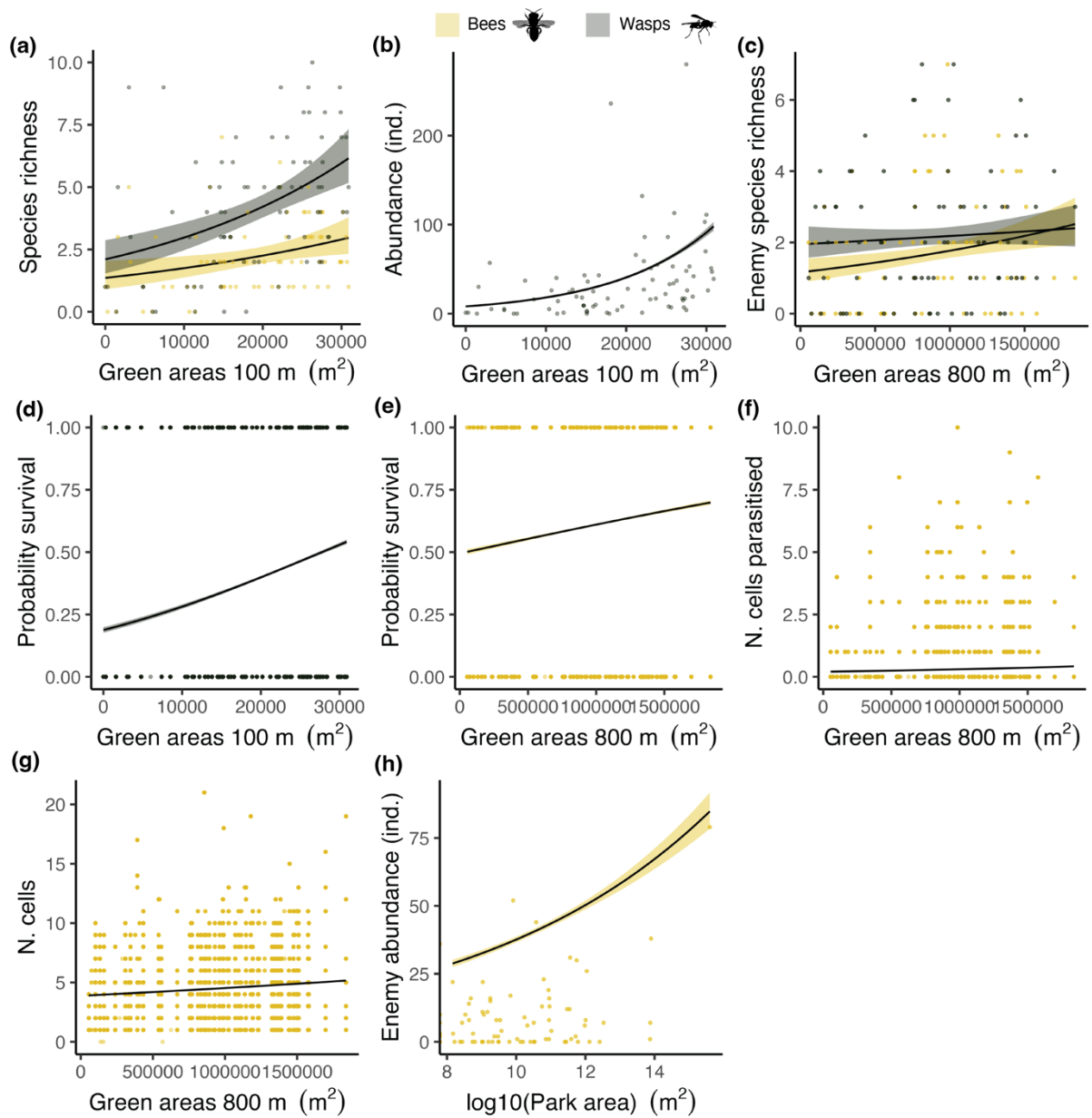
LST 800 = land surface temperature within 800 m; Prox. index = proximity index; Grasslands 32 = proportion of grasslands within a 32 m buffer; Impervious 32 = proportion of impervious surfaces within a 32 m buffer; S = plant species richness; N. parasites = number of parasitized brood cells; Par. Rate = parasitism rate; Host richness = host species richness; Host nest = Number of host nests.



