

City4Bees

For a sustainable coexistence between honeybees and wild bees in cities

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Final Report

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Gewöhnliche Keulhornbiene (*Ceratina cyanea*) sitzt neben einer Honigbiene (*Apis mellifera*) auf einer Wiesen-Flockenblume (*Centaurea jacea*) (©Entomologie/Botanik, ETH Zürich / Foto Albert Krebs - <http://doi.org/10.16902/ethz-a-000018084>)

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Contractor	Swiss Federal Research Institute WSL, Birmensdorf ZH
Authors	Joan Casanelles Abella, Miriam Leimbgruber, Stefanie Müller, Simonetta Selva, David Frey, Marco Moretti With the collaboration of Prof. Bertrand Fournier, University of Potsdam, Germany
Supervision	FOEN: Debora Zaugg Ernst Göhner Foundation: Michaela Gasser This study was commissioned by the FOEN with the support of the Ernst Göhner Foundation. The contractor is solely responsible for the content.

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“You cannot protect what you do not love, and you cannot love what you do not know”

Carlos Herrera
Ecologist specialized in bees

1. ABSTRACT

Background and goals: Wild bees are critical pollinators but are currently declining due to the combined effect of land-use changes, pollution, losses of flowering resources, arrival of pests and pathogens and disrupted interactions. Urbanization represents a major force of land-use change with negative impacts on biodiversity, yet urban areas, particularly in well-studied European cities, can promote and preserve many wild bee species. Nonetheless, the recent increase in urban beekeeping may add a new threat as beekeeping has been shown to enhance intra- and interspecific competition in both honeybees and wild bees in agricultural, natural and, to a minor extent, urban areas. In this report, using Zurich as a model city, we aimed to assess the status of honeybees and wild bees by modelling the distribution of honeybees, wild bees and their relationships with floral resources and studying signs of competition or coexistence between honeybees and wild bees along urban gradients. To address these goals, the report has been divided in four work packages (WP):

WP1 provides a city-scale overview of the distribution and density of honeybees, wild bees, and the floral resources.

WP2 investigates the diet of four wild bee species in five European cities to understand how consistent they were among cities and how this in turn influenced the distribution of the four wild bee species.

WP3 tests for competitive interactions using a wide range of data, both experimental and observational including functional and taxonomic community metrics and reproductive success.

WP4 provides recommendations to stakeholders and city managers to enhance coexistence of honeybees and wild bees in cities.

Methods: We collected honeybee apiary distribution in the city of Zurich for the period 2012-2018. We then assess competition between honeybees and wild bees by crossing honeybees' data with existing data on wild bee species' occurrences, reproductive success metrics and taxonomic and functional community estimates collected in the city of Zurich between the years 2006-2018. We also investigate the level of generalism of wild bees in different cities and the ability to adapt their diet under different environmental condition, including urban densification and floral resources.

Results and discussion: We found Zurich to contain a rich and diverse wild bee community, composed mainly of a vast majority of rare species occurring in few locations in the city, a universal feature of ecosystems that also applies to urban areas. Moreover, wild bees are particularly promoted in allotments, gardens, and brownfields. Nonetheless, we also found honeybee densities have rapidly increased all over the city, to the point that any green area in the city has an apiary in the surrounding. Urban beekeeping has increased throughout Swiss cities between 2012-2018. Concerning competitive interactions, honeybees seem not to interfere with specific guilds such as cavity-nesting bees. In addition, honeybees and wild bees co-occur in high quality urban areas such as low-managed urban gardens where resources are not limited. Conversely, in highly urbanized areas of the city, independently of their local floral richness, green areas tend to have more honeybees because of a concentration effect to favorable patches, and less wild bee species because of a combination of less habitat, environmental stressors and, probably, enhanced competitive interactions.

Implication for the praxis: Overall and based on the existing evidence in agricultural and natural areas, our results suggest that urban beekeeping should not be unconditionally encouraged. At the same time oasis of floral resources should be offered in the denser parts of cities. In general, conservation researchers and city policy makers should work together to manage potential conflicts. On the one hand, researchers should provide evidence-based findings, while city government should intervene through policy and planning mechanisms. A dialectic between scientific research and urban bee policy implementation is critical through intentional science-city partnerships.

2. INTRODUCTION

2.1. Urbanization and conservation of bees

Wild bees are declining globally. Compared to other Central-European countries, Switzerland has an extraordinary high wild bee richness; therefore, the national responsibility to conserve these species may be elevated¹. Wild bees are threatened by land-use change and intensification, global warming, pollution, introduced enemies and pathogens, invasive competitors^{2,3}.

Urbanization is a major driver of land use change, thereby leading to biodiversity loss, primarily through the removal of native vegetation and the destruction of habitats^{4,5}. On the other hand, cities worldwide still contain substantial proportions of native biodiversity, including many rare and endemic species that have a high conservation priority^{6,7}. Hence, there is consensus that biodiversity conservation within urban areas is relevant, and that especially key urban biodiversity areas should be safeguarded⁸.

There is increasing evidence that cities can harbour species- and individual-rich communities of wild bees^{7,9-12}. Moreover, several studies suggest that cities may even serve as source of wild bees and other pollinators for adjacent impoverished agricultural environments^{9,11,13,14}. There are three main reasons for that. First, cities tend to be located within or adjacent to regional and even global biodiversity hotspots¹⁵⁻¹⁷. Second, cities are heterogeneous environments, where green spaces intersect with built ones. They can be described as fine-scaled mosaics consisting of parks, gardens, wastelands, green roofs, buildings with nesting sites, and patches of remnant native vegetation such as forests, shrubland and wetlands. Moreover, due to frequent human disturbances, cities are also temporally very dynamic, which further increases the environment heterogeneity of urban areas. This fine-scale urban habitat mosaic appears to be particularly favourable to many wild bee species^{18,19}. Third, cities are the neuralgic centre of trade routes and movement of people and goods; hence, they are also the arrival point of many exotic species that are deliberately or accidentally released in urban areas. Ornamental plants and the widespread gardening activities have provided wild bees with new types of food sources that might buffer seasonal variation in nectar and pollen¹⁰. Fourth, cities have a warmer microclimate that is favourable for European bees. Consequently, urban areas promise to be a key component for wild bee conservation²⁰.

In the city of Zurich, for instance, the three main studies conducted by the WSL (BiodiverCity 2008-2012), Enhance (2010-2014) and BetterGardens (2015-2019) have found 195 species of bees, 53 (27%) of which are of conservation concern (Swiss Red List of bees⁵⁰); see table 1.

Table 1. Swiss Red List of bees⁵⁰ sampled by the WSL from 2008 to 2019 (Fauna DataBase WSL, 9.7.2019).

Duelli 1994 categories	IUCN categories	N.spp.
0 Ausgestorben oder verschollen	Extinct	1*
1 Vom Aussterben bedroht	Endangered	2
2 Stark gefährdet	Vulnerable	7
3 Gefährdet	Near Threatened	40
4 Potentiell gefährdet	Rare	3
	Total	53 (27%)

* *Andrena alfkenella*

2.2. Beekeeping trends

In the last 20 years, there has been a worldwide increase of beekeeping and therefore of honeybees. This has happened in both countries where beekeeping was not a traditional activity (e.g., countries in Latin America, Asia) but also in several European countries including Switzerland, not only in agricultural land but increasingly in urban areas²¹. Focusing on Switzerland, based on the cantonal apiary register, there has been also an increase in apiaries in several cantons for the period 2012-2018, following the global trend. Conversely, it is unclear how the amount of plants has evolved in the same period and in what magnitude.

2.3. Beekeeping and potential competition with wild bees

Honeybees as a major competitor for plant resources

The increase in managed honeybee individuals might enhance competition with wild pollinators with potential negative effects on the former due to the following reasons. First, honeybees are super-generalist species, with large number of workers (20-60k individuals per colony), efficient foraging behaviour, high food requirements (20-50 kg of pollen/colony)²² and a high mobility (up to 5 km from the colony)²³. Second, the degree to which wild bees and honeybees coexist is mediated by the availability (quantity, quality, variety) of food resources (nectar and pollen). Wild bees have higher pollen requirements for their offspring development. Hence, depletion of pollen resources by more efficient honeybee workers can have important consequences on parasitism rates and on fitness, due to the combined action of inter- and intraspecific competition. Third, honeybees are managed pollinators, which are fed and kept healthy by humans; hence, we expect honeybees to be less influenced by natural selection when compared to wild bees.

Evidence on competitive interactions between honey- and wild bees

There is considerable indirect evidence for competitive interactions between honeybees and wild bees (Table 2). However, experimental evidence is lacking concerning long-term reductions of wild bee populations driven by honeybees²⁴. This is mainly due to the difficulty to convincingly assess competition in these highly mobile species, rather than due to true absence of competition²⁴.

Past studies have investigated competitive interactions mostly in agricultural and natural areas²⁵. These studies have indirectly assessed competition by using correlative and observational methods (Table 2). In contrast, direct evidence of competition (fitness responses, resource use metrics), are still rare²⁶. The few existing studies have found evidence on exploitative competition of honeybees on wild bees²⁷⁻²⁹ in specific contexts (Table 2). Moreover, Herrera (2020)³⁰ has shown declines of wild bee populations in concomitance with increasing honeybee densities over the last 50 years across the Mediterranean Basin³⁰. Finally, some studies have shown that increased honeybee densities not only affect wild bees, but also enhances intraspecific competition and the transmission of pathogens and parasites among hives³¹. Therefore, understanding the ecological consequences of beekeeping is not only relevant for the wild bee conservation, but also for the beekeepers themselves.

It is not clear how the evidence of competition in agricultural areas or wildlands (e.g., nature reserves) can apply to urban ecosystems, which differ from other ecosystem types in many aspects: usually, cities have higher landscape heterogeneity, as patches of habitat are smaller but more diverse due to the small scale of ownership and management decisions. In addition, plant diversity tends to be higher, partly due to the large number of cultivated species^{32,33}, and the naturally high plant species richness in many urban areas¹⁵. Some plant species provide large amounts of flowers that attract honeybees, thereby potentially reducing niche overlap¹². A major challenge is that competitive interactions have been very little studied in urban ecosystems²³, with the only evidence coming from a recent study in the city of Paris³⁴. In Paris, plant-pollinator networks appear to be affected negatively by the presence and abundance of honeybees³⁴. In a recent review, Egerer and Kowarik³⁵ state that *“there is no universal understanding of how the increased density of honeybee colonies impacts the wild insect pollinators (bees, butterflies, flies, etc.) inhabiting cities, or how subsequent shifts in these wild pollinator assemblages may impact urban wild/native plant communities”*. In fact, in cities, urban beekeeping may present both opportunities and risks for wild bee conservation. On one hand, increased competition by managed bees may add to the stressors and disturbances already impacting wild bee populations in urban environments. On the other hand, reports on honeybee declines have had an important influence on society, raising awareness of the effects of human actions and

enhancing willingness to protect “bees”. In fact, people engaged in urban beekeeping often develop a pro-environmental behaviour, for instance by providing habitat for pollinators (pollinator friendly seed mixes) or engaging in politics³⁵.

Finally, there are still important research gaps regarding this topic. Lack of knowledge of city-wide distributions of wild bees, honeybees and plants prevent making precise assessments of the impact of honeybees on wild bees. Second, most of studies have focus only on community-level effects (abundances, species richness) or rough behavioural measures such as visitation rates.

Table 2. Summary of the results of 12 studies on competition between honey- and wild bees performed in Europe. For every study, we provide details on the methodological aspects (the ecosystem type studied, the location, the temporal range, the wild bee species studied, the study type) and the main responses, effects and signals obtained. Overall, 10 studies reported negative effects of honeybees on wild bees and two reported neutral effects.

Study	Ecosystem	Location	Temporal range	Wild bee community	Study type	Response indicator	Effect indicator	Signal
Elbgami et al. 2014	Experimental fields	England	Jul-Set 2010 Jun-Jul 2012	Bumblebees	Experimental	Bumblebee colony weight	Distance honeybee apiaries	☹️
Elbgami et al. 2014	Experimental fields	England	Jul-Set 2010 Jun-Jul 2012	Bumblebees	Experimental	Number of queens	Distance honeybee apiaries	☹️
Elbgami et al. 2014	Experimental fields	England	Jul-Set 2010 Jun-Jul 2012	Bumblebees	Experimental	Proportion of males	Distance honeybee apiaries	😊
Elbgami et al. 2014	Experimental fields	England	Jul-Set 2010 Jun-Jul 2012	Bumblebees	Experimental	Male size	Distance honeybee apiaries	☹️
Wignall et al. 2020	Cultivated	SE England	May-Sep 2017	Bumblebees	Experimental	Presence of bumblebees	Number of honeybees foraging	😐
Wignall et al. 2020	Cultivated	SE England	May-Sep 2017	Bumblebees	Experimental	Number of honeybees foraging	Season	😊
Henry & Rodet 2018	Wildlands	France	2015-2016	All species	Observational	Occurrence wild bee species	Honeybee density	☹️
Henry & Rodet 2018	Wildlands	France	2015-2016	All species	Observational	Nectar foraging success wildbees	Honeybee density	☹️
Henry & Rodet 2018	Wildlands	France	2015-2016	All species	Observational	Nectar harvesting honeybees	Honeybee density	☹️
Henry & Rodet 2018	Wildlands	France	2015-2016	All species	Observational	Pollen harvesting honeybees	Honeybee density	☹️
Ropars et al. 2020	Urban	Paris, France	May-Jul 2014-2016	All species	Observational	Wild bee flower visitation	Honeybee density	☹️
Hudewenz & Klein 2013	Wildlands	Germany	Aug 2012	All species	Observational	Wild bee flower visitation	Honeybee density	☹️
Hudewenz & Klein 2013	Wildlands	Germany	Aug 2012	All species	Observational	Reproductive success wild bees	Distance honeybee apiaries	😐
Hudewenz & Klein 2013	Wildlands	Germany	Aug 2012	All species	Observational	Reproductive success wild bees	Honeybee density	😐
Hudewenz & Klein 2013	Wildlands	Germany	Aug 2012	All species	Observational	Cavity-nesting bee richness	Honeybee density	☹️
Steffan-Dewener & Tschantke 2000	Wildlands	Germany	Apr-Aug 1994	All species	Observational	Wild bee abundance	Honeybee density	😐
Steffan-Dewener & Tschantke 2000	Wildlands	Germany	Apr-Aug 1994	All species	Observational	Wild bee richness	Honeybee density	😐
Herrera 2020	Wildlands, Cultivated	Mediterranean Basin	1963-2017	All species	Observational / Metaanalysis	Proportion of wildbees in flowers	Time	☹️
Herrera 2020	Wildlands, Cultivated	Mediterranean Basin	1963-2017	All species	Observational / Metaanalysis	Honeybee density	Time	😊
Torneé-Noguera et al. 2016	Wildlands	Spain	Mar-Jun 2010	All species	Observational	Wild bee biomass	Distance honeybee apiaries	☹️
Torneé-Noguera et al. 2016	Wildlands	Spain	Mar-Jun 2010	All species	Observational	Pollen consumption	Honeybee visitation	😊
Magrach et al. 2017	Wildlands, Cultivated	SW Spain	2017	All species	Observational	Wildbee visitation on wild flowers	Honeybee density	☹️
Magrach et al. 2017	Wildlands, Cultivated	SW Spain	2017	All species	Observational	Interaction evenness	Honeybee density	☹️
Magrach et al. 2017	Wildlands, Cultivated	SW Spain	2017	All species	Observational	Apparent competition	Honeybee density	😊
Lindström et al. 2016	Cultivated	Sweeden	May-Jun 2011-2012	All species	Experimental	Abundance wild bees	Honeybee density	☹️
Herbertsson et al. 2016	Cultivated	Sweeden	May-Jun 2011-2012	Bumblebees	Experimental	Bumblebee densities	Honeybee density	😐
Cane & Tepedino 2017	Wildlands	-	-	All species	Experimental	Honeybee pollen intake	-	☹️

Goal and conceptual framework

The overall goal of the project is to study and model the distribution of honeybees, wild bees and their relationships with floral resources to elucidate signs of competition between honeybees and wild bees. This goal is part of a large project co-financed by the Federal Office for the Environment (FOEN) and the Ernst Göhner Foundation. The project is composed of four work packages (WP) (see Fig.1).

