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COMMUNITY ECOLOGY – ORIGINAL RESEARCH

Changes in the bee fauna of a German botanical garden between 1997 and 2017, attributable to climate warming, not other parameters

Michaela M. Hofmann[1] · **Andreas Fleischmann**[2] · **Susanne S. Renner**[1]

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Abstract

Botanical gardens represent artificial, but stable environments. With this premise, we analyzed the Munich Botanical Garden's bee fauna in 1997/1999 and again in 2015/2017. The garden covers 20 ha, uses no bee-relevant insecticides, has a protected layout, and on three sides abuts protected areas. Outdoors, it cultivates some 10,871 species/subspecies, many suitable as pollen and nectar sources for bees. The first survey found 79 species, the second 106, or 55% of the 192 species recorded for Munich since 1990. A *Jackknife* estimate for the second survey suggests 115 expected species. Classifying bees according to their thermal preferences (warm habitats, cool habitats, broad preferences, or unknown) revealed that 15 warm-loving species were gained (newly found), two lost (no longer found), and 12 retained, but only one cool-loving species was gained, three lost, and none retained, which multinomial models show to be significant differences. Of the 62 retained species, 27 changed in abundance, with 18 less frequent and nine more frequent by 2017 than they had been in 1997/1999. Retention, gain, or loss were unconnected to pollen specialization and Red List status of bee species. Between 1997 and 2017, average temperatures in Munich have increased by 0.5 °C, and climate warming over the past century is the most plausible explanation for the directional increase in warm-loving and the decrease in cool-adapted species. These results highlight the potential of botanic gardens with their artificially diverse and near-pesticide-free floras as systems in which to investigate climate change per se as a possible factor in shifting insect diversity.

Keywords Botanic gardens · Bee fauna · Climate warming · Repeated monitoring · Stable habitat · Insect faunal change

Introduction

Bee diversity in the United States and Europe appears to be declining (Potts et al. 2010), with bumblebee losses especially well documented (Williams et al. 2007; Goulson et al. 2008). Reasons for the decline are manifold and include stress from parasites and pesticides, habitat loss and fragmentation (affecting nesting sites and food sources), a lack of suitable flowers for oligolectic bees, and climate warming (Williams et al. 2007; Potts et al. 2010; Goulson et al. 2015). Besides the causes, also the direction of faunal change remains poorly understood because few areas have been monitored with consistent methods over longer periods (Hallmann et al. 2017). Data on changes in regional bee faunas are therefore sparse, and where they exist, attribution to specific causes is difficult. Agricultural and urban habitats over the past 100 years have changed in many factors, relating to human construction projects and intensive agriculture. For some bees, urban parks and gardens are becoming refugia, but the relationships between bee diversity and parks are multifactorial, with floristic diversity playing a major role (Hall et al. 2016). By comparison to these habitats, botanic gardens, while also located in urban settings, have a persistent flora that always includes a rich mix of native and foreign species. The basic layout of many older gardens has not changed for the past 50 or even 100 years, and the use of

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✉ Michaela M. Hofmann
michaelahofmann181@gmx.de

✉ Susanne S. Renner
renner@lmu.de

1 Systematic Botany and Mycology, University of Munich (LMU), Menzinger Straße 67, 80638 Munich, Germany

2 Botanische Staatssammlung München, Menzinger Straße 67, 80638 Munich, Germany

insecticides in European public gardens and parks over the past 20 years has become increasingly restricted. Botanic gardens, therefore, provide a setting for not only studying plant responses to climate change (Primack and Miller-Rushing 2009; Zohner and Renner 2014) but also systems for monitoring insect faunas in which directional changes, such an increase or decrease in warm- or cool-loving species, can plausibly be attributed to a change in climate, rather than floristic change or other causes.