1
 2 **FIGURE 1.** Summary of the study design and calculation of the performance traits (survival rate and
 3 parasitism rate) and life-history traits (sex ratio and number of cells per nest) using a nest from *Osmia*
 4 *leaiana* (Kirby, 1802) in Zurich as an example. Each rectangle represents an individual cell in the nest.



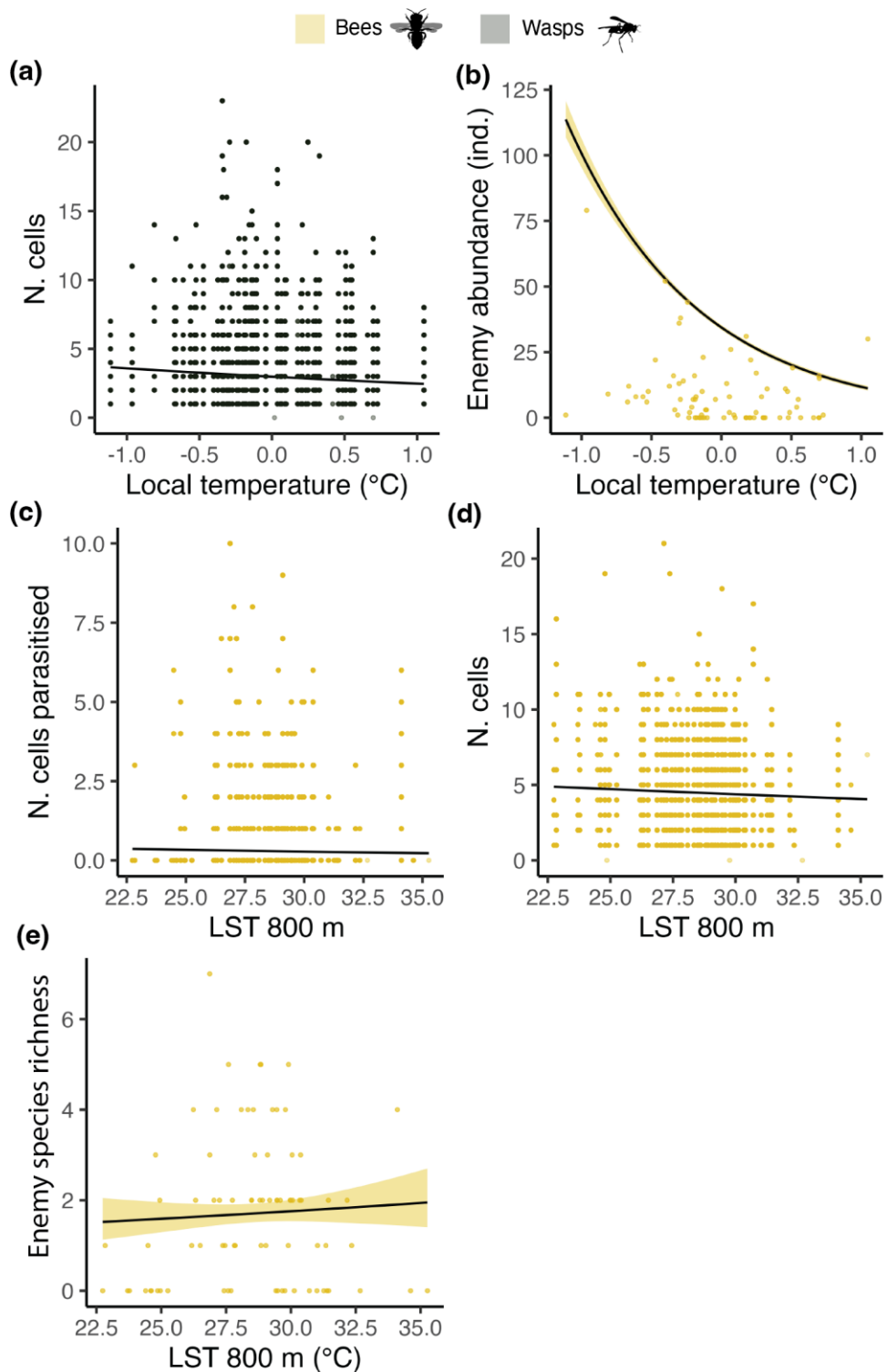
5
6 **FIGURE 2.** Changes in the community structure (a, b, h, i), performance traits (c, e, f) and life-history
7 traits (d, g) of cavity-nesting bees and wasps and their natural enemies, along urban intensity gradients.
8 Points represent the observed data and solid lines represent the predicted values obtained using the best
9 generalised linear mixed effects models ; coloured bands indicate 95% confidence intervals. (j) Loess
10 smoothing between urban intensity and the predictor variables depicting environmental changes at the
11 landscape scale. Urban intensity is inferred through the first PCA axis (see Figure S5) performed on the
12 explanatory variables, which explained ca. 40% of the variability in the data. The influence of specific
13 drivers used to model the responses is shown in Figures 3-6.