More specifically, the project aims to answer the following four research questions (RQ) and relative work packages (WP):

RQ1: How are honeybees and wild bee diversity distributed in cities? [WP1]

RQ2: Which flowers do bees prefer and does their preference change in different cities? [WP2]

RQ3: Do wild bees and honeybees occur together and what are the consequences of an increase in beekeeping and urban densification on wild bees? [WP3]

RQ4: What recommendations can we provide to stakeholders and city managers to enhance the coexistence of honeybees and wild bees in cities? [WP4]

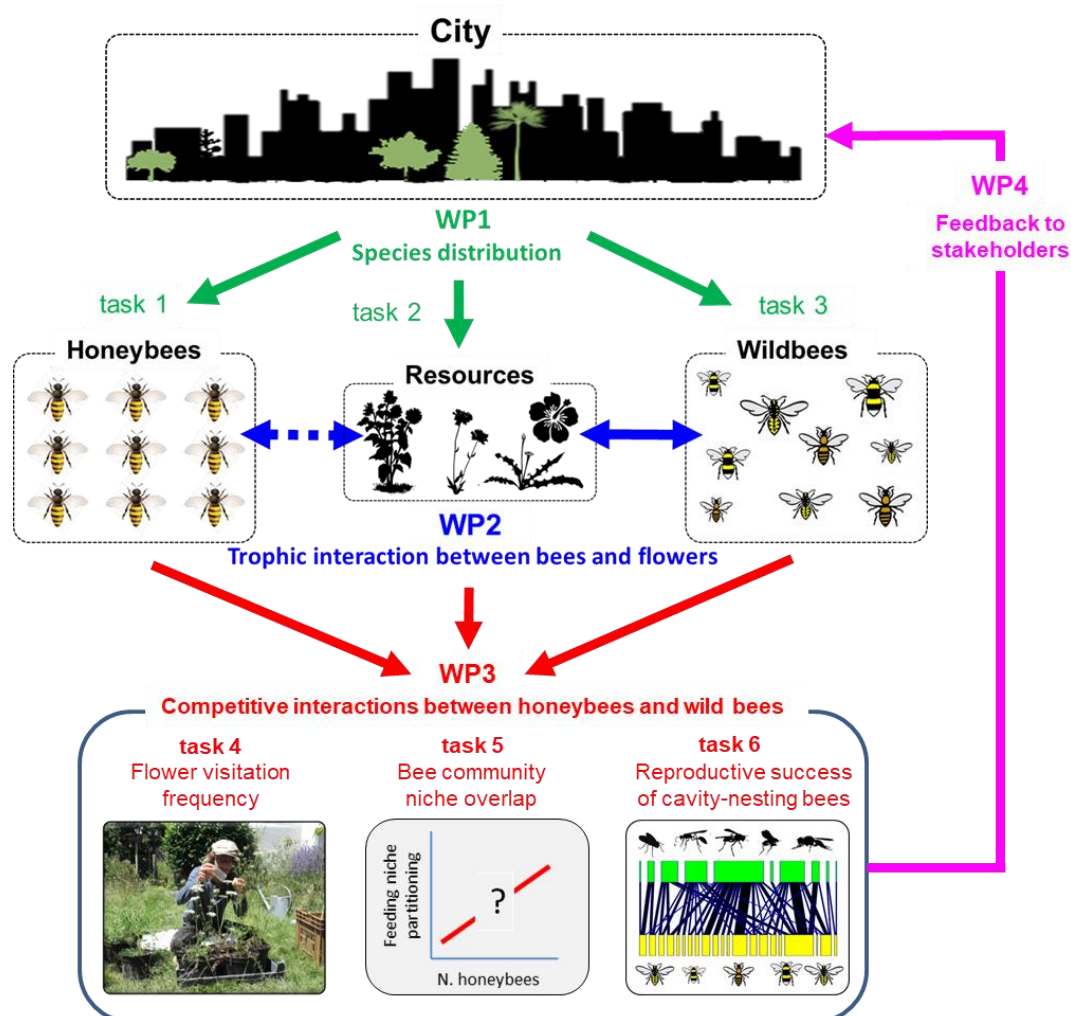


Figure 1. Conceptual framework showing the different work packages (WP) and tasks. Solid arrows: the relationships are directly investigated; Dashed arrows: the relationships are investigated indirectly.

3. WP1: DISTRIBUTION OF BEES AND FLORAL RESOURCES IN THE CITY OF ZURICH

WP1 focuses on the distribution of honeybees, wild bees, and flora resources using the city of Zurich as a case study.

As in any other ecosystem, biodiversity in cities has a spatial organisation, which means that the species are distributed according to both abiotic (climate, pollution) and biotic (presence of food resources, interactions with other organisms such as predators, competitors, mutualists or parasites). In cities, these abiotic and biotic factors are tightly linked to humans and their activities.

WP1 provides a city-scale overview of the distribution and density of honeybees, wild bees and the floral resources. Moreover, it provides practical tools to stakeholders and managers to effectively promote wild bee conservation in cities, in particular with regard to the high wild bee densities associated with nesting site provided by garden owners (“bee hotels”).

WP1 was divided in three tasks: Task 1 - Density maps of honeybees; Task 2 - Heatmaps of floral resources; Task 3 - Wild bee diversity and distribution.

3.1. Task 1: Density maps of honeybees

Goals

Modelling the density of honeybees in the city of Zurich.

Specifically, we aimed to **(1)** understand which factors, such as the city structure, constrain or facilitate honeybee abundance; **(2)** use different available statistical techniques to model and predict the abundance of honeybees and assess their performance, using the available cantonal register of honeybee hives together with an extensive sampling in the city; and finally **(3)** obtain a city-wide map of the predicted abundance of honeybees to locate areas with high- and low-density of honeybees.

Methods

The density maps (or heatmap) of honeybees are a set of modelled maps based on (1) existing honeybee hive distribution and (2) on the field honeybee abundance counts, following different mathematical and ecological assumptions. We obtained the coordinates of the honeybee hives for the years 2012-2018 from the Veterinary Office of the Canton of Zurich. In addition, we conducted a field sampling of honeybee density within the city of Zurich, by dividing the city in 1 x 1Km grid cells and defining one to three 500 m sampling transects, stratified to the number of land covers present. We implemented four modelling approaches to extrapolate the sampled honeybee density to the entire city: distance-based models (Fig. 2-3b), circuitscape-based models (Fig. 3c), abundance models (Fig. 3d) and landscape metrics (Fig. 4). Distance-based models are the simplest model used and only use the spatial distribution of the honeybee hives and infers the density of honeybees using a dispersal function. Circuitscape-based models are an extension of the former models that include landscape resistance to bee movement

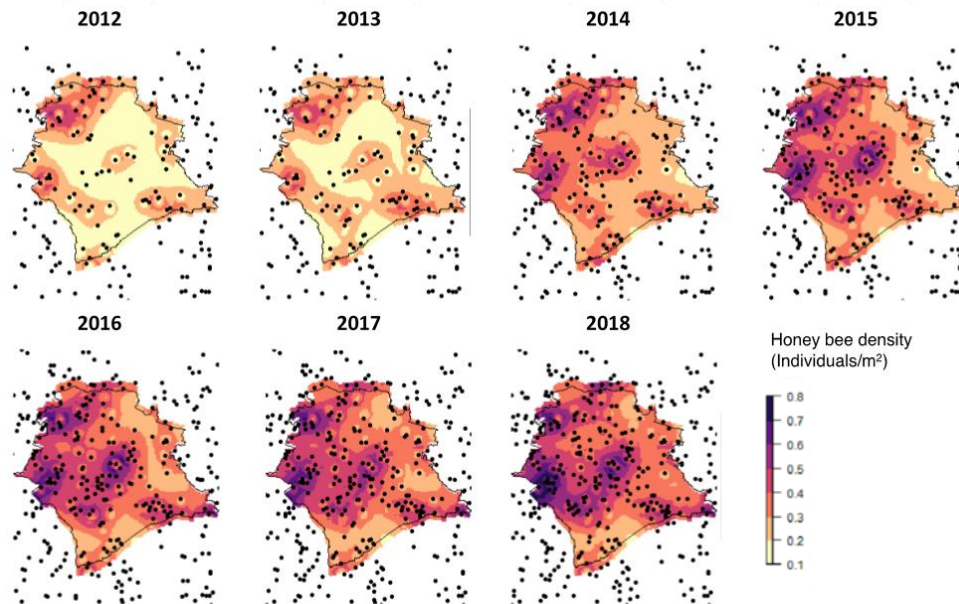


Figure 2. Honeybee density maps for the period 2012-2018 in the city of Zurich. Honeybee densities are calculated following a distance-based model (see also Fig. 3b), which uses the actual distribution of honeybee hives (dots) and computes a dispersal function, where the number of honeybees of each hive decays following a function. In this case, we used a negative exponential function, based on Visscher and Seeley (1982). The color scale of the maps reflects the calculated density of honeybee individuals per ha. **Scale- values:** bright colored areas indicate the lowest densities (yellow indicates ca. 0.1 individuals / ha) and dark colored areas indicate the maximum densities (violet areas indicates ca. 0.8 individuals /ha).

The abundance model is based on species distribution models predicting abundance instead of species occurrence. Finally, we used two types of landscape metrics using the hive distribution data from 2012 and 2018, the distance the nearest beekeeping point and the density of hives at 1000-m radii. All analyses were performed in the R environment and QGIS. For additional information, see the Appendix.

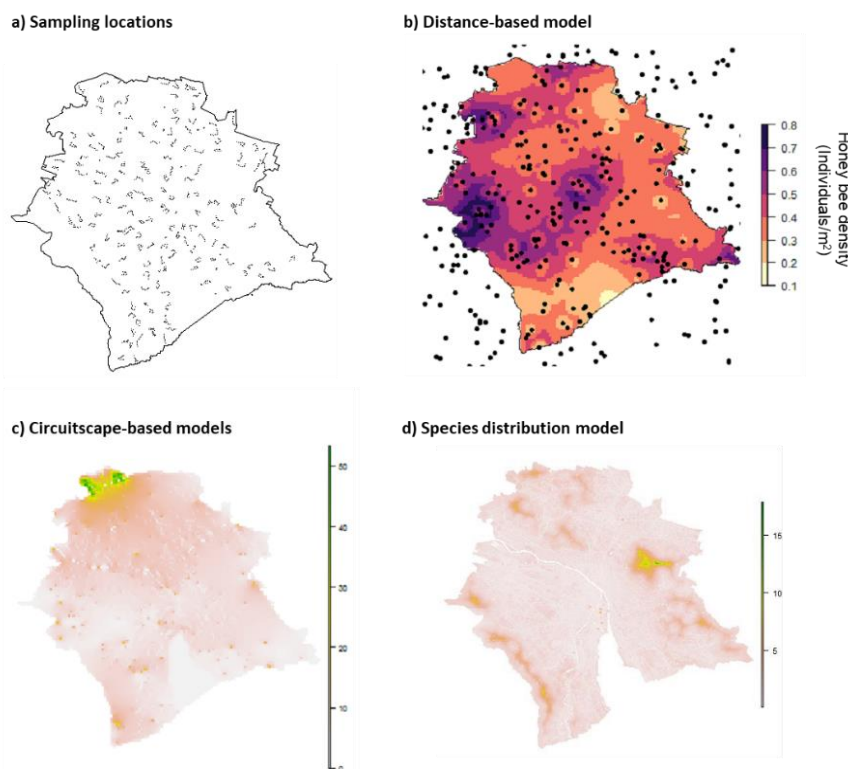


Figure 3. Map (a) shows the sampling locations where honeybee abundance was recorded in 2019. The other maps show predicted honeybee densities calculated using (b) **Distance-based model**, (c) **Circuitscape-based model**, and (d) **Species distribution model**.

Scales show different units according to the model, while differences in range of values relate to very different modelling techniques.

Scale values: (b) dark colored areas (purple) indicate the lowest densities and bright colored areas (white/yellow) indicate the maximum densities (c, d) white colored areas indicate the lowest densities and green colored areas indicate the maximum densities.

Results

We obtained a set of honeybee density maps for the city of Zurich computed following the aforementioned approaches (i.e., distance-based, circuitscape-based and species distribution modelling]. The honeybee sampling, the hive distribution and our density maps indicate that honeybees are present all over the city, at least at coarse spatial scales, likely due to the rapid increase in the number of honeybee hives in the recent years (Fig. 2]

However, none of the applied modelling procedures was able to predict honeybee distribution in the city with a satisfying precision or accuracy at finer resolutions (< 100 m]. A combination of factors hinders a more realistically estimate of the small-scale honeybee densities:

- (1) the number of honeybee hives, which are currently present in all districts and cover most of the city extension (see Fig. 2]. That means there are almost no absences but rather a nearly 100% coverage in the city.
- (2) the biology of honeybees, which are considered to be “super” generalists, meaning they can forage on a wide range of plant species present in the city. In addition, honeybees have large foraging ranges, a highly developed social structure, an advanced scouting behaviour to locate resources, and can share information about the direction and distance to patches of flowers with other hive members. This makes them less susceptible to habitat isolation and fragmentation, allowing them to access a wide range of foraging patches (areas where there are flowers]. Taken together, the high mobility of honeybees and the urban landscape structure may cause transient concentrations or dilution of foraging honeybees³⁶.
- (3) A lack of knowledge on the influence of the different elements of the urban landscape on honeybee movement

Our results indicate two main points: *First*, honeybees seem to be able to reach any area within the city, as any point in the city has a hive in at least 1000 m (Fig. 4b], a distance easily covered by honeybee workers. Moreover, due to their advanced scouting behaviour, honeybee colonies can rapidly allocate their workers to the available food patches that are within their foraging range (which can extend to at least 5 km]. This implies that **competitive interaction with wild bees can potentially occur within the entire urban area of Zurich, also at sites that could be important for wild bee conservation**. Hence, no sanctuaries for wild bees currently exist in the metropolitan area of Zurich. As honeybees prefer to use the most abundant floral resource, the spatial distribution of honeybee abundance will follow temporal dynamics (concentration or dilution], coupled with the phenology of the city plants. *Second*, the current situation on honeybee density is very recent. As shown in Fig. 2, the number of honeybee hives has markedly increased between 2012 and 2018 (data prior to 2012 is not available] and so has the honeybee density. Although these models have a low accuracy at detailed spatial resolutions and make important assumptions about the bee movement, at the general city level they indicate a rapid increase in honeybee density, particularly after 2014.

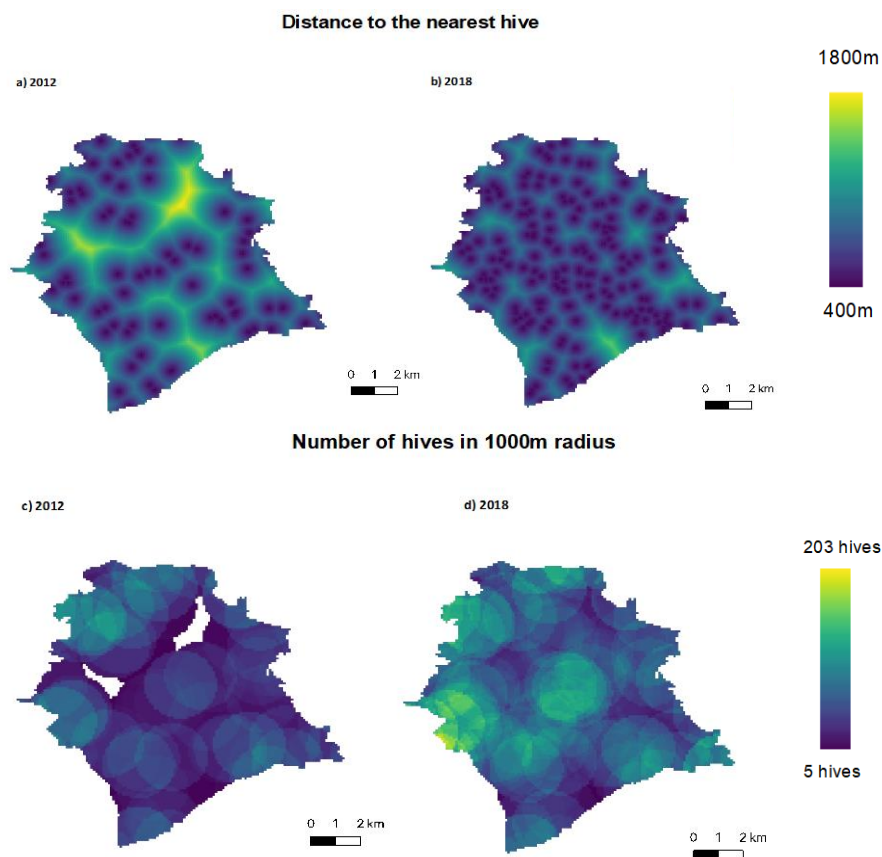


Figure 4. Honeybee hives density maps for the city of Zürich. The maps show the distance to the nearest hive for the years 2012 (a) and 2018 (b), and the number of hives in a 1000 m radius for 2012 (c) and 2018 (d). Maps are calculated at the centroids of each raster cell in a resolution of 1 hectare.

Scale- values: For (a) and (b), warm colored areas (yellow) indicate the largest distances from a cell to the nearest honeybee hives (1800 m), and cold colored areas (purple and blue) indicate the lowest distances from a cell to the nearest honeybee hive (400 m). For (c) and (d), white colored areas indicate no hives, cold colored areas (purple and blues) indicate the lowest densities of hives in 1000 m radius (5 hives) and warm colored areas (yellow) indicate the maximum densities (203 hives).

Summary points of task 1

- Honeybees are able to reach any area within the city
- The number of honeybee hives have increased fast between 2012-2018.