Here, we use two inventories, carried out 20 years apart, of the bees of the Munich Botanic Garden to investigate the possible impact of climate warming per se on an urban bee fauna. The garden's bees were inventoried in 1997–1999 (Bembé et al. 2001) and again in 2015–2017. The garden's paths and flower bed layout are protected; its seasonally changing flower displays over the past 20 years have not changed, hardly any pesticides have ever been used, and the flora and buildings surrounding the garden have essentially not changed, since it opened in May 1914 (details in "Methods"). Average temperatures during the vegetation season in Munich have increased by 0.5 °C over the past 20 years (compare Fig. 1), and winters have become shorter by almost 4 weeks (Zohner and Renner 2014). We, therefore, expected that bee diversity might have shifted to more warm-loving species.

Methods

Study area, bee monitoring and identification, and scoring of bee species traits

The Munich Botanic Garden opened in May 1914 and covers about 20 ha (Renner 2014). It is situated next to the

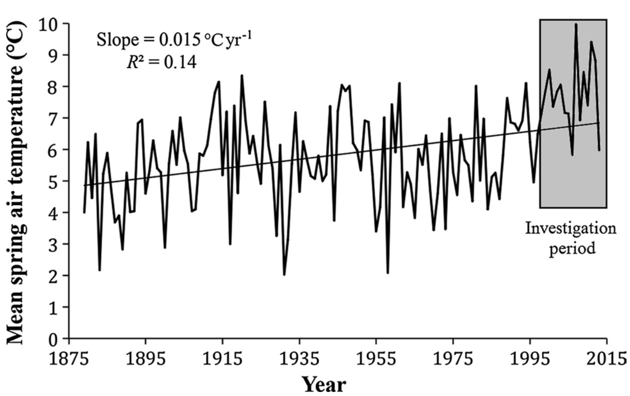

Fig. 1 Average spring (March and April) temperatures in Munich, with the slope revealing a mean temperature increase of 0.015 °C per year. Data from the weather stations Munich Botanical Garden (1879–1954), Munich-Nymphenburg (1955–1998), and Munich downtown (1999–2013) modified from Zohner and Renner (2014, Fig. S1)

Nymphenburg Palace Park at 48°09′45″N, 11° 30′06″E at an altitude of ca.500 m above sea level. On three of its sides, it borders on the 210-ha-large Palace Park and the orchard of a Catholic Nunnery; on its fourth side is a heavily travelled road that separates the garden from a hospital that opened at almost the same time as the garden. The garden currently cultivates 10,871 species and subspecies outdoors (data from the garden's living plant database, accessed by SSR on 1 Nov. 2017). The only pesticides used over the past 20 years are occasionally Neudorff Spruzit against molluscs and Neudorff Loxiran against ants (http://www.neudorff-handel.de, last accessed 3 Sep. 2017). Both have no known negative effects on bees. The layout of the garden and its visitor paths (Online Supporting Material Figure S1) are protected, as is the layout and all paths in the Nymphenburg Palace Park. Two large and several small nesting aids, consisting of bamboo, wood, and bricks, have long been used in the garden.

Between spring and fall 1997, 1998, and 1999, Bembé et al. (2001) carried out 56 biweekly monitoring walks, mostly between 9:00 and 12:00, recording bees by hand-netting (with most netting effort in 1998). As customary in the 1990s, species identification was based on morphological features. Between spring and September 2015, 2016, and 2017, we carried out biweekly monitoring walks, resulting in 184 walks and 290 h of observation (2015: 38 walks, 59 h; 2016: 107 walks, 159 h; 2017: 72 walks, 72 h). Like Bembé et al. (2001), we did not follow a strict route, but instead focused on patches with numerous flowering plants (throughout the garden), and on the morning hours of warm and dry days rather than overcast or humid days. Depending on bee abundance and weather, our mapping walks lasted between half an hour and 4 h.