14

15 **FIGURE 3.** Generalised linear mixed effects models (GLMMs) depicting the relationship between
 16 proxies of habitat amount (amount of green areas at 100 and 800 m, and park area) and (a-b) host
 17 community structure, (c & h) enemy community structure, (d-f) host performance traits, and (g) life-
 18 history traits. Note that habitat amount proxies did not affect natural enemies. Points represent the
 19 observed data and solid lines represent the predicted values obtained using the best GLMMs; coloured
 20 bands indicate 95% confidence intervals. Model results are shown in Table S6. Additional relationships
 21 can be found in Figures S8-S10.

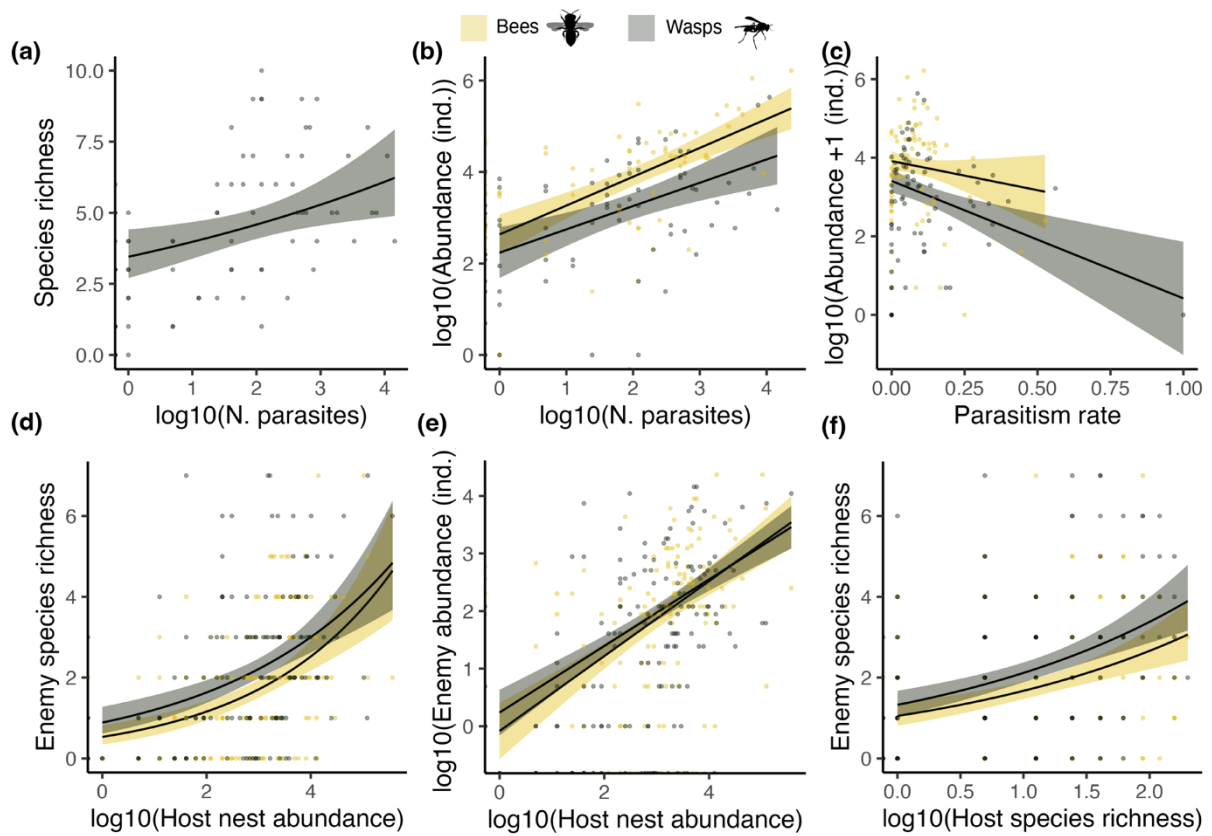
22



23

24 **FIGURE 4.** Generalised linear mixed effects models (GLMMs) depicting the relationship between
 25 proxies of temperature (local temperature and LST at 800 m) and (a-c) host performance traits, (d-e)
 26 natural enemy community structure. Points represent the observed data and solid lines represent the
 27 predicted values obtained using the best GLMMs; coloured bands indicate 95% confidence intervals.
 28 Model results are shown in Table S6. Additional relationships can be found in Figures S8-S10. LST =

29 Land Surface Temperature; Local temperature depicts the anomalies of the local temperature, (see
30 methods section).
31



32

33

34

35

36

37

FIGURE 5. Generalised linear mixed effects models (GLMMs) depicting the relationship between proxies of biotic interactions for hosts (a-c) and natural enemies (d-f). Points represent the observed data and solid lines represent the predicted values obtained using the best GLMMs; coloured bands indicate 95% confidence intervals. Model results are shown in Table S6. Additional relationships can be found in Figures S8-S10.

38 **References**

- 39 Albrecht, M., P. Duelli, B. Schmid, and C. B. Müller. 2007. Interaction diversity within
40 quantified insect food webs in restored and adjacent intensively managed meadows.
41 *Journal of Animal Ecology* 76:1015–1025.
- 42 Alós Ortí, M., J. Casanelles-Abella, F. Chiron, N. Deguines, T. Hallikma, P. Jaksi, P. K.
43 Kwiatkowska, M. Moretti, B. Muysshondt, Ü. Niinemets, P. Pinho, M. J. Pinto, P. Saar, R.
44 Samson, P. Tryjanowski, A. Van Mensel, and L. Laanisto. 2022. Negative relationship
45 between woody species density and size of urban green spaces in seven European
46 cities. *Urban Forestry & Urban Greening* 74:127650.
- 47 Aronson, M. F. J., C. H. Nilon, C. A. Lepczyk, T. S. Parker, P. S. Warren, S. S. Cilliers, M. A.
48 Goddard, A. K. Hahs, C. Herzog, M. Katti, F. A. La Sorte, N. S. G. Williams, and W.
49 Zipperer. 2016. Hierarchical filters determine community assembly of urban species