3.2. Task 2: Heatmaps of floral resources

Goals

Floral resources encompass a wide range of plants that potentially could be used by insects. These plants are a key feeding resources for both wild bees and honeybees. Furthermore, floral resources in cities largely depend on human management and preferences and include native, horticultural and exotic species, and thus may be linked to specific types of land-use and land-covers. In task 2, we specifically attempt to use the existing datasets on floral resources collected in different types of land-uses to create city-wide heatmaps summarising different aspects, such as the abundance of flowers or the number of plant species.

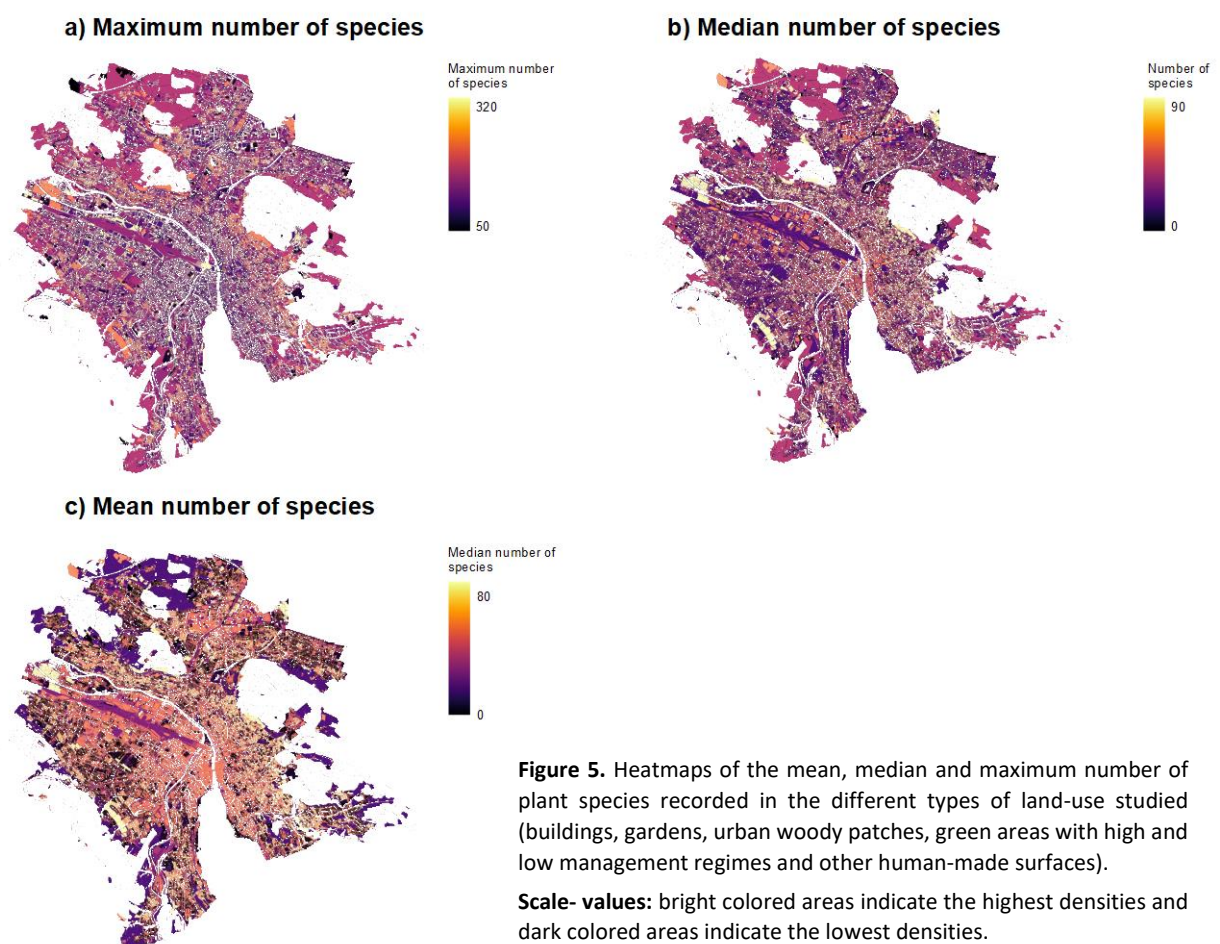
Methods

The floral resource map has been created using records of plant species, counts of flowers and habitat distribution. The approach is based on Baldock¹¹, which elaborated floral resource maps for four cities in the U.K. We assigned a land-use category to each plant plot done and then use the available information to calculate land-use based summary statistics (i.e., mean, median and

maximum number of plant species per land-use). The summary statistics were then plotted using the habitat map of the city of Zurich, excluding the categories of water and forest (Fig. 5).

Results

More than 1500 plant species have been recorded across different land cover types of the city in approx. 150 sites set in different types of land-uses (e.g., cemeteries, parks, meadows, green roofs, ruderal sites, gardens). The number of plant species is composed of more than 50% exotic and ornamental species, many of which found in private properties (gardens) or as trees and shrubs. Plant species have been recorded and digitalized in a database. **Gardens had the highest mean, median and maximum number of plant species recorded**, whereas urban woody patches and green areas with intensive management regimes (i.e., mainly lawns) had the lowest.



Summary points of task 2

- Gardens have the highest mean, median and maximum number of plant species recorded, whereas urban woody patches and green areas with high management regimes (i.e., mainly lawns) have the lowest.

3.3. Task 3: Wild bee diversity and distribution

Goals

In task 3, we studied the wild bee diversity in Zurich. Specifically, we **(1)** analysed the abundance and occurrence patterns of wild bees to find out which species are more common and which ones are more rare, **(2)** modelled the occurrence and species richness of wild bees using a wide range of environmental predictors through predictive machine learning models and obtain city-wide richness maps, and **(3)** examined how wild bee richness is distributed in different urban green areas.

Related publications:

Casanelles-Abella, J., Chauvier, Y., Zellweger, F., Villiger, P., Frey, D., Ginzler, C., Moretti, M. & Pellissier, L. (2021) Applying predictive models to study the ecological properties of urban ecosystems: A case study in Zürich, Switzerland. *Landscape and Urban Planning*, **214**, 104137. <https://doi.org/10.1016/j.landurbplan.2021.104137>

Related datasets:

The data is deposited in the repository EnviDAT under <https://doi.org/10.16904/envidat.172>

Methods

To study the species abundance and occurrence, we used the abundance and occurrence of 177 bee species sampled in 251 sites in Zurich during four urban ecology projects run between 2009 and 2018. Specifically, we applied ‘rank-abundance and rank-occurrence diagrams’, which show the distribution of abundances and occurrences of the different bee species. We used common thresholds to classify the species according to their abundance and occurrence in three categories: 1) ‘very common’ for bees that were very abundant and very widespread; 2) ‘common’ for bees that were abundant and widespread; and 3) ‘rare’ for bees that were scarce and locally-occurring.

To model the city-wide distribution of wild bees and obtain species richness maps, we applied predictive models using two different variables. For common species, which had sufficient presences and absences, we ensemble Species Distribution Models obtaining distribution maps for each species. Then we stacked the individual maps of the modelled species to obtain a single map with the predicted species richness of common species (Fig. 7c). For rare and very common species, which had insufficient number of either absences or presences to be modelled with an SDM, we ensemble Species Richness Models (SRM) and obtained city-wide maps of their distribution (Fig. 7b and 7d). Additionally, we also did a SRM containing all the bee species present (Fig. 7a). For more information concerning model calibration, validation, and ensemble, see the Appendix.

Results

The analyses of the bee species abundance and occurrence have shown that urban bees in Zurich follow universal ecological diversity patterns, meaning that **most bee species in Zurich are rare and locally distributed**, as shown in Fig. 6. Conversely, very common species are only a handful and are distributed all over the city. In addition, bee species richness in Zurich is considerably high, comprising around 31% of the species with respect to the species pool⁷ (Fig. 6).

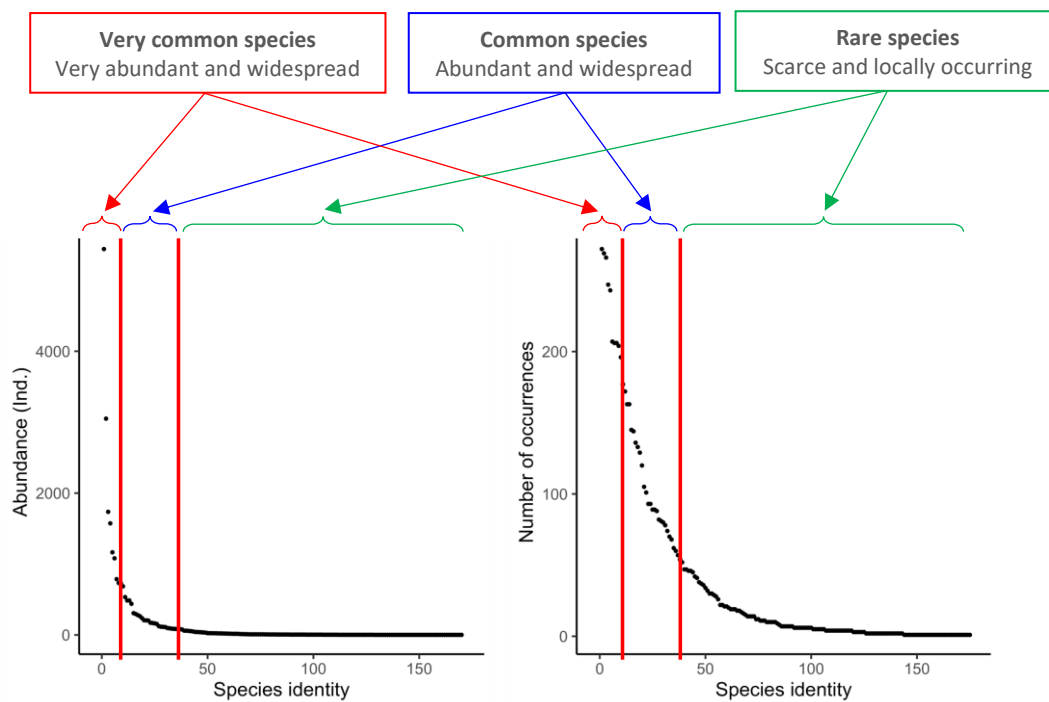


Figure 6. Diversity distributions of urban bees in the city of Zürich. Rank-abundance (a) and rank-occurrence (b) diagrams on 177 bee species. Red lines delimit the species classified on three main classes: very common, common and rare species.

We have obtained city-wide predicted species richness maps for all, very common, common and rare species, where we located areas with high and low species richness (Fig. 7). Very common species are widely distributed in the city, probably due to their traits that make them thrive in urban areas (feeding or nesting behaviours, movement capacity, xero-thermophily, etc.). Common species are also widely distributed, but their richness decreases with increasing urban intensity (e.g., overwarming, pollution, grey covers). Finally, **rare species display clear richness gradients over the city, with their richness decreasing in highly urbanized areas. Nonetheless, highly urbanized areas still contain a low number of rare species.** Their presence might indicate that local scale factors allow them to survive and maintain scattered populations, for instance, due to small-sized green areas (gardens, green roofs, balconies, tree pits) and specific management decisions.

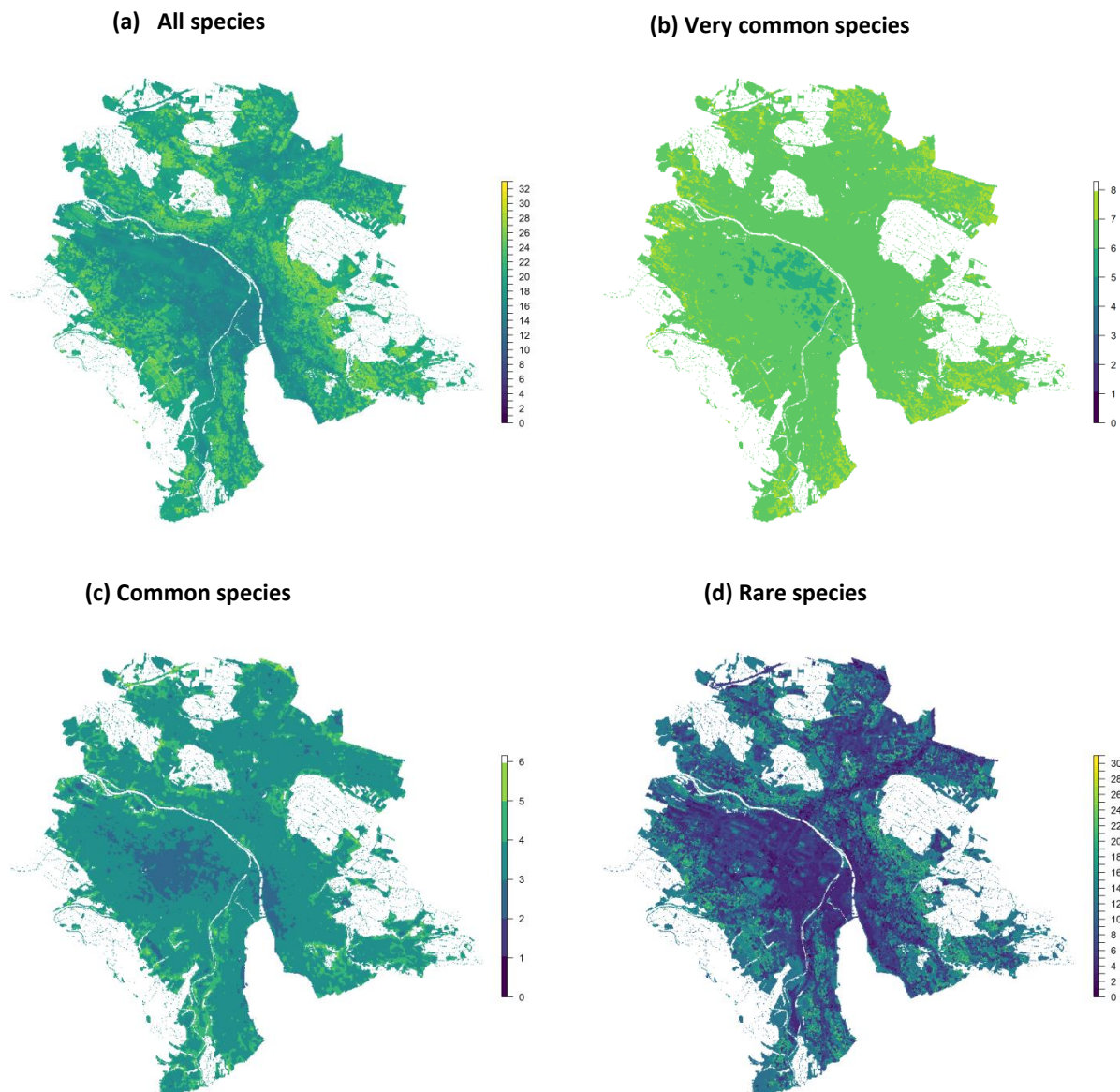


Figure 7. Predicted richness bee maps. Maps showing the predicted number of species of **(a)** all bee species, and only considering **(b)** very common, **(c)** common and **(d)** rare species, indicating hot- and coldspots of bee richness. **Scale-values:** cold colored areas (purple and blue) indicate low values of species richness, whereas warm colors (yellow) indicate high values of species richness. Note that woodlands have been excluded in the map as they have not been sampled properly and are poor bee habitats for Central European bees. Copied from Casanelles-Abella *et al* ⁴⁹

Concerning the value of the different urban green areas for supporting wild bees, a recent study in Zurich⁷ **found wild bee richness and diversity peaked in gardens, allotments and brownfields** (Fig. 8). In addition, the authors found that **different urban green areas selected and filtered for different bee traits and thus species**, indicating the importance of maintaining different types of urban green areas to promote richer communities. For example, gardens and allotments selected for species with short tongue while parks, green roofs and brownfields selected for generalist active longer and sooner in the season. Note that some urban habitats (e.g., ruderal sites in railways) have been poorly sampled but are suspected to be favourable for many wild bee species.

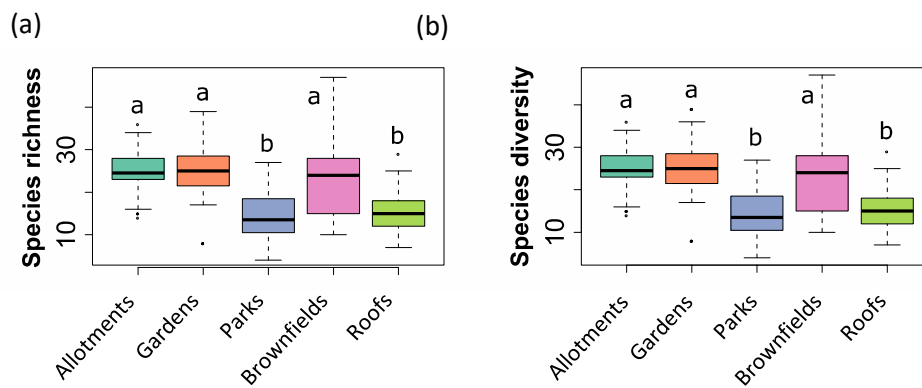


Figure 8. Boxplots showing differences among urban green areas in **(a)** species richness and **(b)** diversity of urban bees. See how allotments, gardens and brownfield have the highest species richness and diversity. Letters show differences among urban green areas (Tukey's Honest Significant Difference tests). Copied from Fournier, Frey and Moretti²⁴.