We recorded easily recognizable bee taxa, such as Megachilidae, by photography (in situ, but also close-ups of caught individuals chilled down to 4 °C for several hours and then released after photography), focusing on mandibles, coloration, hair and facial patterns, and tergite markings. For identification, we used keys by Dathe (1980), Amiet et al. (1999, 2001, 2004, 2007), Amiet and Krebs (2014), von Hagen and Aichhorn (2014), and Falk and Lewington (2015). Bees from genera that are difficult to identify were caught with a magnifying cup, chilled down to 4 °C for microscopic examination, and, in some cases, killed by storing them in a freezer at − 20 °C for later DNA isolation and barcoding, relying on the primers of Schmidt et al. (2015) who have barcoded 546 of the 571 bee species that occur in Germany; our lab procedure is described in the Online Supporting Materials, which also list GenBank accession numbers and details on vouchers deposited in the State Zoological Collection in Munich (ZSM; collecting permit StmUV Az.62 g-U8645.8-2014/1-2 v.10.11.2014). For the *Bombus lucorum* species complex, we used dead bees found below linden trees in large numbers in July and August (Baal et al. 1994); these partly damaged specimens were not deposited in the ZSM. Our bee taxonomy and nomenclature follow Scheuchl and Willner (2016).

To compare the 1997–1999 and 2015–2017 surveys, we assigned species to one of three categories, namely "lost", "retained", and "gained", with lost referring to species only found in the first survey, retained referring to species found in both surveys, and gained referring to species found only in the recent survey. Bee temperature preferences were scored based on habitat preferences in Switzerland (Amiet et al. 1999, 2001, 2004, 2007; Amiet and Krebs 2014) and Central Europe (Westrich 1989; Scheuchl and Willner 2016). Bee pollen foraging specialization was scored based on Scheuchl and Willner (2016), with oligolecty defined as pollen foraging restricted to closely related species and polylecty as pollen foraging on diverse (unrelated) species. Following Bembé et al. (2001), we scored abundance using the following categories: category 0 for species not seen; category I for species observed with fewer than 5 individuals; category II for 5–20 individuals, and category III for more than 20 individuals per year. Since the abundance estimates in the first (1997–1999) and second survey (2015–2017) were done by different people, we did not model the possible importance of abundance for 'predicting' extinction (Results). Red List categories follow Westrich et al. (2011), with 0 meaning extinct, 1 critically endangered, 2 endangered, 3 vulnerable, NT near threatened, G threat of unknown magnitude, and an asterisk for least concern. A list of all species and their traits can be found in the Online Supporting Materials (Table S1).

Correlations between bee species gain, loss, or retention and thermal habitat niche, pollen specialization, and Red List status were analyzed using multinomial models implemented in the R-package VGAM (Yee 2010), excluding all species with unknown thermal habitat niche. Since a first model with the independent variables "foraging preference" and "endangerment" indicated no significant influence of pollen specialization or Red List status on abundance changes, we excluded these factors and calculated a second model with only "temperature preference" as independent variable. In this model, the category "retained" was used as reference category. Due to low numbers of wild bees with preferences for cooler habitat, a third model without these species was calculated to check whether the coefficients of the other thermal preferences stay stable despite high variation for the factor "cooler habitats."

To assess our sampling success, we used the *Jackknife* method of Haeseler and Ritzau (1998), whereby the expected number of species for an area can be calculated using the formula $Sj = S + K \times \frac{n-1}{n}$, with S being the number of recorded species, K being the number of singletons, and n being the number of survey walks (we used the number of walks in 2016).

Results

Increase in warm-loving bees over the past 20 years and correlation with species traits

The 1997–1999 survey yielded 79 species, the more recent survey 106, in both cases including the honeybee (Table S1, Online Supporting Materials). The species number expected for the garden, using *Jackknife* estimation, is 115 ("Methods") for 2015–2017, which is close to the 106 so far found. A *Jackknife* estimation based on the 1997 monitoring efforts yields 97 expected species. The 106 species belong to 23 of the c. 45 genera of bees currently accepted for Germany (Schmidt et al. 2015; Scheuchl and Willner 2016).

Whether a species is warm-habitat preferring, cool-habitat preferring, or has broad habitat preferences significantly affected whether it was retained, lost, or newly gained: by 2017, we found 15 warm-loving species that were not present in 1997 (i.e., species that spread into the garden). The geographic ranges and habitat preferences of these 15 species are detailed in the "Discussion". In addition, 12 warm-preferring species were retained between the two surveys, and two lost. In comparison, three cool-preferring species were lost, one cool-loving species was gained, and none retained. For the geographic ranges and habitat preferences of the cool-adapted species, see the "Discussion".