50 pools. *Ecology* 97:2952–2963.
- 51 Aronson, M. F., C. A. Lepczyk, K. L. Evans, M. A. Goddard, S. B. Lerman, J. S. MacIvor, C.
52 H. Nilon, and T. Vargo. 2017. Biodiversity in the city: key challenges for urban green
53 space management. *Frontiers in Ecology and the Environment* 15:189–196.
- 54 Attwood, S. J., M. Maron, A. P. N. House, and C. Zammit. 2008. Do arthropod assemblages
55 display globally consistent responses to intensified agricultural land use and
56 management? *Global Ecology and Biogeography* 17:585–599.
- 57 Banaszak-Cibicka, W. 2014. Are urban areas suitable for thermophilic and xerothermic bee
58 species (Hymenoptera: Apoidea: Apiformes)? *Apidologie* 45:145–155.
- 59 Barton, K., and I. Šímová. 2015. Package ‘mumin’.
- 60 Bascompte, J., P. Jordano, C. J. Melián, and J. M. Olesen. 2003. The nested assembly of
61 plant-animal mutualistic networks. *Proceedings of the National Academy of Sciences of*
62 *the United States of America* 100:9383–9387.
- 63 Beyer, N., J. Kulow, and J. Dauber. 2023. The contrasting response of cavity-nesting bees,
64 wasps and their natural enemies to biodiversity conservation measures. *Insect*
65 *Conservation and Diversity*.
- 66 Brooks, M., K. Kristensen, K. van Benthem, A. Magnusson, C. Berg, A. Nielsen, H. Skaug,
67 M. Maechler, and B. Bolker. 2017. glmmTMB Balances Speed and Flexibility Among
68 Packages for Zero-inflated Generalized Linear Mixed Modeling. *The R Journal* 9:378–
69 400.
- 70 Burks, J. M., and S. M. Philpott. 2017. Local and landscape drivers of parasitoid abundance,
71 richness, and composition in urban gardens. *Environmental Entomology* 46:201–209.
- 72 Burnham, K. P., D. R. Anderson, and K. P. Huyvaert. 2011. AIC model selection and
73 multimodel inference in behavioral ecology: Some background, observations, and
74 comparisons. *Behavioral Ecology and Sociobiology* 65:23–35.
- 75 Butt, N., D. F. Shanahan, N. Shumway, S. A. Bekessy, R. A. Fuller, J. E. M. M. Watson, R.
76 Maggini, and D. G. Hole. 2018. Opportunities for biodiversity conservation as cities
77 adapt to climate change. *Geo: Geography and Environment* 5:e00052.
- 78 Casanelles-Abella, J., D. Frey, S. Müller, C. Aleixo, M. Alós Ortí, N. Deguines, T. Hallikma,
79 L. Laanisto, Ü. Niinemets, P. Pinho, R. Samson, L. Villarroya-Villalba, and M. Moretti.
80 2021. A dataset of the flowering plants (Angiospermae) in urban green areas in five
81 European cities. *Data in Brief* 37:107243.
- 82 Casanelles-Abella, J., S. Müller, A. Keller, C. Aleixo, M. Alós Orti, F. Chiron, N. Deguines, T.
83 Hallikma, L. Laanisto, P. Pinho, R. Samson, P. Tryjanowski, A. Van Mensel, L.
84 Pellissier, and M. Moretti. 2022. How wild bees find a way in European cities: Pollen