Summary points of task 3

- In Zurich, the vast majority of bee species occur in few places and in low abundance; only a handful of species are widespread and very abundant (e.g., *Bombus pascuorum*, *Bombus terrestris*).
- The city of Zurich presents cold- and hotspots of bee diversity, which could orient management.
- Gardens (allotments, private) and green areas with low management regimes have the highest numbers of predicted bee species, hence protect these types of green areas should be a key management priority.

4. WP2: FLORAL RESOURCES AND BEES

In WP2 we investigated the diet of bees in two different projects. **First**, by implementing a modelling framework, we have assessed the sustainability of urban beekeeping in Swiss cities, by examining if the available floral resources are sufficient to satisfy the demands of the existing honeybee populations. **Second**, we studied the diets of wild bees in urban areas. First off, we investigated the diet of four wild bee species in five European cities to understand how consistent they were among cities and how this in turn influenced the distribution of the four wild bee species. Furthermore, we also investigate the diet of *Bombus pascuorum* and *B. lapidarius*, being quite similar to honeybees with respect to morphology and flower visiting behavior. Whereas the massive widespread distribution of honeybees in the city of Zurich (see task 1) led us to use different approaches to investigate competition between honeybees and wild bees (see WP3).

Related publications:

- Casanelles-Abella, J., & Moretti, M. (2022). Challenging the sustainability of urban beekeeping using evidence from Swiss cities. *Npj Urban Sustainability*, **2**, 1-5. <https://doi.org/10.1038/s42949-021-00046-6>
- Casanelles-Abella, J., Müller, S., Keller, A., Aleixo, C., Alós Orti, M., Chiron, F., Deguines, N., Hallikma, T., Laanisto, L., Pinho, P., Samson, R., Tryjanowski, P., Van Mensel, A., Pellissier, L., & Moretti, M. (2022). How wild bees find a way in European cities: Pollen metabarcoding unravels multiple feeding strategies and their effects on distribution patterns in four wild bee species. *Journal of Applied Ecology*, **59**, 457–470. <https://doi.org/10.1111/1365-2664.14063>
- Casanelles-Abella, J., Keller, A., Müller, S., Aleixo, C., Alós-Orti, M., Chiron, F., Laanisto, L., Myczko, Ł., Pinho, P., Samson, R., Tryjanowski, P., Van Mensel, A., Villarroya-Villalba, L., Pellissier, L., & Moretti, M. (2022). Wild bee larval food composition in five European cities. *Ecology*, **103**, e3740. <https://doi.org/10.1002/ecy.3740>

Related datasets:

The raw data is deposited in the repository EnviDAT under <https://doi.org/10.16904/envidat.210>

Goal 1: sustainability of urban beekeeping in Swiss cities

To evaluate the magnitude of urban beekeeping growth and its sustainability, we analysed data on beehives and available resources in 14 Swiss cities from 2012–2018 and modelled the sustainability of urban beekeeping under different scenarios of available floral resources and carrying capacities.

Methods

Study cities: We selected a total of 14 cities and urban agglomerations in Switzerland.

Urban beekeeping: Annual data on the spatial distribution of beekeeping locations and the number of hives at each location in the studied areas were obtained from the cantonal veterinary offices. The considered period was 2012–2018. As exceptions, data were only available from 2012–2014 for Basel and from 2013–2018 for Lausanne (Supplementary Table 3). The data from each veterinary office were checked separately and only records of beekeeping locations with reliable coordinates were included. For Chur and Geneva, where the beekeeping locations did not have precise coordinates, and in Basel, we only used the available data to study the increase in the number of hives over time.

Available urban greenspace: Data on available urban greenspace (UGS) were obtained from a continental-scale European Land-Cover map (ELC1011). We considered the following land- cover

classes as UGS: cropland, woodland, shrubland, grassland and wetland. For simplicity, we assumed (1) equal floral resources in all these land-cover classes, although they are expected to vary greatly, and (2) the same land cover composition in 2012 and 2018. We additionally simulated increases in the amount of available UGS by adding percentages to the original values in intervals of 10%, ranging from 0 to 100%. Spatial data process, including calculations on UGS and number of hives and beekeeping locations was done in QGIS v.3.10.

Modelling: We calculated the required UGS and the UGS balance for 2013 and 2018 in Lausanne, and for 2012 and 2018 in the remaining 10 cities. In a given city, for each cell and each year, we first calculated the total number of honeybee hives. We then calculated the required UGS in each cell according to the number of hives present and an estimated carrying capacity value, i.e., the maximum number of honeybee hives that can be sustain in 1 km² of UGS.

The UGS balance in a given year was calculated by subtracting the required UGS in a given cell from the available UGS in that cell. Equation (1) shows the calculation of the available UGS, equation (2) shows the calculation of the required UGS and equation (3) shows the calculation of the UGS balance:

$$\text{Available UGS}_{ij} = \text{AvailableECL10}_{ij} + \text{AvailableECL10}_{ij} * I \quad (1)$$

$$\text{Required UGS}_{ij} = \frac{N_{ij}}{CCV} \quad (2)$$

$$\text{Balance UGS}_{ij} = \text{Available UGS}_{ij} - \text{Required UGS}_{ij} \quad (3)$$

where i is the cell, j is the city, I is the simulated percentage of increase (in decimal form) in available UGS, N is the number of hives, CCV is the assumed carrying capacity and AvailableECL10 is the amount of available UGS based on the European Land-Cover, ECL10 map, without an increase.

The UGS balance was calculated for the different carrying capacity scenarios and increases in available UGS. Finally, for each city we calculated the proportion of cells with a positive balance (i.e. the required UGS for beekeeping was smaller than the available UGS) and with a negative balance (i.e. the required UGS for beekeeping was larger than the available UGS).

Results

We found large increases in hives numbers across all cities from 3139 hives in total in 2012 to 6370 in total in 2018 (Fig. 9) and observed that available resources are insufficient to maintain present densities of beehives, which currently are unsustainable.

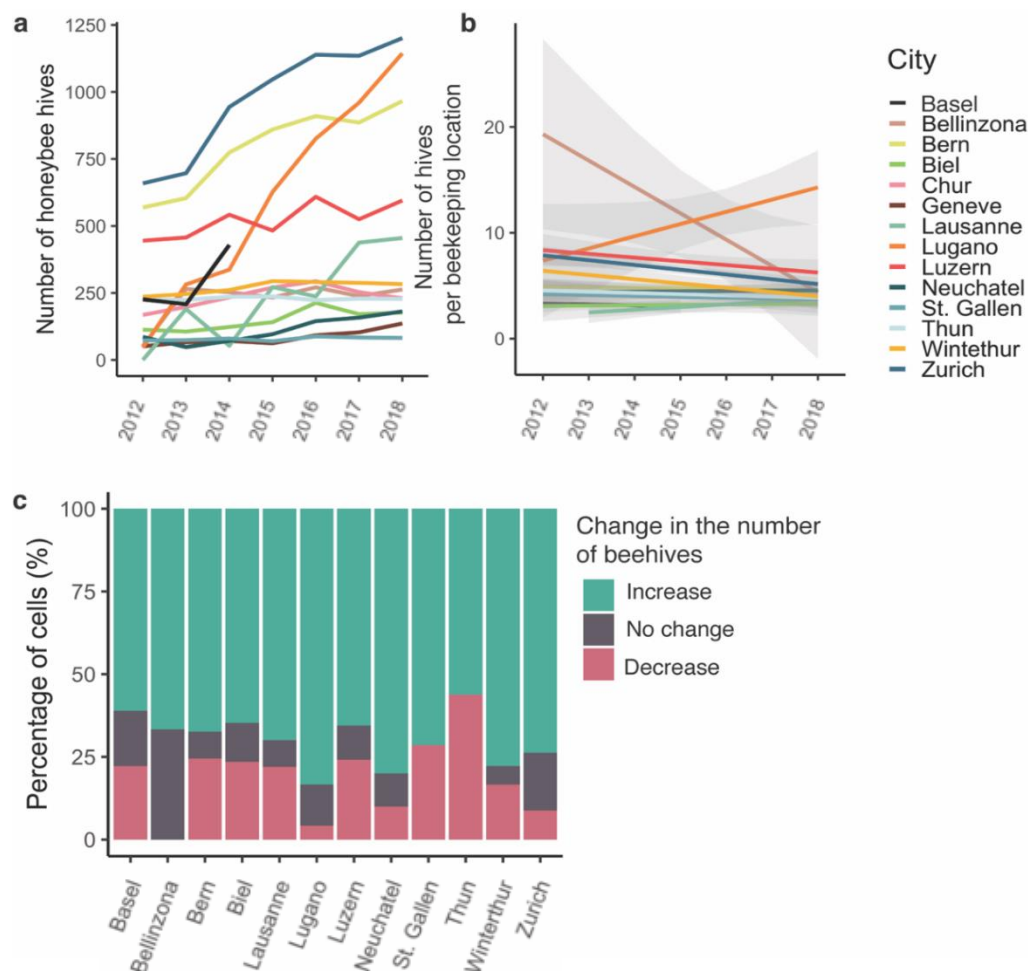


Figure 9. Urban beekeeping trends in Swiss cities for the period 2012–2018. **a)** Number of honeybee hives per year for all 14 Swiss cities. Each line and colour represent a single city. **b)** Response curves showing the number of hives per beekeeping location per year for all of the Swiss cities except Geneva and Chur (where spatially explicit data were of low quality). Lines represent linear models and bands indicate 95% confidence intervals. Each line and colour represents a single city. **c)** Percentage of cells in each city with an increase (green), decrease (red) or no change (dark grey) in the number of hives.

Goal 2: wild bee diets

We investigated the larval diet and distribution patterns of four solitary wild bee species with different diet specialization (i.e., *Chelostoma florissomne*, *Osmia bicornis*, *O. cornuta* and *Hylaeus communis*) along urban intensity gradients in five European cities (Antwerp, Paris, Poznan, Tartu, and Zurich) using two complementary analyses. Specifically, using trap-nests and pollen metabarcoding techniques, we characterized the species' larval diet, assessed diet consistency across cities, and modelled the distribution of wild bees using species distribution models (SDMs).

In addition to these four solitary wild bees, we also investigate the diets of *Bombus pascuorum* and *B. lapidarius* in urban and rural landscapes across three regions in Switzerland (Zurich, Basel, and Bern) to study the link between intraspecific trait variability in the tongue and body size and the diet composition, and to test the influence of urban landscapes in shaping bumblebee dietary choices. The reason why we selected these six bee species is that they show a different degree of trait similarity to the honeybee (see Fig. 16a in WP 3 "Competitive interactions between honeybees and wild bees"). Since honeybee is a super-generalist, we do not expect a species-specific diet, except when hives are moved to specific locations with a high abundance of single plant species, e.g., rape fields, apple, or acacia trees, which never the case in cities.

Methods

Study design: 80 sites distributed in five cities: 32 in Zurich and 12 in each of the remaining five European cities. Sites varied in their size and in the amount of green spaces in the surroundings.

Three rural sites and three urban sites in the regions of Basel, Bern, and Zurich.

Bee and pollen sampling: Wild bees and pollen were sampled with trap-nests (Fig. 10)

Pollen metabarcoding: We performed DNA metabarcoding to identify the plant species present in the larval pollen depositions for the four studied bees (463 samples in total). Pollen metabarcoding was done by AllGenetics & Biology SL, A Coruña, Spain. The bioinformatic analysis has been performed by PD Dr. Alexander Keller, University of Würzburg, Germany, based on an academic collaboration.

Species Distribution Models (SDM): SDM was used to investigate the distribution of Wild bee in cities. Additional details on the methods can be found in Casanelles-Abella *et al.*³⁷.

For the pollen identification, we used a standardized genetic procedure explained at figure 10.

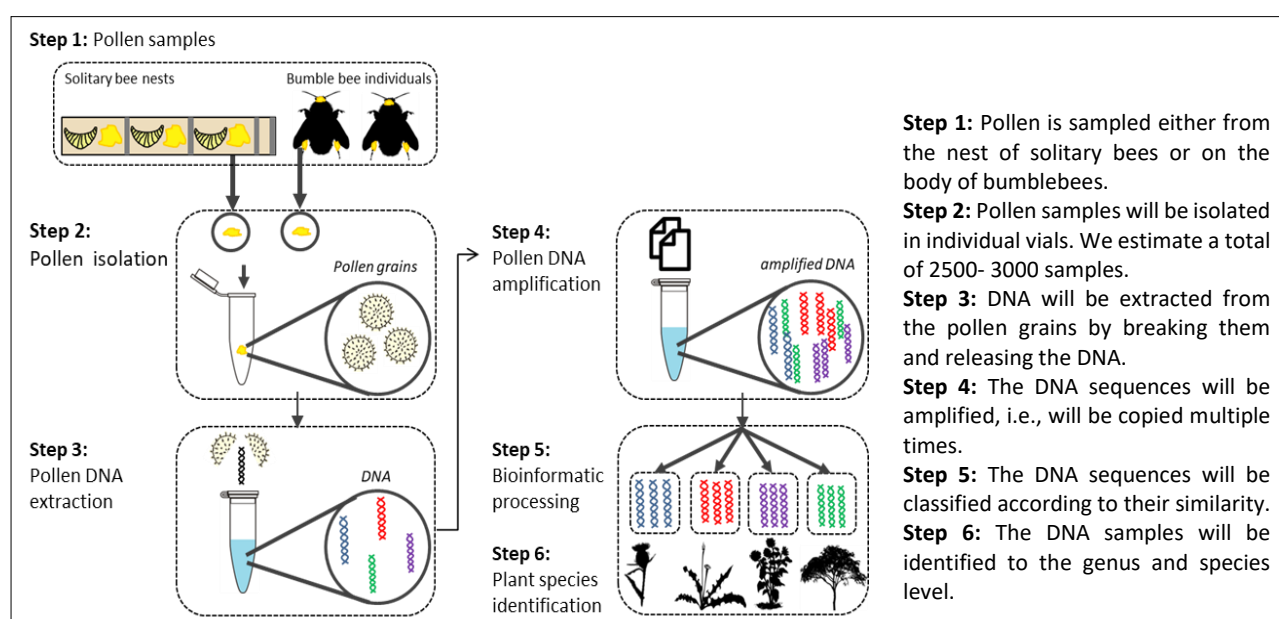


Figure 10. Workflow of the technique and related steps that enables to identify on which plant species the bees have.

Results

Solitary wild bees

A total of 41 plant families, 93 genera and 135 species were identified from the nests of the four wild bee species (Fig. 11). Over half of the species were native (55%), there were more herbs (42%) than trees (34%), and dish-bowl blossoms were more common (56%). The number of plant species per bee nest was similar among bee species. The total number of collected plant taxa varied greatly among bee species, reflecting their differences in diet specialization: 1 family and 4 species in *Chelostoma florissomme*, 12 families and 33 species in *Osmia cornuta*, 18 families and 51 species in *O. bicornis*, and 32 families and 81 species in *Hylaeus communis*. **We found different levels of diet conservatism across cities at the plant family and plant genus level, according to the bee specialization degree and taxonomic resolution of the plant taxa (Fig. 11).**

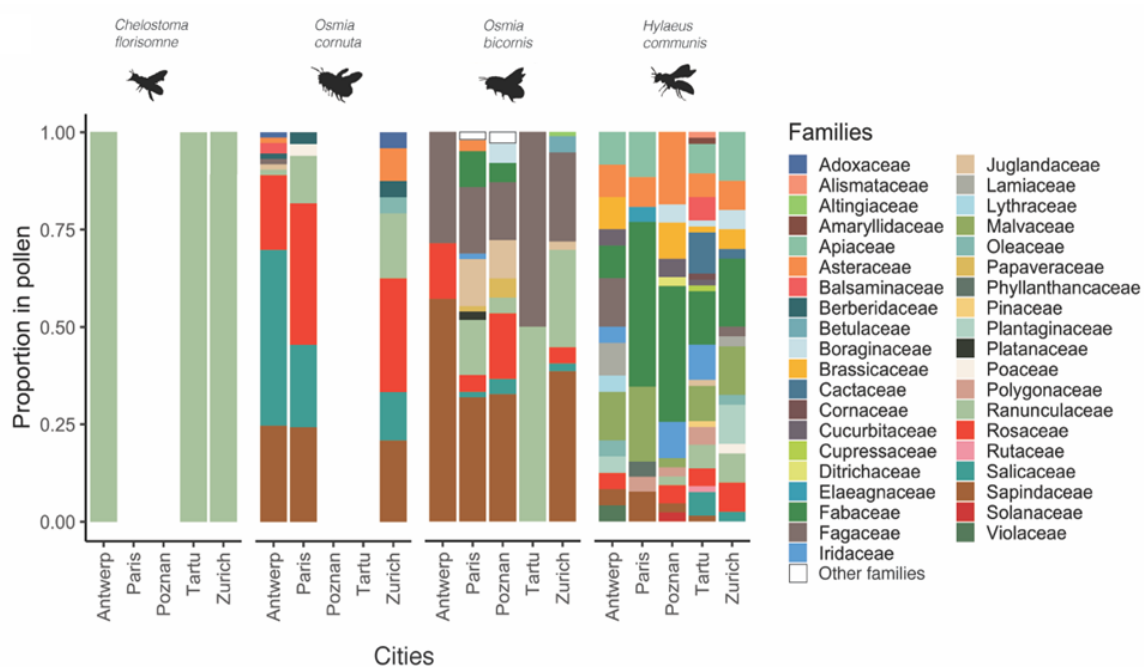


Figure 11. Bee larval diet composition in the studied cities. For each bee species, the proportion in the pollen of the different collected plant families in the studied cities is shown. Only families with a proportion in pollen ≥ 0.01 are plotted, whereas the remaining ones are represented in the category “Other families”. Copied from Casanelles-Abella et al. ³⁷.