Of the species with broad habitat preferences, 20 were gained, 7 lost, and 47 retained (Tables 1, S1; multinomial model including thermal habitat preferences, foraging specialization, and Red List status: $p = 0.010$; multinomial model including only thermal habitat preferences: $p = 0.022$; multinomial model excluding cool-loving species: $p = 0.022$). The 16 species recorded in 1997 and no longer found by 2017 (Table S1, online supporting material) mostly belong to *Hylaeus* and *Lasioglossum*, and are small-bodied bees.

We then tested for a correlation between pollen specialization and species persistence, gain, or loss (Tables 1, S1). Two of 17 species lost by 2017 were oligolectic, 12 were polylectic, and three were cuckoo bees. Of the species gained by 2017, 10 are oligolectic, 23 polylectic, and 11 kleptoparasitic. This does not argue for pollen specialization having contributed to bee species loss. Two oligolectic species decreased in abundance, two others increased, and 11 did not change in abundance (see Table 1). Of the 62 retained species, 27 changed in abundance, with 18 less frequent and nine more frequent by 2017 than they had been in 1997. Finally, of the species no longer found by 2017, 14 had the Red List status "least concern", two were

Table 1 Foraging specialization, thermal habitat preferences, Red List status, and abundance categories of bee species lost, retained, or gained in faunistic surveys of the Munich Botanical Garden in 1997/1999 and 2015/2017

	Lost ($n=17$)	Retained ($n=62$)	Gained ($n=44$)
Foraging specialization			
Oligolectic	2	15	10
Polylectic	12	37	23
Parasitic	3	10	11
Thermal preferences			
Broad range	7	47	20
Cooler habitats	3	0	1
Thermophilic	2	12	15
Unknown	5	3	8
Red List status			
Least concern (*)	13	52	33
Threat of unknown magnitude (G)	0	1	1
Near threatened (NT)	2	4	3
Vulnerable (3)	0	4	5
Endangered (2)	1	1	1
N/A	1	0	1
Abundance categories			
I (<5 individuals)	9		29
II (5–20 individuals)	6		12
III (>20 individuals)	2		3
Increase in abundance		9	
Equal abundance		35	
Decrease in abundance		18	

	Increasing abundance ($n=9$)	Equal abundance ($n=35$)	Decreasing abundance ($n=18$)
Foraging preferences			
Oligolectic	2	11	2
Polylectic	7	21	9
Parasitic	0	3	7
Thermal preferences			
Broad range	6	25	16
Thermophilic	3	7	2
Unknown	0	3	0
Red List status			
Least concern (*)	8	28	16
Threat of unknown magnitude (G)	1	0	0
Near threatened (NT)	0	2	2
Vulnerable (3)	0	4	0
Endangered (2)	0	1	0

"near threatened", and one was "endangered" (this species was already found only once in 1997–1999). Most of the species gained are categorized as "least concern" ($n=33$), but, additionally, the garden gained three species that are "near threatened", five that are "vulnerable", and one that with the Red List status "endangered".

The 23 genera of bees recorded from the garden are distributed throughout the phylogeny of bees known from Germany that is shown in Appendix S6 of Schmidt et al. (2015), which includes 514 species from 45 genera. We refrained from testing for phylogenetic signal in the retention, gain, or loss of species from the Munich Botanical Garden over the past 20 years. Such a signal may well be present in a larger region, for example, southern Germany or the Alps, but is unlikely in a 21-ha garden, studied over 20 years.

Discussion

Of 515 species of bees known from Bavaria (Scheuchl and Schwenninger 2015), 192 have been recorded for Munich since 1990 (Bräu and Nützel 2010), so that the garden's 106 species represent some 55% of the city's species. Similar-sized gardens in Southern Germany and Switzerland have between 70 and 150 recorded species (Zurbuchen and Müller 2012).