85 metabarcoding unravels multiple feeding strategies and their effects on distribution
86 patterns in four wild bee species. *Journal of Applied Ecology* 59:457–470.

87 Classen-Rodríguez, L., R. Tinghitella, and K. Fowler-Finn. 2021. Anthropogenic noise affects
88 insect and arachnid behavior, thus changing interactions within and between species.
89 *Current Opinion in Insect Science* 47:142–153.

90 Colding, J. 2007. ‘Ecological land-use complementation’ for building resilience in urban
91 ecosystems. *Landscape and Urban Planning* 81:46–55.

92 Dainese, M., V. Riedinger, A. Holzschuh, D. Kleijn, J. Scheper, and I. Steffan-Dewenter.
93 2018. Managing trap-nesting bees as crop pollinators: Spatiotemporal effects of floral
94 resources and antagonists. *Journal of Applied Ecology* 55:195–204.

95 Dale, A. G., and S. D. Frank. 2018. Urban plants and climate drive unique arthropod
96 interactions with unpredictable consequences. *Current Opinion in Insect Science*
97 29:27–33.

98 Diamond, S. E., G. Bellino, and G. G. Deme. 2023, June 1. Urban insect bioarks of the 21st
99 century. Elsevier Inc.

100 Dormann, C. F., J. Elith, S. Bacher, C. Buchmann, G. Carl, G. Carré, J. R. G. Marquéz, B.
101 Gruber, B. Lafourcade, P. J. Leitão, T. Münkemüller, C. McClean, P. E. Osborne, B.
102 Reineking, B. Schröder, A. K. Skidmore, D. Zurell, and S. Lautenbach. 2013.
103 Collinearity: a review of methods to deal with it and a simulation study evaluating their
104 performance. *Ecography* 36:27–46.

105 Ebeling, A., A. M. Klein, W. W. Weisser, and T. Tschardtke. 2012. Multitrophic effects of
106 experimental changes in plant diversity on cavity-nesting bees, wasps, and their
107 parasitoids. *Oecologia* 169:453–465.

108 EEA. 2012. Urban Atlas.

109 Fabian, Y., N. Sandau, O. T. Bruggisser, A. Aebi, P. Kehrl, R. P. Rohr, R. E. Naisbit, and L.
110 F. Bersier. 2014. Plant diversity in a nutshell: Testing for small-scale effects on trap
111 nesting wild bees and wasps. *Ecosphere* 5:1–18.

112 Fahrig, L. 2013. Rethinking patch size and isolation effects: The habitat amount hypothesis.
113 *Journal of Biogeography* 40:1649–1663.