Urban wild bees display different successful strategies to exploit existing urban floral resources: not only broad generalism (i.e., *H. communis*), but also intermediate generalism, with some degree of diet conservatism at the plant family or genus level (i.e., *O. cornuta* and *O. bicornis*), or even strict specialization on widely available urban pollen hosts (i.e., *C. florissomme*).

Wild bee distribution ranges inside urban ecosystems ultimately depend on their degree of specialization, and that broader diets result in less sensitivity to urban intensity (Fig. 12).

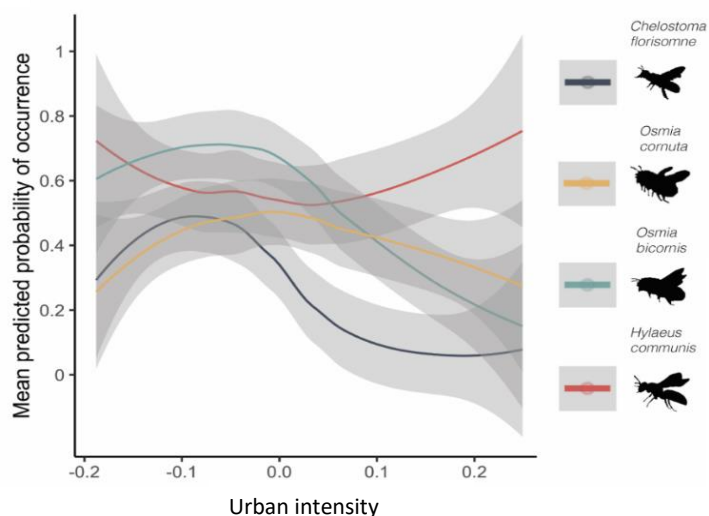


Figure 12. Loess models of the predicted probability of occurrence of the 4 bee species studied along an urban intensity gradient. Higher levels of urban intensity are related with higher temperature, larger amounts of grey surfaces, less vegetation and less water. Grey bands indicate the 95% confidence interval. Copied from Casanelles-Abella et al. ³⁷.

Bumblebees

We found a total of 230 plant species belonging to 47 families across all sites and regions carried by *Bombus pascuorum* and *B. lapidarius* on their bodies and corbicula (Figs. 13, 14). We observed significant differences in the pollen load and diet between urban and rural bumblebees (Figure 13). Urban bumblebees had a more diverse and abundant pollen load, suggesting a more varied diet compared to rural bumblebees. Urban bumblebees also visited a wider range of plant families, while rural bumblebees tended to forage from a more limited number of families. Furthermore, there were notable variations in the diet of bumblebees across different regions. For instance, bumblebees from the rural area in Bern had a limited diet, with *B. lapidarius* only visiting 8 taxa and *B. pascuorum* visiting 9 taxa. In contrast, bumblebees in the urban region of Zurich had a much more varied diet, with *B. lapidarius* collecting 100 taxa and *B. pascuorum* 97 taxa. Compared to solitary wild bees (above) both bumblebee species collected pollen from many different taxa. The median in cities was for *B. lapidarius* 77 and for *B. pascuorum* 86, compared to 4, 33, 51 and 81 species in the respective solitary bee.

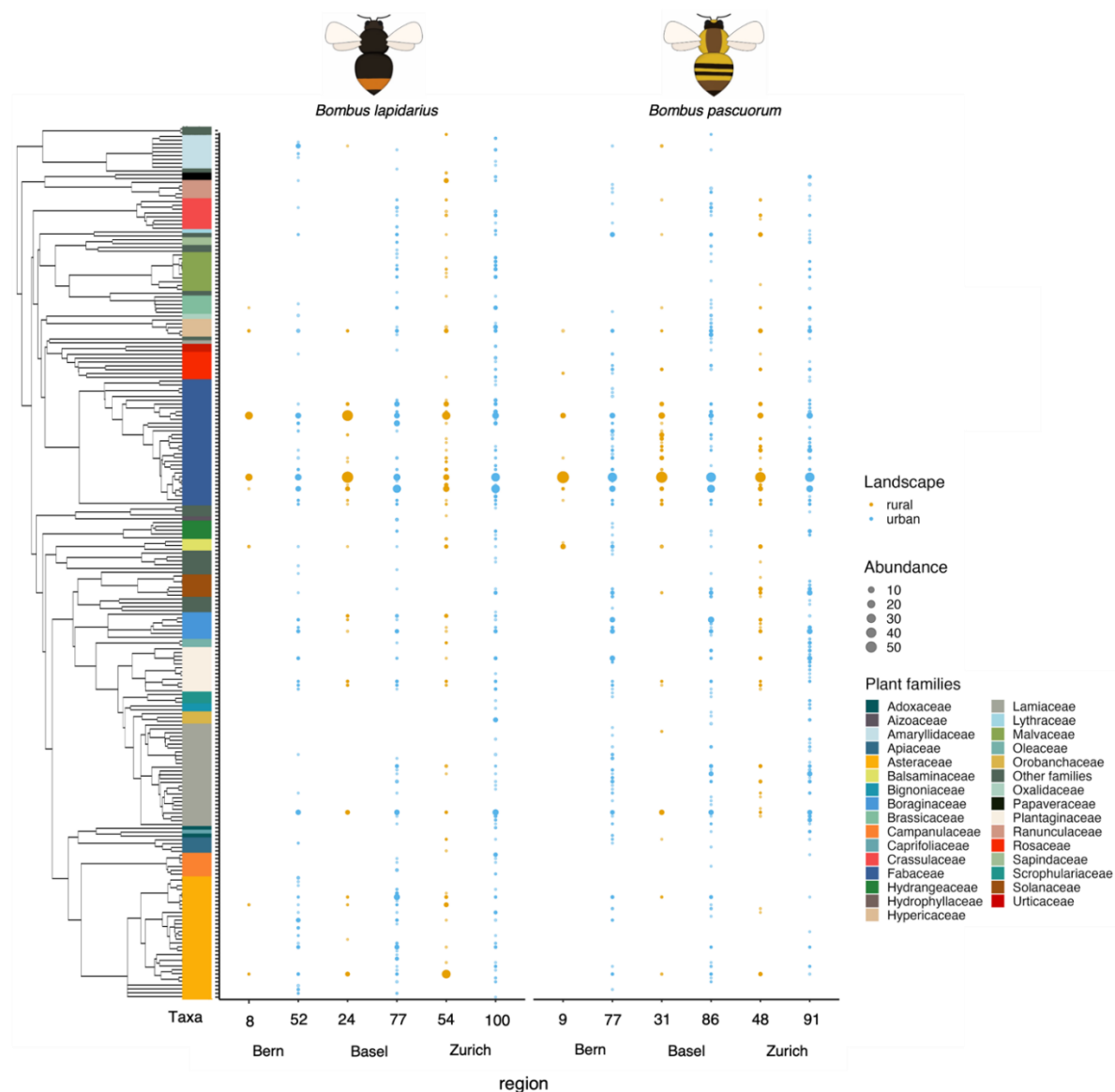


Figure 13. Urban bumblebees have a richer and more diverse diet than rural bumblebees. Diet composition of *Bombus pascuorum* and *B. lapidarius* in the studied rural (orange) and urban (blue) areas of the three regions. Dot size reflects the abundance of pollen species carried by the two bumblebee species in the different study sites and the dot color corresponds with the landscape (see legend). The dendrogram on the left shows the phylogenetic relationships among plant species visited by the bumblebees, while the colors reflect the plant families (see legend).

As anticipated, species from the family Fabaceae were the most prevalent in the diet of bumblebees, with the genus *Trifolium* (clover) being widely distributed and vital for bees (Fig. 14). Additionally, our study also found that the two bumblebee species in question foraged for different plant families. In addition to Fabaceae, *B. lapidarius* also collected a significant amount of Asteraceae, while *B. pascuorum* preferred Boraginaceae. We additionally found that bumblebees primarily foraged from flag-shaped flowers. However, a greater diversity of flower shapes was observed in urban areas. *B. pascuorum* was found to forage from a broader range of flower shapes, which is counterintuitive with its more specialised nature. In terms of growth form, we found that the majority of the plants visited by bumblebees were herbs, which is not unexpected. There is however again a higher diversity in growth form visited by the bumblebees in urban areas. Regarding the origin status of the plants, our findings were surprising. We did not find a significant increase in the number of exotic plants in urban areas compared to rural areas.

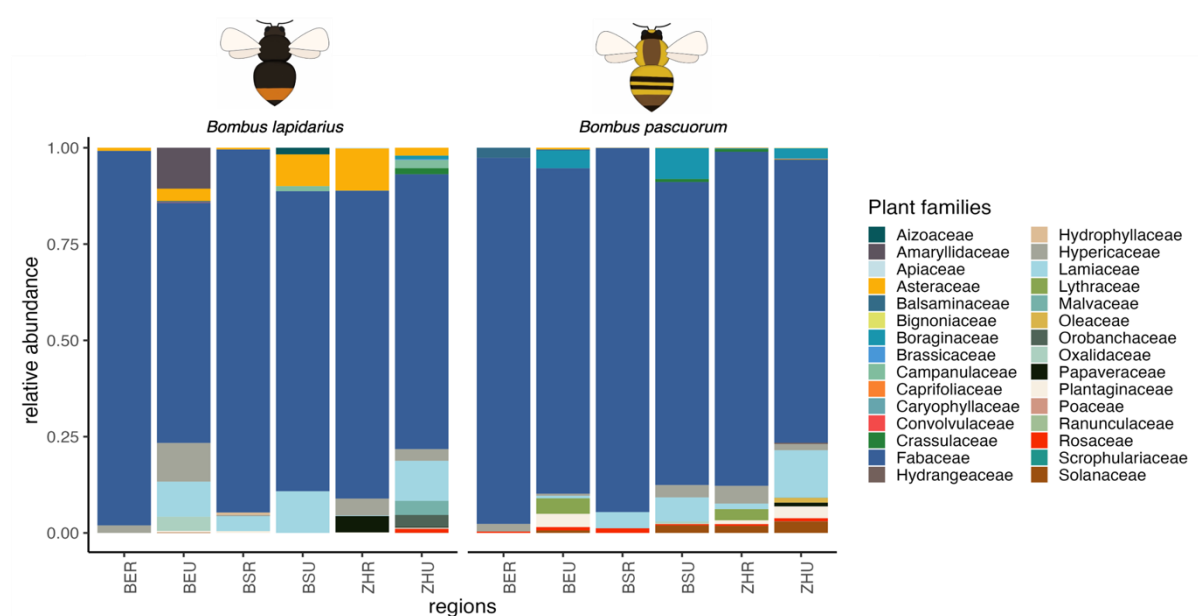


Figure 14. Diet composition of *Bombus pascuorum* and *B. lapidarius* grouped in plant families (see legend) in the studied rural (R) and urban (U) areas of the three regions (Bern BE; Basel BS; Zurich ZH. Example: BER= Bern-Rural; ZHU= Zurich-Urban).

Summary points of WP2

- Successful wild bees in cities can have different feeding strategies, ranging from specialisation to widespread flowers to broad generalism.
- While urban trees represent a very important source of food for wild bees as compared to typical weeds (e.g., clover, dandelion), clover was very important for bumblebee species, especially in rural landscape. Conservation strategies aimed to promote wild bees in cities should also include tree species, while a diversity of flowers should be enhanced for bumblebees.
- Identifying larval floral preferences (e.g., using pollen metabarcoding) of other wild bee species is extremely helpful to identify key plant taxa and plant traits for bee survival and for improving strategies to develop bee-friendly cities
- Urban bees have a more diverse and richer diet than rural ones.

5. WP3: COMPETITIVE INTERACTIONS BETWEEN HONEYBEES AND WILD BEES

In WP3 we aimed to test for competitive interactions using a wide range of data, both experimental (5.1 Flower visitation frequency; task 6), observational from the whole community (5.2 Bee community niche overlap; task 7) and using specific guilds (5.3 Reproductive success of cavity-nesting bees; task 8). In this WP we extended the analysis techniques and datasets used, improving our understanding on three complementary aspects in bee ecology: (1) behavioral aspects, (2) functional aspects, and (3) aspects related to reproductive success and thus the fitness of wild bees.

Related publications:

- Casanelles-Abella et al., 2023. Low resource availability drives feeding niche partitioning between wild bees and honeybees in a European city. *Ecological Applications*, **33**, e2727. <https://doi.org/10.1002/eap.2727>
- Casanelles-Abella & Moretti, 2022. Challenging the sustainability of urban beekeeping using evidence from Swiss cities. *Npj Urban Sustainability*, **2**, 1-5. <https://doi.org/10.1038/s42949-021-00046-6>

Related datasets:

The raw data is deposited in the repository EnviDAT under <https://doi.org/10.16904/envidat.253>

5.1. Task 4: Flower visitation frequency

Goals

In task 6 we studied the visitation frequencies of pollinator communities (wild pollinators and honeybees) on flowers of standardized arrays of plants (pollination experiment).

Methods

Study design: See Appendix for a detailed description of the methods. In brief, we sampled 24 urban gardens in the city of Zurich to vary independently in their flower species richness from the proportional amount of impermeable surface in their surrounding landscape.

Experimental set-up: An array of four plant species was set up in each garden. Each pot contained one plant of one of the following insect-pollinated plant species: wild carrot (*Daucus carota* L.), radish (*Raphanus sativus* L.), common sainfoin (*Onobrychis viciifolia* Scop.) and common comfrey (*Symphytum officinale* L.).

Plant-pollinator interactions: Flower-visiting insects were sampled on each plant of each of the four plant species during their peak flowering time between June 15 and July 20, 2016. In each garden, flower visitors were sampled by two or three people simultaneously for nine full and consecutive hours between 9:00 to 18:00 h under sunny weather conditions and no wind. Each of these sampling rounds was repeated at least three times in each garden.

Results

During a total of 1244 sampling hours, which corresponded to 92 observation rounds on 18 sampling dates, 5504 native insect pollinators belonging to 157 taxa were sampled. Most pollinators were bees (Hymenoptera: Anthophila; 66%) and hoverflies (Diptera: Syrphidae; 29%). Honeybee (*Apis mellifera* L.) made up about 9% of all pollinators.

Our models predicted an average reduction in total pollinator visits by 52% at high urbanization levels (80% impervious surface), when compared to landscapes with low urbanization levels (20% impervious surface; Fig. 15). Specifically, **apart from the honeybee, these declines were consistently**

and significantly negative –or showed a negative trend– across all investigated pollinator groups and standardized arrays of potted plants.