The 15 warm-loving species first recorded by 2017 include (1) *Xylocopa violacea,* which has its main distribution in southern Europe. It has been documented north of the Alps in the Danube valley and other warm regions since 1850 (Hage 2005; Schmalz 2005; Bußler 2007), perhaps arriving with imported wood from the south or foehn winds from the Inn Valley (Knoerzer 1941). From the Munich area, including the botanic garden, *X. violacea* was recorded by 1980 (Burmeister in Bembé et al. 2001), but since 2000, it is becoming more frequent in Bavaria and other states, as far north as Hesse (Schmalz 2005; Bußler, 2007). (2) *Osmia cornuta* is a Mediterranean species that nests in sun-exposed loess and clay walls (Scheuchl and Willner 2016); in the Munich Botanic Garden, sun-exposed wooden nesting aids are intensely populated by *O. cornuta* (> 100 individuals). (3) *Eucera nigrescens* is a bee of Southern and Central Europe where it occurs mostly at elevations < 500 m (Westrich 1989; Falk and Lewington 2015; Scheuchl and Willner 2016). (4) The western Palearctic species *Anthophora bimaculata* may be a new record for the Munich area (http://www.buw-bayern.de/show.php?artid=601, last accessed: 3 Sep. 2017); it occurs in dry, warm locations with sand or clay, where it can dig nests. (5) *Anthidiellum strigatum* is restricted to sunny, warm forest edges (Scheuchl and Willner 2016). (6 and 7) *Halictus scabiosae* and *H. subauratus* both are distinctly thermophilic (Westrich 1989; Scheuchl and Willner 2016), and the former has rapidly expanded its range since 2000, most likely linked to climate warming (Frommer and Flügel 2005; Hopfenmüller 2014). (8) Another new arrival since 1997–1999, *Hoplitis adunca*, is strictly oligolectic on a thermophilic plant (*Echium vulgare*) that has become more abundant as winters have become shorter and temperatures warmer.

The three cool-habitat-adapted species no longer found are (1) *Andrena intermedia*, which has its main area of distribution in mountain regions and occurs north to the polar circle and south to Turkey and the Peloponnese (Scheuchl and Willner 2016); (2) *Megachile ligniseca,* which, in Southern Germany, occurs in cool habitats in forests up to the subalpine area (Westrich 1989; Scheuchl and Willner 2016); and (3) *M. nigriventris*, which is distributed in Northern Europe and the Alps, usually > 500 m a.s.l. (Dorn and Weber 1988; Westrich 1989). All three of these were already rare in 1997/1999 (Table S1), however, and over its 100 years of existence, the botanical garden may never have harbored many cool-habitat-adapted species.

What best explains the disappearance of three cool-loving species and the arrival of 15 thermophilic species over the past 20 years? Since the man-made flora of the botanical garden and the protected flora of its surroundings (namely, the 210 ha-large Nymphenburg Palace Park, the orchard of a Catholic nunnery, and a street and hospital) have not changed over the past 20 years, the loss of habitat and food plants for oligolectic bees seems an unlikely explanation for bee species disappearance, and this agrees with the absences of a statistical correlation between pollen specialization and retention or loss from the garden over the 20 years between the two surveys. We also found no significant difference in Red List status between the categories gained, lost, and retained ("Results").

Thus, over the past 20 years, plant diversity and availability of nesting sites in the garden and its adjacent areas have remained essentially identical, and the distinct increase in warm-loving species that we detected is, therefore, most likely due to climate warming (Fig. 1), with the novelty of our study being that we have used an artificial, but stable 'ecosystem' to link insect fauna changes to climate warming per se. No other environmental parameter in the Munich botanical garden matches the directional increase in warm-loving species documented in our study. This study thus highlights the potential of botanic gardens as systems in which to investigate the effects of climate on insect faunas, controlling for insecticides, habitat fragmentation, and other human-impact factors. Our findings also underscore the importance of urban gardens as bee habitat (Hernandez et al. 2009; Hall et al. 2016).

Author contribution statement MH, AF, and SSR designed the experiment, and MH and AF performed the fieldwork. MH and SSR analyzed the data, and all authors contributed to the manuscript.

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Compliance with ethical standards

Conflict of interest The authors declare that there is no conflict of interest.

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