114 Fitch, G., P. Glaum, M. C. Simao, C. Vaidya, J. Matthijs, B. Iuliano, and I. Perfecto. 2019.
115 Changes in adult sex ratio in wild bee communities are linked to urbanization. *Scientific*
116 *Reports* 9:1–10.

117 Fournier, B., D. Frey, and M. Moretti. 2020. The origin of urban communities: From the
118 regional species pool to community assemblages in city. *Journal of Biogeography*
119 47:615–629.

120 Gathmann, A., and T. Tschardtke. 2002. Foraging ranges of solitary bees. *Journal of Animal*
121 *Ecology* 71:757–764.

122 Geppert, C., A. Cappellari, D. Corcos, V. Caruso, P. Cerretti, M. Mei, and L. Marini. 2022.
123 Temperature and not landscape composition shapes wild bee communities in an urban
124 environment. *Insect Conservation and Diversity*:1–12.

125 Gustafson, E. J., and G. R. Parker. 1994. Using an index of habitat patch proximity for
126 landscape design. *Landscape and Urban Planning* 29:117–130.

127 H, W., and X. Y. 2022. evaluate: Parsing and Evaluation Tools that Provide More Details
128 than the Default.

129 Hamann, E., C. Blevins, S. J. Franks, M. I. Jameel, and J. T. Anderson. 2021, February 1.
130 Climate change alters plant–herbivore interactions. Blackwell Publishing Ltd.

131 Hartig, F. 2022. DHARMA: Residual Diagnostics for Hierarchical (Multi-Level / Mixed)
132 Regression Models.

- 133 Hassell, M. P. 1982. Patterns of parasitism by insect parasitoids in patchy environments.
134 *Ecological Entomology* 7:365–377.
- 135 Hassell, M. P. 2000. Host-parasitoid population dynamics*. *Journal of Animal Ecology*
136 69:543–566.
- 137 Holm, S. 1979. A Simple Sequentially Rejective Multiple Test Procedure A Simple
138 Sequentially Rejective Multiple Test Procedure. Source: *Scandinavian Journal of*
139 *Statistics* 6:65–70.
- 140 Hutchinson, G. E. 1957. Concluding Remarks. *Cold Spring Harbor Symposia on Quantitative*
141 *Biology* 22:415–427.
- 142 Jamieson, M. a., a. M. Trowbridge, K. F. Raffa, and R. L. Lindroth. 2012. Consequences of
143 Climate Warming and Altered Precipitation Patterns for Plant-Insect and Multitrophic
144 Interactions. *Plant Physiology* 160:1719–1727.
- 145 Kendall, L. K., J. M. Mola, Z. M. Portman, D. P. Cariveau, H. G. Smith, and I. Bartomeus.
146 2022. The potential and realized foraging movements of bees are differentially
147 determined by body size and sociality. *Ecology* 103:e3809.
- 148 Krewenka, K. M., A. Holzschuh, T. Tschardt, and C. F. Dormann. 2011. Landscape
149 elements as potential barriers and corridors for bees, wasps and parasitoids. *Biological*
150 *Conservation* 144:1816–1825.
- 151 Levi, T., M. Barfield, S. Barrantes, C. Sullivan, R. D. Holt, and J. Terborgh. 2019. Tropical
152 forests can maintain hyperdiversity because of enemies. *Proceedings of the National*
153 *Academy of Sciences* 116:581–586.
- 154 Lihoreau, M., J. Buhl, M. A. Charleston, G. A. Sword, D. Raubenheimer, and S. J. Simpson.
155 2015. Nutritional ecology beyond the individual: A conceptual framework for integrating
156 nutrition and social interactions. *Ecology Letters* 18:273–286.
- 157 Liu, X., Y. Huang, X. Xu, X. Li, X. Li, P. Ciais, P. Lin, K. Gong, A. D. Ziegler, A. Chen, P.
158 Gong, J. Chen, G. Hu, Y. Chen, S. Wang, Q. Wu, K. Huang, L. Estes, and Z. Zeng.
159 2020. High-spatiotemporal-resolution mapping of global urban change from 1985 to
160 2015. *Nature Sustainability* 3:564–570.
- 161 Lüdtke, D., M. Ben-Shachar, I. Patil, P. Waggoner, and D. Makowski. 2021. performance:
162 An R Package for Assessment, Comparison and Testing of Statistical Models. *Journal*
163 *of Open Source Software* 6:3139.
- 164 Mayr, A. V., M. K. Peters, C. D. Eardley, M. E. Renner, J. Röder, and I. Steffan-Dewenter.
165 2020. Climate and food resources shape species richness and trophic interactions of
166 cavity-nesting Hymenoptera. *Journal of Biogeography* 47:854–865.
- 167 Melian, C. J., and J. Bascompte. 2002. Food web structure and habitat loss. *Ecology Letters*
168 5:37–46.
- 169 Müller, N., W. Kuttler, and A. B. Barlag. 2014. Counteracting urban climate change:
170 Adaptation measures and their effect on thermal comfort. *Theoretical and Applied*
171 *Climatology* 115:243–257.
- 172 Nakagawa, S., and H. Schielzeth. 2013. A general and simple method for obtaining R² from
173 generalized linear mixed-effects models. *Methods in Ecology and Evolution* 4:133–142.
- 174 Orr, M. C., A. C. Hughes, D. Chesters, J. Pickering, C.-D. Zhu, and J. S. Ascher. 2021.
175 Global Patterns and Drivers of Bee Distribution. *Current Biology* 31:451-458.e4.
- 176 Ostap-Chec, M., J. Kierat, K. Kuszewska, and M. Woyciechowski. 2021. Red mason bee
177 (*Osmia bicornis*) thermal preferences for nest sites and their effects on offspring
178 survival. *Apidologie* 52:707–719.