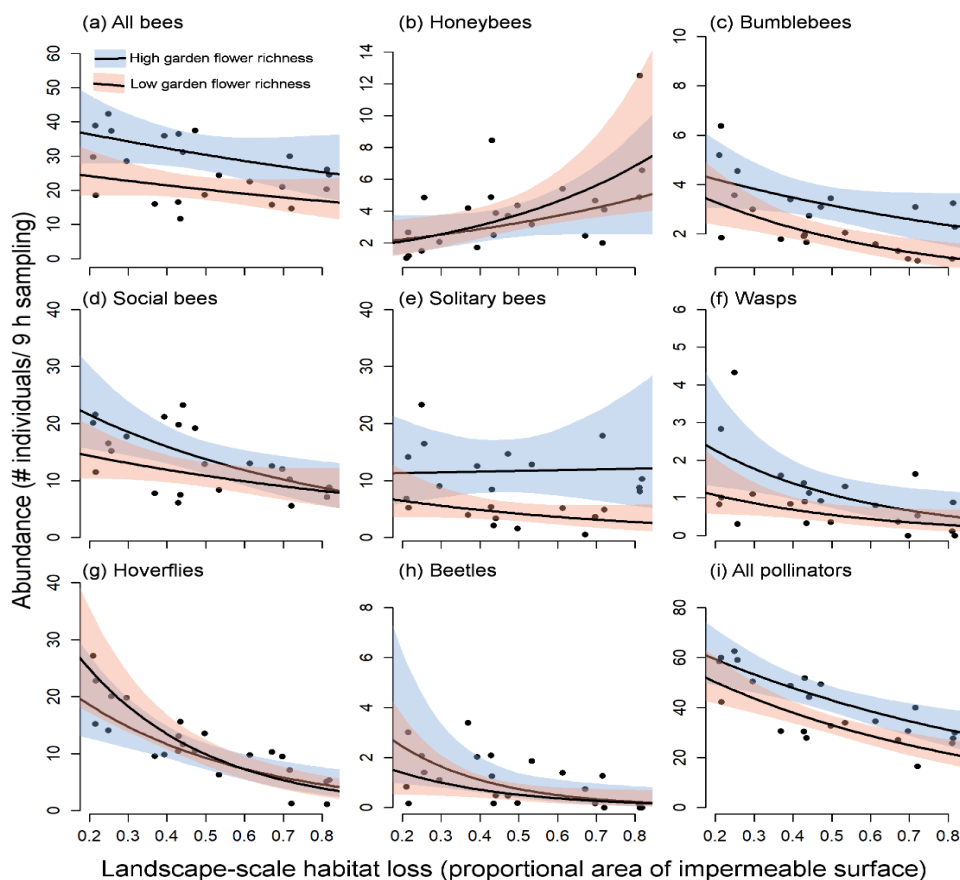


Figure 15. Effect plots depicting the effects of landscape-scale habitat loss (i.e., the proportional area of impermeable surface within 500-m radius circles) on the flower visitor frequency across standardized arrays of potted plants. Mean values and their 95% credible intervals (CI) were predicted for low and high garden-scale plant species richness of insect pollinated plants, corresponding to the 20% (red CI) and the 80% (blue CI) percentiles of the observed garden flower richness.

Garden flower species richness significantly increased overall visitation frequencies by 23% on average and to a lesser extent also pollinator species richness (Fig. 15). This effect was independent from those of landscape-scale urbanization level.

Summary points of task 4

- Honeybees are the only pollinator group that responds positively to landscape-scale loss of foraging habitat (measured by the proportional area of impermeable surface covers)
- Honeybee visitation frequency does not depend on the flower richness of gardens.

5.2. Task 5: Bee community niche overlap

Goals

In task 7 we studied the feeding niche overlap between honeybees and the remaining wild bees as a sign of possible competition between the two.

Methods

We used bee data collected in the city of Zurich using a subset of 24 sites from the pollination experiment of the BetterGardens project. We selected traits that we expected to play a role in competitive interactions, classified in the following four groups: foraging range, feeding specialisation degree, phenology, and daily activity. Feeding niche partitioning was measured as the mean pairwise trait distance between wild bees and honeybees in the community, which indicates how functionally similar are the two communities. Higher values of the mean pairwise distance indicate that the two groups, honey- and wild bees, are becoming more dissimilar with respect of their trait values, hence indicating higher niche partitioning as the honeybee and wild bee individuals overlap less in the use of the floral resources. We expect feeding niche partitioning (i.e., the strength of competitive interactions) between wild bees and honeybees to be driven by the beekeeping intensity and the resource availability at both local and spatial scales. To model this, we used Structural Equation Models (SEM).

Results

We found an increase in the feeding niche partitioning with increasing number of flowers (plant S) (Fig. 16 d) and species richness of wild bees (Fig. 16 e) in the experimental gardens. This can be explained by the fact that the greater the number of wild bee species in the community, the greater the likelihood that functional species distinct from honeybees increase the overall feeding niche partitioning (see lower part of Fig. 16a). **However, the feeding niche partitioning also tended to increase in the experimental gardens when the availability of resources at the local (100 m) and landscape (500 m) levels decreased (Fig. 16 b-c), that is, when there were fewer green areas available nearby, which for this reason attracted greater abundances of honeybees (Figs. 17 a,c).** However, **beekeeping intensity at the local and landscape scales did not directly influence community feeding niche partitioning or wild bee species richness (Fig. 16 f,g).**

Overall, we found wild bee species richness and honeybee abundance to be affected by resource availability at different spatial scales (Fig. 17). Wild bee species richness was positively influenced by local plant species richness (Fig. 17 f). Predicted wild bee species richness indicated maximum wild bee species richness when resource availability at the local scale (i.e., plant species richness) was also maximal (Fig. 17g), and to a minor extent, at intermediate levels of resource availability at the local scale when resource availability at the landscape scale was maximal (Fig. 17g). By contrast, the number of honeybees at the site covaried negatively only with resource availability at the landscape scale (Fig. 17h). Honeybee abundance showed that honeybees concentrated at the local sites when resource availability at the landscape scale was low (Fig. 17h).

Our results indicate a major role of resource availability in driving both the density of honeybees and wild bee species richness patterns (Fig. 17), and ultimately in driving feeding niche partitioning between wild bees and honeybees at the community level (Fig. 16). In that regard, cities

could engage in schemes to monitor resource availability spatially and temporally, as it fluctuates seasonally and depending on weather conditions and urban planning decisions. In addition, because the responses to changes in resource availability and beekeeping intensity might have a lag period, cities should also monitor wild bee populations to better assess the temporal trends and legacies in wild bee populations. These monitoring schemes could help in the planning and regulation of urban beekeeping, e.g., guiding where and where not to perform beekeeping, and could promote actions to enhance floral resources in order to safeguard urban pollinators.

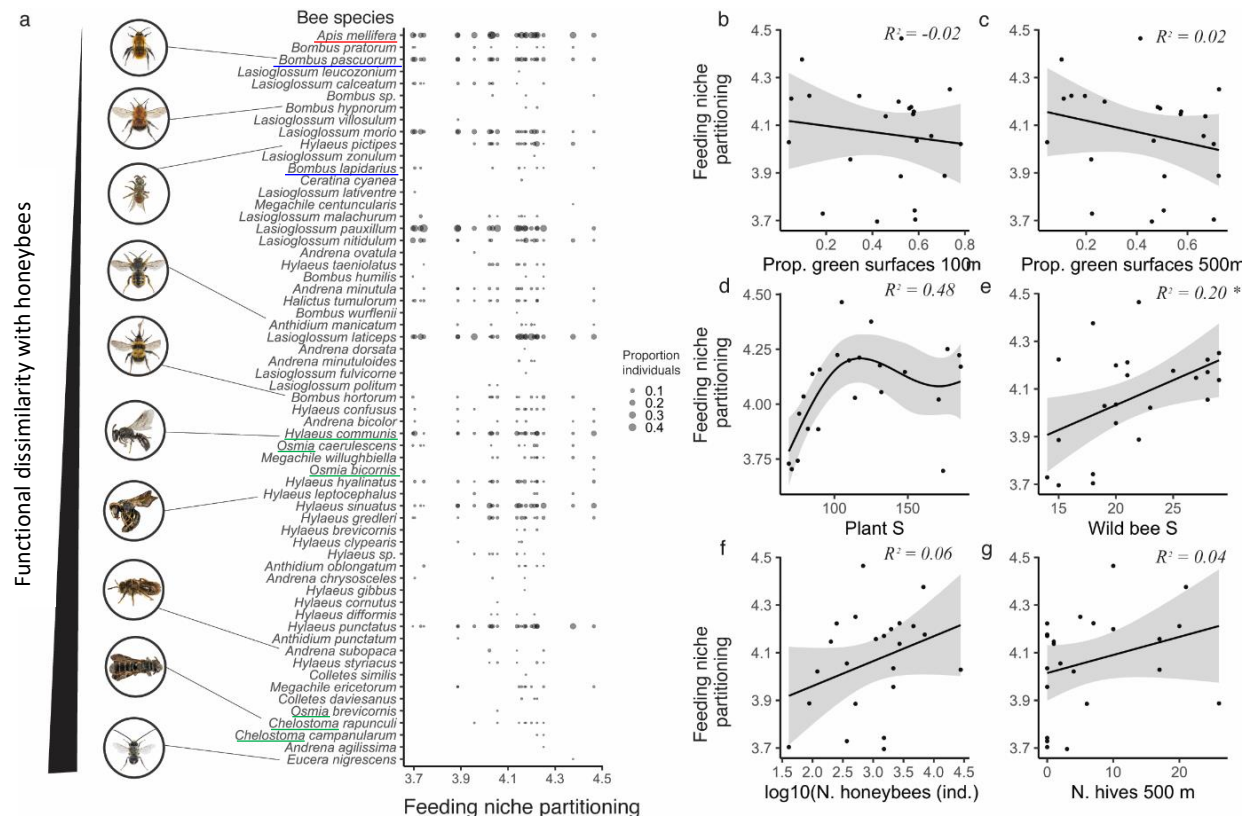


Figure 16. Changes in feeding niche partitioning. (a) Wild bee species composition in relation to feeding niche partitioning value at each site, i.e., the mean pairwise distances between wild bees and honeybee individuals (at the very top) in a given site. Wild bee species are sorted according to their functional dissimilarity with honeybees, with functionally similar species on the top and functionally dissimilar species on the bottom. The size of each dot represents the proportion of individuals sampled at a given site. (b-g) Linear (b,c,f,g) and generalised additive models (GAM, d,e) with the adjusted R^2 between feeding niche partitioning and resource availability at the landscape scales (b,c), resource availability at local scale (Plant species richness S) (d), wild bee species richness, S (e), and urban beekeeping at local (N. honeybees ind.) (f) and landscape scales (N. hives 500m) (g). Smooth terms in GAMs are calculated using cubic regression splines. Grey bands indicated 95% confidence intervals. Significance values: * = $0.01 < p < 0.05$. Underlined in red colour: honeybee; in green: *Chelostoma spp.*, *Osmia bicornis*, *Osmia spp.* and *Hylaeus communis* (link with WP2 ‘Flora resources and bees’; in blue: *Bombus pascuorum* and *B. lapidarius* (link with WP2).

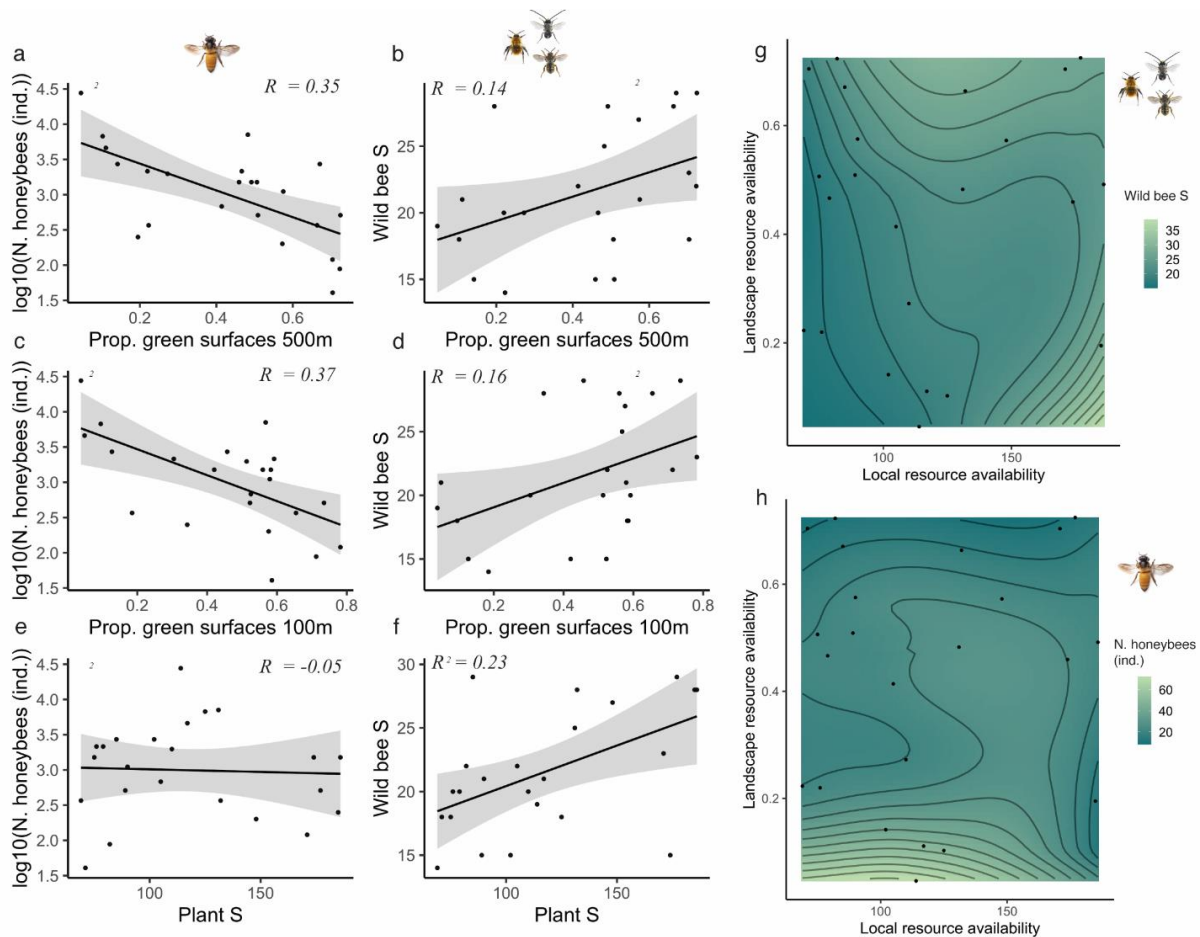


Figure 17. Influence of landscape and local resource availability on the number of honeybee individuals and wild bee species richness in the 24 studied gardens. Linear models depicting the relationship between the number of honeybees (a, c, e) and the wild bee species richness (b, d, f) with the proportion of green surfaces in a 500 m radius (a, b) and 100 m radius (c, d), and the local plant species richness (e, f). For each linear model, the adjusted R² is provided. Grey bands indicate the 95% confidence intervals. Contour plots of the predicted number of wild bee species (g) and the number of honeybees (h) with respect to resource availability at the local and landscape scale, showing that wild bee species richness and honeybee abundances are influenced by resource availability at different spatial scales (local and landscape scale, respectively). Contour plots are based on a loess model on the plant species richness (local resource availability) and proportion of green surfaces in a 500 m radius (landscape resource availability). Black dots represent the study gardens. S = species richness

Summary points of task 5

- Lower resource availability at the local scale leads to high abundances of honeybees in local sites. This seems to cause an exclusion of wild bee species that share similar traits with honeybees and thus potential food resources. In these circumstances, honeybees could be competitively excluding those wild bee species.
- Wild bee species richness was positively influenced by local resource availability, while local honeybee abundance by resource availability at the landscape scale.
- Direct competition for resources between honeybees and wild bees was not a main driver of the wild bee community.

5.3. Task 6: Reproductive success of cavity-nesting bees

Goals

In task 8 we studied the links between local- and landscape scale resource availability, honeybee abundance and parameters of wild bee fitness: reproductive success (number of brood cells), survival probability and parasitism risk.

Methods

Study design: We sampled 85 urban gardens in the city of Zurich two independent local- and landscape-scale gradients to separate the effects of local resource availability and potential foraging habitat landscape spatial scales. Local resource availability was assessed as gardener-provided nesting and feeding resources for cavity-nesting solitary bees and wasps.

Trap nests: Before the activity period of wild bees, in February 2016, we fixed three trap nests each garden. In October 2016, we collected the nests and stored them at 6°C to simulate winter conditions. Between November and February 2017 all tubes were opened. Tubes with brood cells were transferred into labelled test glasses and all emerging host and enemy individuals were successively recorded and determined to species level. Wild bee reproductive success was quantified as the sum of all brood cells per garden. Furthermore, we assessed offspring survival rate (i.e., probability) at the level of individual nests as the number of emerging adults out of the total the number of brood cells per nest and species. Parasitism risk was the number of brood cells attacked by an enemy out of the total number of brood cells per nest and host species.

Honeybee sampling: We sampled honeybees in each garden with three one-litre bowl traps fixed on a 1.5 m triangular wooden pole run for 14 consecutive weeks between May 18 and August 19, 2015 and were emptied weekly.

Statistical analyses: We used Poisson and binomial generalized linear mixed effect models in a Bayesian framework to test for the effects of local- and landscape-scale resource availability and honeybee abundance on total, garden-scale wild bee reproductive success, and survival probability and parasitism risks at the level of nests.

Results

Of the 85 gardens, 83 (98%) could be successfully evaluated (249 trap nests). About 58'000 tubes were opened, revealing a total of 23'602 brood cells (approx. 6'000 nests). Wild bees were found in all gardens, and about 15'400 brood cells (79%) could be attributed to this group (mean number of brood cells per garden = 185.8, range = 3–931). Honeybees were found in all 85 gardens. The mean number of honeybees per garden was 116 (range = 4–326).

We found that local- and landscape scale resource availability positively influenced reproductive success (number of brood cells), while natural enemies negatively influenced survival probability. Parasitism risk was (positively) host density dependent; hence, it was indirectly positively influenced by local and landscape-scale resource availability. Wild bee fitness parameters and honeybee abundance showed (weak) positive associations (Figs. 18, 19).

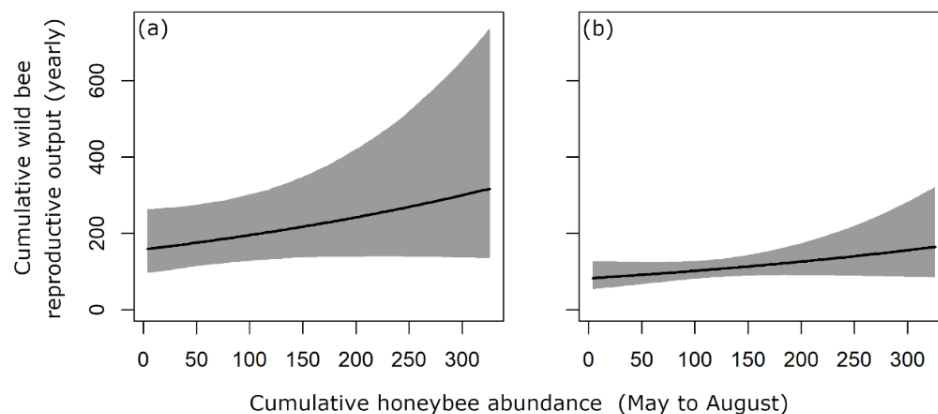


Figure 18. Effect plots of partial linear regressions with 95% credible intervals illustrating the association between honeybee abundance and wild bee reproductive output (number of brood cells) in 83 urban gardens in (a) gardens with artificial nesting aids and (b) gardens without artificial nesting aids. Gardens with artificial nesting aids have a significantly higher number of brood cells. There is a tendency for a positive association between honeybee abundance and wild bee reproductive output. The effect of honeybee abundance is plotted by keeping the additional variable in the model (garden- and landscape-scale foraging habitat cover) constant at average values.

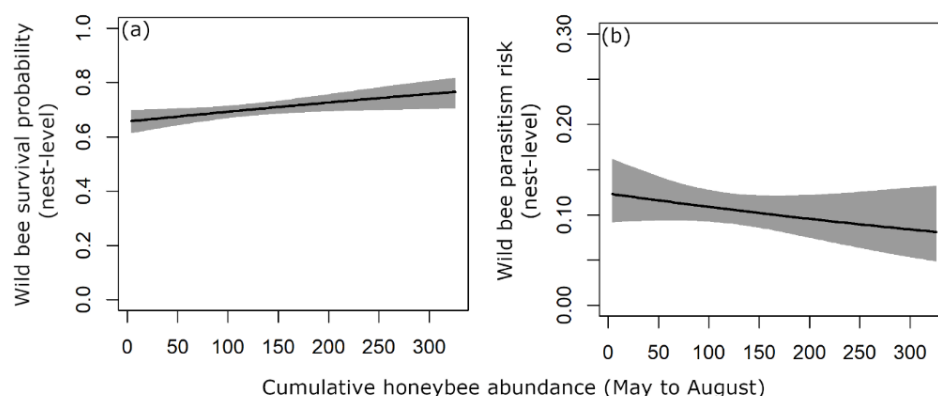


Figure 19. Effect plots of partial linear regressions with 95% credible intervals illustrating the association between honeybee abundance and (a) wild bee survival rate and (b) wild bee parasitism rate in 4013 nests collected from 83 urban gardens. There are tendencies for higher survival probabilities and lower parasitism risk with increasing honeybee abundance.

Summary points of task 6

- We found that local- and landscape scale resource availability positively influenced reproductive success (number of brood cells), while natural enemies negatively influenced survival probability.
- No evidence of negative effects of honeybee density on the reproductive success of cavity-nesting bees has been found; rather, we found positive associations between correlates of wild bee fitness and honeybee densities. However, these positive correlations were very weak and certain, as seen by the broad credible intervals.
- The weak positive association between the correlates of wild bee fitness and honeybee density could be explained by an increased honeybee foraging activity in good quality, resource-rich wild bee habitats, and by the absence of competition due to a surplus of resources during the peak activity of cavity-nesting species.

6. WP4: FEEDBACK TO STAKEHOLDERS

6.1. Summary results

Concerning honeybees

- Honeybee densities in Zurich have substantially increased between 2012 and 2018 (Fig. 2).
- Honeybee hives are distributed all over the city, also in the city centre (Fig. 3-4).
- Honeybees can reach any type of urban green area in the city, due to the distribution of beehives all over the city and the large foraging range of honeybees.
- Honeybees are present in any place of the city as long as foraging resources are available.
- Honeybees are the only pollinator group that their visitation frequency increased with urban intensity (Fig. 15b) due to likely human facilitation and their foraging traits.

Concerning wild bees

- Zurich has a large diversity of wild bee species (Fig. 6), which are distributed in the different urban green areas all over of the city (Fig. 7-8).
- The wild bee diversity of Zurich is composed mainly of scarce (i.e., with low abundances) and locally occurring bee species (Fig. 6), with a minority of species widely distributed over the city (Fig. 6-7).
- Less intense management like mowing and a high flower species richness leads to higher number and densities of wild bees (Fig. 8).
- Several urban green areas have high plant richness, and several districts contain a large proportion of green spaces, enhancing available habitat for wild bees.
- Wild bees have different feeding strategies that make them successful city dwellers, from specialization to broad generalism.
- Urban trees represent a main source of larval pollen.
- Wild bee species richness on some ruderal areas (e.g., railway areas) of Zurich is likely underestimated and deserves further attention.

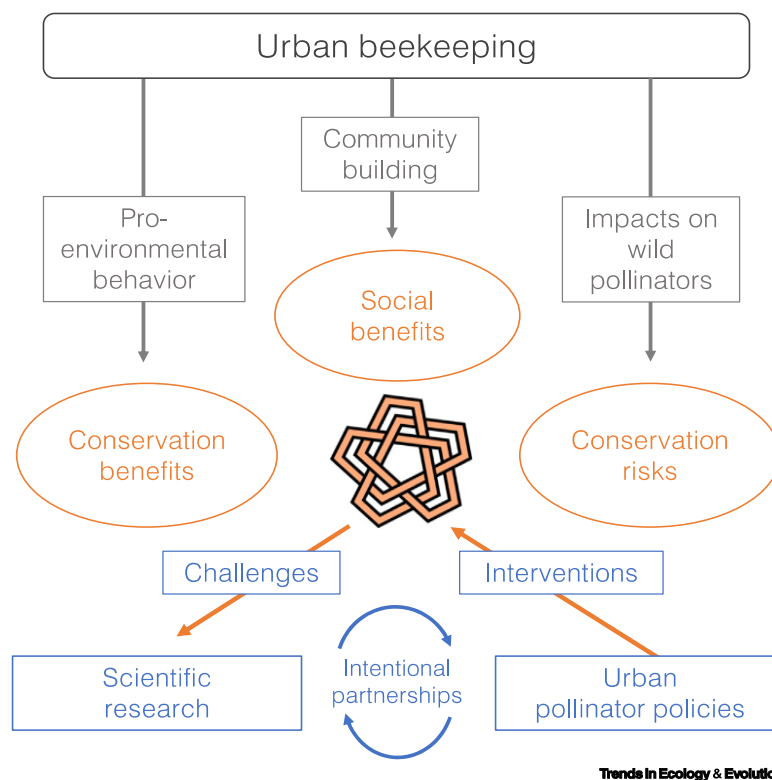
Coexistence and competition between honeybees and wild bees

- Honeybees seem not to interfere with specific guilds such as cavity-nesting bees (Figs. 18, 19). This could be explained by an increased honeybee foraging activity in good quality, resource-rich wild bee habitats, and by the absence of competition due to a surplus of resources during the peak activity of cavity-nesting species.
- Honeybees and wild bees co-occur in high quality urban areas such as low-managed urban gardens. This is likely due to the high floral availability at the local scale but also the high density of honeybee hives at the landscape scale.
- Several districts of Zurich have both high floral resources and predicted wild bee richness. This might indicate that in these city areas, the carrying capacity has not yet been exceeded.
- Sites in highly urbanized areas of the city, independently of their local floral richness, have more honeybees because of a concentration effect to favorable patches and less wild bee species, which might be due to a combination of habitat loss and fragmentation, lack of resources and perhaps competitive interactions.
- Sites in highly urbanized areas of the city host wild bee communities composed of species with more different traits (and probably foraging preferences) than honeybees, compared with sites in less urbanized areas of the city that are surrounded with larger and more divers types of habitats.

6.2. Take home messages to the stakeholders

The pros and cons of urban beekeeping

Urban beekeeping, as beekeeping in general, has both benefits and risks for wild bees and the environment. The main benefits are that honeybees have served as an **umbrella species to raise awareness of pollinators and promote pro-environmental behaviors**, which includes gardening for pollinators, providing nesting sites, reducing use of harmful management practices (e.g., mowing, herbicides). In fact, **often urban beekeepers do also promote actively wild bees** through their activities and might be committed to their conservation³⁵. On the other hand, **beekeeping still poses important conservation risks not only to wild bees but can also extend to other pollinator groups and plants**^{29,31}. Although these risks have been little explored in cities, they have been documented in natural environments and agricultural areas across Europe. **The results consistently show the risks of beekeeping on other species**, although there is a lack of experimental evidence testing for competition and explicit effects (e.g., fitness). Long-term effects have been little assessed³⁰. The existing and competing benefits and risks, and the number of agents and players involved make the regulation of urban beekeeping a complex topic that has been recently named as a Gordian knot (Fig. 20). To manage this Gordian knot, both researchers, society and government must work together, by establishing a dialogue that link scientific findings and translate them into managing and planning actions. The following paragraphs will discuss what can be applied.



Trends in Ecology & Evolution

Figure 20. Tying Urban Beekeeping's Gordian Knot (framework published in Egerer and Kowarik ³⁵). Through social and ecological means (gray boxes and arrows), urban beekeeping produces tensions among three spheres (orange): (i) the social benefits it provides to urban residents; (ii) direct or tangential conservation benefits; and (iii) conservation benefits and risks, for example, competition with wild pollinators. This tension creates a 'Gordian Knot' (orange knot diagram).

Conservation researchers and city policy makers must work together to manage this knot (blue boxes and orange arrows). Here, the knot presents challenges for researchers to study and generate scientific findings (e.g., WSL), while city government (or higher institution such as BAFU) must intervene through policy and planning mechanisms (orange arrows). A dialectic between scientific research and urban bee policy implementation is critical through intentional science–city partnerships (curved linked blue arrows).

Legal basis for managing beekeeping and wild bees in cities: What is needed? What kind of problems can be anticipated?

To better manage and plan urban green areas for wild bees, some problems can be anticipated. There are three aspects to be considered. First, although the substantial increases detected between 2012 and 2018 of urban beekeeping in several Swiss cantons, industrial beekeeping was typically not occurring in Swiss cities. That means that beekeeping was mainly done as a recreational activity, which might make beekeepers more willing to adapt their beekeeping practices to meet wild bee conservation goals if awareness is raised. **Nonetheless, this situation seems to be changing in the city of Zurich, where there are signals of economically-motivated urban beekeeping.** Second, cities such as Zurich still contain important amounts of floral resources (Frey & Moretti³²). The availability of floral resources determines the pollinator carrying capacity of the urban ecosystem and hence the balance between coexistence and competition. This has important implications for the actions (e.g., type, cost) that can be taken. Third, pollinators are declining worldwide and at an alarming rate³⁸⁻⁴⁴, and will continue as drivers of their declines will worsen (mainly land-use change and intensification⁴⁵⁻⁴⁷, but also pollution, altered biotic interactions and global warming). **This makes urgent to anticipate future problems and solve them when there is still time^{26,48,49}.** Urban beekeeping might not yet be main stressor of wild bees in Zurich, but this situation can change rapidly if honeybee densities keep raising. In fact, it is important to remember that managed honeybees have been shown to be a stressor on wild bees in other ecosystems. In addition, stressors do not act solitarily, they combine synergistically with each other. Therefore, the next question is: what problems can be anticipated and specifically, through what actions?

Lack of knowledge on wild bees is a major constraint for developing management and conservation strategies. There is little knowledge on the conservation status of many wild bee species (whether they are declining or not) both at the European and Swiss level, which hampers establishing conservation priorities. Concerning the case of urban ecosystems, there is no information on the citywide distribution of wild bee richness, of honeybee densities and of the flowering plants. In this report, we have done a first attempt to surmount these limitations by providing citywide estimates. With this information we suggest the following:

- **Create urban bee sanctuaries.** Citywide maps of wild bees together with the specific information on urban habitats of interest for wild bees (e.g., family gardens, gardens) should be used to define “wild bee sanctuaries” in the cities. This kind of sanctuaries would be zones of high conservation priority based on the wild bee richness, and particularly on the occurrence of red list species and national priority species that are off limits for beekeepers (within a certain buffer zone).
- **Urban beekeeping should not unconditionally be encouraged.** Honeybee hives have dramatically increased at least in the period between 2012-2018 and are now present all over the city. Urban wild bee sanctuaries could guide policy makers by delimiting areas without urban beekeeping. This could be particularly important in central urban habitats, where wild bees may have their habitat value reduced because of the number of honeybees using those “green oasis”. A possibility is to avoid financial incentives and subsidies to further increase honeybee densities in cities, as well as professional honeybee keeping in cities.

These measures are not only going to positively affect wild bees but also honeybees. Competition not only occurs with other species (interspecific competition) but also among individuals of the same species (intraspecific competition). In the case of honeybees, different hives can compete if resources are scarce, generally having negative effects for both colonies. Finally, controlling honeybee densities would reduce pest risk and the transmission of diseases.

What can Swiss cities do for wild bee management and conservation?

Zurich is a good example for how cities still harbor important levels of native biodiversity – at least in certain taxonomic groups such as wild bees. Hence, cities have a duty to protect, manage and even enhance their biodiversity. This inevitably involves not only regulating beekeeping but also enhancing suitable habitat for bees. Our predicted richness maps have showed cold- and hotspots of wild bees in the city. Such maps can help preserving and promoting wild bees by establishing main simple solutions as explained in Kawahara *et al.*⁴⁸, which include the **conversion of public lawns into diverse natural habitats, promotion of native plants, avoiding the use of herbicides and increasing local public awareness and appreciation for insects**. Particularly, biodiversity maps could inform where to define priority conservation areas (a sort of wild bee sanctuaries, focusing on specific habitats such as allotment gardens, ruderal areas or brownfields), and also, spot which areas of the city have low levels of biodiversity. **These biodiversity-poor areas will likely suffer from a deficit of green spaces, have larger amounts of stressors (e.g., pollution) affecting residents, and could be considered priority targets for greening the city** (for instance, this will complement ongoing projects such as the *Fachplanung Hitzeminderung*⁵⁰). Converting lawns into other habitat types (i.e., by reducing mowing regimes) and promoting native plants in existing green land covers (while also increasing their areas), for instance by integrating them into the existing infrastructures, might be a solution to boost urban biodiversity. Grey land covers frequently incorporate novel habitats (e.g., planted trees, road verges or flowerpots, and green roofs and/or walls) that could be designed and extended to maximize the amount of habitats and their ecological connectivity. In addition, most rare and threatened species in Switzerland are ground nesting bees, which specially suffer from loss of nesting sites due to land-use changes⁵¹. Hence, it is of major importance to promote urban habitats that offer ground nesting sites by maintaining open spaces and bare soil. These actions could increase the amount of available habitat without major transformations of the cityscape, whilst having positive effects on biodiversity and city-dwellers⁵².

6.3. Publications and outreach activities

Below we list the publications produced and the outreach activities carried out as part of this project or closely related to it.

Peer reviewed publications

- Casanelles-Abella, J., Fontana, S., Fournier, B., Frey, D. & Moretti, M. 2023. Low resource availability drives feeding niche partitioning between wild bees and honeybees in a European city. *Ecological Applications*, **33**, e2727, <https://doi.org/10.1002/eap.2727>
- Casanelles-Abella, J., Keller, A., Müller, S., ... & Moretti, M. 2022. Wild bee larval food composition in five European cities. *Ecology*, **103**, e3740, <https://doi.org/10.1002/ecy.3740>
- Casanelles-Abella & Moretti, 2022. Challenging the sustainability of urban beekeeping using evidence from Swiss cities. *Npj Urban Sustainability*, **2**, 1-5, <https://doi.org/10.1038/s42949-021-00046-6>
- Casanelles-Abella, J., Müller, S., Keller, A... & Moretti, M. (2022). How wild bees find a way in European cities: Pollen metabarcoding unravels multiple feeding strategies and their effects on distribution patterns in four wild bee species. *Journal of Applied Ecology*, **59**, 457–470. <https://doi.org/10.1111/1365-2664.14063>
- Casanelles-Abella, J., ... & Moretti, M. 2021. A dataset of the flowering plants (Angiospermae) in urban green areas in five European cities. *Data in Brief*, **37**, 107243, <https://doi.org/10.1016/j.dib.2021.107243>

Outreach activities

Beside the scientific publication we provided a series of initiatives that contributed to bridge the gap between Science with Society.