179 Papanikolaou, A. D., I. Kühn, M. Frenzel, and O. Schweiger. 2017. Semi-natural habitats
180 mitigate the effects of temperature rise on wild bees. *Journal of Applied Ecology*
181 54:527–536.

182 Parreño, M. A., C. Alaux, J.-L. Brunet, L. Buydens, M. Filipiak, M. Henry, A. Keller, A.-M.
183 Klein, M. Kuhlmann, C. Leroy, I. Meeus, E. Palmer-Young, N. Piot, F. Requier, F.
184 Ruedenauer, G. Smagghe, P. C. Stevenson, and S. D. Leonhardt. 2022. Critical links
185 between biodiversity and health in wild bee conservation. *Trends in Ecology & Evolution*
186 37:309–321.

187 R Core Team. 2022. R: A language and environment for statistical computing. Vienna,
188 Austria.

189 Raubenheimer, D., S. J. Simpson, and D. Mayntz. 2009. Nutrition, ecology and nutritional
190 ecology: Toward an integrated framework. *Functional Ecology* 23:4–16.

191 Requier, F., and S. D. Leonhardt. 2020. Beyond flowers: including non-floral resources in
192 bee conservation schemes. *Journal of Insect Conservation* 24:5–16.

193 Ricklefs, R. E., and M. Wikelski. 2002. The physiology/life-history nexus. *Trends in Ecology
194 & Evolution* 17:462–468.

195 da Rocha-Filho, L. C., P. C. Montagnana, D. Boscolo, and C. A. Garófalo. 2020. Green
196 patches among a grey patchwork: the importance of preserving natural habitats to
197 harbour cavity-nesting bees and wasps (Hymenoptera) and their natural enemies in
198 urban areas. *Biodiversity and Conservation* 29:2487–2514.

199 da Rocha-Filho, L. C., L. S. Rabelo, S. C. Augusto, and C. A. Garófalo. 2017. Cavity-nesting
200 bees and wasps (Hymenoptera: Aculeata) in a semi-deciduous Atlantic forest fragment
201 immersed in a matrix of agricultural land. *Journal of Insect Conservation* 21:727–736.

202 Rombough, P. 2003. Modelling developmental time and temperature. *Nature* 424:268–269.

203 Rosenberg, D. K., and K. S. McKelvey. 1999. Estimation of Habitat Selection for Central-
204 Place Foraging Animals. *The Journal of Wildlife Management* 63:1028.

205 Rosenheim, J. A. 1990. Density-Dependent Parasitism and the Evolution of Aggregated
206 Nesting in the Solitary Hymenoptera. *Annals of the Entomological Society of America*
207 83:277–286.