Own articles

- Leimgruber, M., Casanelles-Abella, J. & Moretti, M. 2020. Bieneschutz in der Stadt: “More than honey”. *N+L Inside* 1: 19.
- Casanelles-Abella, J. 2021: Uncovering what urban wild bees are feeding on to better promote them in cities. *The Applied Ecologist* <https://appliedecologistsblog.com/>

Documentaries

- Fröhlich, B. Das Imkern in der Stadt boomt. NANO. <https://www.3sat.de/wissen/nano/220520-bienen-nano-104.html>

Press releases

- Galliker, F., 2022. Excessive beekeeping in Swiss cities could be detrimental for wild bees and honeybees. WSL News <https://www.wsl.ch/en/news/2022/02/excessive-beekeeping-in-swiss-cities-could-be-detrimental-for-wild-bees-and-honeybees.html>
- Casanelles-Abella, J. Ed. Kusma, S., 2021. What urban bees feed on. News WSL. Link: <https://www.wsl.ch/en/news/2021/11/what-urban-bees-feed-on.html>
- Bose, L., 2021. Zurich home to some rare species. WSL News. Link: <https://www.wsl.ch/en/news/2021/09/zurich-home-to-some-rare-species.html>

Interviews

- Interview for Dezeen: Hahn, J., 2022. “Study finds cities lack green spaces to support “unsustainable” beekeeping boom”. Link: <https://www.dezeen.com/2022/01/27/urban-beekeeping-sustainability-study/>
- Interview for Bloomberg CityLab: Matteucci, L., 2022. “Urban bees face a flower deficit, says Swiss study”. Link: <https://www.bloomberg.com/news/articles/2022-01-14/urban-bees-lack-pollen-says-new-study-of-14-swiss-cities>
- Interview for Corriere del Ticino: Mantovan, J., 2021. “Le città sono vive, lo sappiamo grazie alle api” by Jona Mantovan. Link: <https://www.cdt.ch/news/le-citta-sono-vive-lo-sappiamo-grazie-alle-api-270970>

Potcasts

- Episode 115: The Growth of Urban Beekeeping <https://podcasts.apple.com/at/podcast/episode-115-the-growth-of-urban-beekeeping/id1494010558?i=1000578748761>

Other contributions

Bienen Medienreview 2022-2023 of the WSL, state 14.2.2023 (**See attached documents**)

- **Print:** 20 interviews/articles
- **TV:** 3 interviews
- **Radio:** 5 interviews
- **News Websites:** 44 news

Published datasets

- Casanelles-Abella, J., Moretti, M. 2021. Challenging the sustainability of urban beekeeping: evidence from Swiss cities. *EnviDat*. <https://doi.org/10.16904/envidat.239>.
- Casanelles-Abella, J., Fontana, S., Fournier, B., Frey, David J., Moretti, M. 2021. Niche partitioning between wild bees and honeybees. *EnviDat*. <https://doi.org/10.16904/envidat.253>.
- Casanelles-Abella, J., Moretti, M., et al. 2021. Larval food composition of four wild bee species in five European cities. *EnviDat*. <https://doi.org/10.16904/envidat.249>.
- Casanelles-Abella, J., et al., Moretti, M. 2021. Flowering Plants (Angiospermae) in Urban Green Areas in five European Cities. *EnviDat*. <https://doi.org/10.16904/envidat.210>.

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8. APPENDIX

Supplementary methods

1. Density of honeybees

Sampling honeybees: To sample the honeybee density within Zurich, the city has been divided into 98 grid cells of 1 x 1 km. In every cell one to three transects of 500 m have been defined, stratified to the number of land covers present. The transects have been measured and predefined using ArcGIS. By adding transects at already given sampling sites for wild bees this study design resulted in 180 transects (10 points/transect = 1800 sampling points) spread all over the city of Zurich. During fieldwork, a sample of the honeybees present within one square meter was taken every 50 meters along the predefined transects to optimize accuracy and sampling time. The 50 meters between each sampling location were measured by step counting or the use of the app «GPS Distance Meter». The sampling plot was selected subjectively as the most bee friendly square meter within a radius of 3 meters around the sampling location. Within this sampling plot the abundance of honeybees was counted. If no honeybees were present at the beginning, a maximum waiting period of three minutes until continuing to the next sampling plot was applied. Sampling was carried out during sunny days without wind between 8:30 to 16:30.

Modelling: To extrapolate the sampled honeybee density to the entire city, four modelling approaches have been implemented:

1. **Distance-Based Model:** this is the simplest model and only uses the spatial distribution from the honeybee hives. This model assumes that honeybees can move and forage at any direction following a dispersal function, that is, a function that measures the probability of a honeybee to be foraging in a certain range from their hive. We considered three types of dispersal function: linear, exponentially modified Gaussian distribution and an exponential function following previous studies (Visscher and Seeley, 1982)(Figs. 2-3).
2. **Circuitscape-based Model:** this model is a modification of the distance-based model that considers the landscape surrounding the honeybee hives to not be homogenous and hence to impose different levels of resistance to movement. This model is based on Circuit Theory⁴⁸, where individuals represent a current flux and the different landscape elements represent different resistances (Fig. 3).

3. Abundance Model: we used a modification of the Species Distribution Models used in macroecology to model the sampled abundance of honeybees and predict it in the city. This model combines the sampled abundance with a set of environmental predictors (e.g., temperature, landscape metrics) to predict the honeybee hives in city areas we did not visit (Fig. 3).
4. Landscape metrics: In this case, we calculated the distance to the nearest beekeeping point and the density of hives in 500- and 1000-m buffers without considering honeybee movement (Fig. 4).

2. Wild bee diversity and distribution

Species abundance and occurrence: we used the abundance and occurrence of 177 bee species sampled in 251 sites in Zurich during four urban ecology projects run between 2009 and 2019.

Species diversity patterns: we studied the species abundance and occurrence patterns by using ‘rank-abundance and rank-occurrence diagrams’, which show the distribution of abundances and occurrences of the different bee species decreasingly. We used common thresholds to classify the species according to their abundance and occurrence in three categories: 1) ‘very common’ for bees that were very abundant and very widespread; 2) ‘common’ for bees that were abundant and widespread; and 3) ‘rare’ for bees that were scarce and locally-occurring.

Modelling species richness: Two types of model were calibrated: (i) Species Distribution Models (SDMs) for the individual bee species with sufficient occurrences and absences, and (ii) Species Richness Models (SRMs), aggregating the richness of rare, common and very common bees. Depending on the type of model, two distinct probability distributions were used: Binomial for SDMs and Poisson for SRMs. Each SDM and SRM was calibrated using an ensemble of four common modelling techniques to account for model uncertainty and specificity: Generalized Linear Models (GLM), Generalized Additive Models (GAM), Random Forests (RF) and Gradient Boosting Machines (GBM). GLMs and GAMs are models based on linear regression. While GLMs assume a parametric relationship between response and predictors, GAMs focus on flexible nonparametric smoothing functions. RFs and GBMs are defined as tree-based models and show a higher complexity in their response than GLMs and GAMs. Each modelling technique was parameterized in the following way: GLMs were calibrated with second-order polynomials, GAMs with a spline smoothing term of intermediate complexity ($k=3$), RF with a node size of 5 ($nodesize=5$) and 1000 trees, and GBM with an interaction depth of 1, a shrinkage of 0.001 and 1000 trees. In addition, we set GBM shrinkage at 0.001. The models were computed using the R packages *mgcv* version 1.8-30, *RandomForest* version 4.6-14, and *gbm* version 2.1.5.

For each SDM and SRM, species records were split randomly into two sets containing 80% and 20% of the data. The former was used to calibrate the model and the latter for evaluation. This procedure was replicated five times. Model performance was assessed with True Skill Statistic (TSS) for SDMs, and with Pseudo- R^2 for SRMs. TSS evaluates model skill in distinguishing absences from presences. Pseudo- R^2 provides a measure of predictive performance by determining the ratio between model error and variance of the response variable. Both performance metrics range from 0 to 1, with 1 indicating perfect models. Models were then filtered according to their predictive performances. For SDMs, model predictive performance was considered reliable at $TSS > 0.4$, a commonly used threshold. For SRMs, the quartile distribution of performance metrics was calculated and models with the 25% worst performance were removed.

For each of species, retained models among the initial 25 (5 repetitions * 4 algorithms) were projected over the study area. Each model prediction was then converted into binary output using the value that yielded the maximum TSS as a threshold. Finally, binary layers of presences/absences (PA) were stacked and the final species PA layer was formed by applying a threshold of 50%, above which cells were assigned species presence. Finally, we combined the distribution maps of the 272 species into the respective taxonomic groups to form group richness maps of common species.

Species richness in urban land covers: Citywide maps of predicted species richness were then created considering all species, as well as very common species only and rare species only. More details in Casanelles-Abella et al. ⁴⁹.

3. The pollinator experiment

Study design: We sampled 24 urban gardens in the city of Zurich along two independent local- and landscape-scale gradients to separate the effects of local resource availability and potential foraging habitat landscape spatial scales. Specifically, we selected the gardens to vary independently in their flower species richness from the proportional amount of impermeable surface in their surrounding landscape. All gardens were open, with at least 7-9 h of daily sun exposure during the experiment.

Experimental set-up: An array of 19 pots of four plant species (also called “phytometer plants”) was set up in the centre of each garden. Each pot contained one plant of one of the following insect-pollinated plant species: wild carrot (*Daucus carota* L.; five pots), radish (*Raphanus sativus* L.; six pots), common sainfoin (*Onobrychis viciifolia* Scop.; five pots) and common comfrey (*Symphytum officinale* L.; three pots). The four species were selected based to their expected variation in flower visitor specificity because of their differences in floral types (i.e., access to nectar): (a) a flower with exposed nectar (“allophilous”), wild carrot, (b) a flower with partially concealed nectar (“hemiphilous”), radish, (c) a flower with concealed nectar (“euphilous”), sainfoin, and (d) a flower with deeply concealed nectar (“euphilous”), comfrey.

Insect sampling: Flower-visiting insects were sampled on each plant of each of the four plant species during their peak flowering time between June 15 and July 20, 2016. In each garden, flower visitors were sampled by two or three people simultaneously for nine full and consecutive hours between 9:00 to 18:00 h under sunny weather conditions and no wind (or low wind speed, <2m/sec). Each of these sampling rounds was repeated at least three times in each garden. This enabled us to determine flower visitation frequency by each insect species (or flower visitor group, respectively) during each of nine consecutive hours during each sampling day. To achieve this, 37 volunteers were recruited and trained. This allowed us to sample up to nine gardens in parallel the same day. Volunteers were randomly allocated to gardens for each sampling round, but no volunteer could work twice in the same garden. Insects were collected after landing on an open flower using a 50 mm by 100 mm polypropylene beaker with a foam plug (Semadeni AG, Ostermundigen). Each insect was transferred individually under a sweep net from the tube to an 8 ml glass tube, which was labelled with the respective phytometer plant and capturing time window and put on cooling elements in cooling bags. Flower visitors were transferred to the lab after each observation round and kept under -20°C until determination by taxonomic experts. The four most abundant flower visitor taxa: bees (Hymenoptera: Anthophila), hoverflies (Syrphidae), wasps and beetles

(Coleoptera: several families) were determined to species level, sexed and re-transferred to -20°C immediately after identification.

4. Niche partitioning analyses

Bee data: We used bee data collected in the city of Zurich using a subset of 24 sites from the pollination experiment of the BetterGardens project.

The bee data from the *city level* (164 sites) were sampled during the research projects ENHANCE (2010) and BetterGardens (2015) and contain bee at community level (species and abundances) sampled with standard interception traps (coloured pan traps) during 10-13 weeks from May to August. The bee data collected in the subset of experimental sites (24 sites) of the project BetterGardens contains bee community data sampled by hand on the four different phytometer plant species presented in the previous section (3.1-Pollination experiment). All the sites were selected to follow gradients of urban intensity at the landscape scale (500 m radius around the sampling points) and of floral resource availability at the local scale.

Functional traits: For the 164 sites, trait data was obtained from available databases and measured at the species level. For the subset of 24 sites, trait data was measured at the individual level. We selected traits that we expected to play a role in competitive interactions, classified in the following four groups: foraging range, feeding specialisation degree, phenology, and daily activity.

As proxies for this four groups we used the following traits: *intertegular distance (ITD)* for mobility; *lecty* and *relative tongue length* (i.e., tongue length corrected by the ITD) for degree of feeding specialisation; *phenology starting, ending and duration* for phenology; *daily activity time* as feeding hour of the day. We calculated Pearson and Spearman correlations among candidate traits and selected those that were correlated by less than 0.7.

Functional metrics – Niche overlap was measured as the mean pairwise trait distance between wild bees and honeybees in the community, which indicates how functionally similar are the two communities. Higher values of the mean pairwise distance indicate that the two groups, honey- and wild bees, are becoming more dissimilar with respect of their trait values, hence indicating higher niche partitioning as the honeybee and wild bee individuals overlap less in the use of the floral resources.

Analyses – We expect niche overlap (i.e., the strength of competitive interactions) between wild bees and honeybees to be driven by three main predictors: (1) the density of honeybees (the potential competitor); (2) the amount of habitat or the resource availability at the local scale (where the taxa was samples); (3) the amount of habitat or the resource availability at the landscape scale. To infer these three main predictors, we used the following proxies: (1) *sampled honeybees in the study site* as a proxy of honeybee density; (2) *floral resources at the study site and management intensity at the study site* as a proxies of resource availability at the local scale; (3) *amount of available habitat* (e.g., proportion of green land covers) *at the landscape scale* (500 m radius around the sampling points) and *local overwarming at the landscape scale* (500 m radius around the sampling points).

5. Reproductive success of cavity-nesting bees

Study design: We sampled 85 urban gardens in the city of Zurich two independent local- and landscape-scale gradients to separate the effects of local resource availability and potential

foraging habitat landscape spatial scales. Local resource availability was assessed as gardener-provided nesting and feeding resources for cavity-nesting solitary bees and wasps. Specifically, we i) scored the presence or absence of (functional) nesting aids, and ii) quantified the proportion of land-cover that gardeners spared as foraging grounds: as the sum of wildflower meadows, perennial flowers, wild area and shrub cover (hereafter called 'foraging area'). To assess the amount of foraging habitat of hosts at landscape spatial scales, we used the urban habitat map of the city of Zurich (Grün Stadt Zürich, 2010). Specifically, we quantified the cover of potential host foraging habitat as the sum of urban gardens, shrubland, permanent grasslands and farmland within the main foraging ranges of trap-nesting bees and wasps, in 50-, 100-, 250-, and 500-m radius circles (i.e., buffers) around each garden.

Trap nests: Standardized trap nests are an experimental approach to investigate the consequences of local habitat properties and land-use intensity gradients for fitness components of aculeates, solitary bees, wasps and their natural enemies. Before the activity period of wild bees, in February 2016, we fixed a trap nest on a wooden pole at a height of 1.5 m in a central and sunny place in each garden. Each trap nest consisted of two plastic pipes (20 cm long, 10 cm diameter), filled with about 200 internodes (hereafter called 'tubes') of common reed (*Phragmites australis* (Cav.) Steud.). One additional plastic pipe was filled with 7.5 mm diameter paperback tubes (WAB Mauerbienenzucht, Konstanz, Germany). Trap nests were covered with a wooden roof (30 cm × 40 cm) and directed eastwards to shelter from rain. After the end of the flying period of hosts, in October 2016, we collected the nests and stored them at 6°C to simulate winter conditions. Between November and February 2017 all tubes were opened. If present, brood cells and enemies were recorded, while keeping tubes on ice. Tubes with brood cells were transferred into labelled test glasses, which were sealed with cotton wool and transferred back to 6°C. In March 2017, test glasses were moved to an unheated room, and all emerging host and enemy individuals were successively recorded and determined to species level.

Wild bee reproductive success was quantified as the sum of all brood cells per garden. Furthermore, we assessed offspring survival at the level of individual nests. Survival rate was the number of emerging adults out of the total the number of brood cells per nest and species. Parasitism risk was the number of brood cells attacked by an enemy out of the total number of brood cells per nest and host species.

Honeybee sampling: We sampled honeybees in each garden with three one-litre bowl traps fixed on a 1.5 m triangular wooden pole. Each bowl was dyed with either UV-bright blue, white or yellow paint (Sparvar Leuchtfarbe, Spray-Color GmbH, Merzenich, Germany). All traps were three quarters filled with 0.2% Rocima solution (bactericide and fungicide; Acima, Buchs, Switzerland), run for 14 consecutive weeks between May 18th and August 19th 2015 and were emptied weekly.

Statistical analyses: We used Poisson and binomial generalized linear mixed effect models in a Bayesian framework to test for the effects of local- and landscape-scale resource availability and honeybee abundance on total, garden-scale wild bee reproductive success, and survival probability and parasitism risks at the level of nests.

6. Bienen Medienreview_2022_2023

See attached document















Annex to the "City4Bees" Final Report

Bienen Medienreview_2022_23







14.02.2023

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