208 RStudio Team. 2020. R studio: Integrated Development for R. Boston, MA.

209 Ryser, R., J. Häussler, M. Stark, U. Brose, B. C. Rall, and C. Guill. 2019. The biggest losers:
210 Habitat isolation deconstructs complex food webs from top to bottom. *Proceedings of
211 the Royal Society B: Biological Sciences* 286.

212 Schielzeth, H. 2010. Simple means to improve the interpretability of regression coefficients.
213 *Methods in Ecology and Evolution* 1:103–113.

214 Srivastava, D. S., and J. H. Lawton. 1998. Why More Productive Sites Have More Species:
215 An Experimental Test of Theory Using Tree-Hole Communities. *The American
216 Naturalist* 152:510–529.

217 Staab, M., G. Pufal, T. Tschardt, and A.-M. M. Klein. 2018. Trap nests for bees and wasps
218 to analyse trophic interactions in changing environments—A systematic overview and
219 user guide. *Methods in Ecology and Evolution* 9:2226–2239.

220 Steffan-Dewenter, I., and S. Schiele. 2008. Do resources or natural enemies drive bee
221 population dynamics in fragmented habitats? *Ecology* 89:1375–1387.

222 Theodorou, P. 2022. The effects of urbanisation on ecological interactions. *Current Opinion
223 in Insect Science* 52:100922.

224 Trøjelsgaard, K., and J. M. Olesen. 2013. Macroecology of pollination networks. *Global
225 Ecology and Biogeography* 22:149–162.

226 Tscharrntke, T., A. Gathmann, and I. Steffan-Dewenter. 1998. Bioindication using trap-
 227 nesting bees and wasps and their natural enemies: Community structure and
 228 interactions. *Journal of Applied Ecology* 35:708–719.

229 Uchida, K., R. V. Blakey, J. R. Burger, D. S. Cooper, C. A. Niesner, and D. T. Blumstein.
 230 2021. Urban Biodiversity and the Importance of Scale. *Trends in Ecology & Evolution*
 231 36:123–131.

232 Vaudo, A. D., J. F. Tooker, C. M. Grozinger, and H. M. Patch. 2015. Bee nutrition and floral
 233 resource restoration. *Current Opinion in Insect Science* 10:133–141.

234 Vega, K. A., and C. Küffer. 2021. Promoting wildflower biodiversity in dense and green cities:
 235 The important role of small vegetation patches. *Urban Forestry & Urban Greening*
 236 62:127165.

237 Venter, Z. S., and M. A. K. Sydenham. 2021. Continental-Scale Land Cover Mapping at 10
 238 m Resolution Over Europe (ELC10). *Remote Sensing* 13:2301.

239 Vidal, M. C., and S. M. Murphy. 2018. Bottom-up vs. top-down effects on terrestrial insect
 240 herbivores: a meta-analysis. *Ecology Letters* 21:138–150.

241 Villalta, I., C. Bouget, C. Lopez-Vaamonde, and M. Baude. 2022. Phylogenetic, functional
 242 and taxonomic responses of wild bee communities along urbanisation gradients.
 243 *Science of the Total Environment* 832:154926.

244 Violle, C., M.-L. Navas, D. Vile, E. Kazakou, C. Fortunel, I. Hummel, and E. Garnier. 2007.
 245 Let the concept of trait be functional! *Oikos* 116:882–892.

246 Wagner, D. L., E. M. Grames, M. L. Forister, M. R. Berenbaum, and D. Stopak. 2021. Insect
 247 decline in the Anthropocene: Death by a thousand cuts. *Proceedings of the National*
 248 *Academy of Sciences of the United States of America* 118:1–10.

249 Wickham, H. 2016. *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag, New
 250 York.

251 Zumwald, M., B. Knüsel, D. N. Bresch, and R. Knutti. 2021. Mapping urban temperature
 252 using crowd-sensing data and machine learning. *Urban Climate* 35:100739.

253 Zuo, W., M. E. Moses, G. B. West, C. Hou, and J. H. Brown. 2012. A general model for
 254 effects of temperature on ectotherm ontogenetic growth and development. *Proceedings*
 255 *of the Royal Society B: Biological Sciences* 279:1840–1846.

256 Zuur, A. F., E. N. Ieno, and C. S. Elphick. 2010. A protocol for data exploration to avoid
 257 common statistical problems. *Methods in Ecology and Evolution* 1:3–14.

258